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**PLANT MORPHOGENESIS AS THE BASIS
FOR SCIENTIFIC MANAGEMENT
OF RANGE RESOURCES**

**Proceedings
of
The Workshop of the United States-Australia
Rangelands Panel
Berkeley, Calif., March 29-April 5, 1971**

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**PLANT MORPHOGENESIS AS THE BASIS FOR
SCIENTIFIC MANAGEMENT OF RANGE RESOURCES**

**Proceedings of the Workshop of
the United States-Australia Rangelands Panel
Berkeley, California
March 29-April 5, 1971**

Coordinated by

**Kermit W. Kreitlow, former Agricultural Administrator
and Richard H. Hart, Agronomist
Agricultural Research Service
U.S. Department of Agriculture**

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Kermit W. Kreitlow, senior coordinator of these proceedings, died September 21, 1971. He had served the U.S. Department of Agriculture since 1941, when he joined the Forage and Range Research Branch at the U.S. Regional Pasture Research Laboratory, University Park, Pa., as a plant pathologist. In 1950, he transferred to Beltsville, Md., where he supervised the work of the Branch's plant pathologists at experiment stations throughout the country, and advised agronomists, plant breeders, and geneticists on plant diseases. In 1964, he was named Assistant Chief of the Branch. By this time he had authored over 100 publications, and was recognized as one of the world's authorities on forage crop diseases.

In 1969, Dr. Kreitlow was named chairman of an ad hoc committee of U.S. scientists, which met with a group of Australian scientists to organize the U.S.-Australia Rangelands Panel, with R. A. Perry of Australia and Dr. Kreitlow as cochairmen. Dr. Kreitlow was a leader in organizing the Panel's first workshop and was chosen to coordinate the proceedings but was stricken by his final illness before he could carry out the task.

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PLANT MORPHOGENESIS AS THE BASIS FOR SCIENTIFIC MANAGEMENT OF RANGE RESOURCES

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INTRODUCTION

By R. A. Perry¹

Australia and the United States both have large areas of rangelands which in the past have been used mainly for grazing stock, but which in the future will be increasingly valuable for other purposes, including recreation. The rangelands of the two countries differ considerably in latitude, topography, and climate, but the general principles and importance of good range management apply equally in both countries.

The main objective of range management is the maintenance of the natural resources on which present and future productivity depend. Range management is concerned with complex ecosystems in which vegetation has a central role, in that it both provides forage for animals and protects the landscapes from wind and water erosion. It is implicit that if vegetation is managed correctly then so is the ecosystem. Management of vegetation needs to be based on a knowledge of the biology of the component species, in relation to the physical and chemical environment and their reaction to grazing.

The tolerance of ecosystems to utilization by man, and their ability to regenerate following misuse, decreases as the physical environment becomes more extreme, for example, as aridity or slope increases. The more extreme the environment, the greater the need for careful management and for flexibility in management systems. Viewed against these considerations, the intensity of stocking on many Australian rangelands is too high and too inflexible, at least under existing

broad scale management practices. In many cases, lower stocking intensities probably would be more profitable in the long term.

Normally the management of multispecific plant communities is concerned with maintaining a balance between species. This particularly applies in the case of mixed woody and herbaceous elements, where the desirable balance is one which contains enough individuals of woody species to provide landscape protection and reserve forage in adverse periods, but not so many that they seriously reduce herbaceous production at other times. The balance needs to be maintained within reasonably narrow limits, because if it is allowed to swing too far towards undesirable species, it is difficult to reverse by grazing management alone. It is impossible to eliminate undesirable species by any practical grazing management.

Range management is commonly considered as being concerned with native vegetation. However, since new herbivores have been introduced to most rangelands, scope exists for exploring plant genetic material in terms of its grazing and nutrient response and compatibility with other plant species. Woody perennials may be more important than they have been considered to be in the past.

The primary tool of range management is grazing control, involving variations in intensity of use, season of use, distribution of animals, and kind and class of animals. Other tools include burning, selective biocides, mechanical treatments to land or vegetation, and fertilizing. In Australia, these all need assessing at more sophisticated levels, particularly in matching specific practices to individual sites and seasonal conditions.

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Grazing systems should be designed for specific objectives, and need to be flexible (in stock numbers and season of use) to match climatic variations and, therefore, plant responses. Flexibility should also be adequate to allow for periods of environmental stress, such as droughts. In designing management systems, all factors and constraints affecting the entire management plan should be considered, for example, location of fences, water, and alternative areas for stock. Allowance should be made for animals other than domestic stock.

In all the examples mentioned at the meeting, experimental rotational grazing systems were inferior to, or no better than, yearlong grazing. However, it was recognized that considerable scope exists for applying flexible, seasonal grazing practices designed from a knowledge of plant responses. One reason for the lack of good research data on such practices is the difficulty of designing experiments involving flexible treatments.

Research results from the short grass plains and the California annual grass type in the United States, and from Mitchell grass in Australia indicate that there is a critical level or amount below which vegetation cannot be grazed without impairing its recuperative capacity. The specific critical levels are 300 pounds per acre of blue grama for the short grass plains, 500 pounds per acre of mulch in the annual type, and a 5-inch stubble for Mitchell grass. There was a strong suggestion that such a critical level exists for each range type, and that it is the most important factor affecting range management.

An associated aspect, on which there was general agreement, is that insufficient attention has been given to the region a few centimeters above and below the soil surface. It is in this region that rainfall is partitioned into runoff and soil

water, that most decomposer activity occurs, and that seeds and nutrients accumulate. The conditions in this region, therefore, have a profound effect on the future of the ecosystems.

The importance of managing for maximum seed crops has been over-emphasized in the past. Annual plants will produce adequate seed supplies under most grazing systems and certainly under yearlong grazing. Some perennials do not need to produce seeds and most others only need to seed occasionally.

Different range types require different criteria for judging condition and trend and, therefore, for assessing success or otherwise of management. The original or climax condition is not necessarily the best. Care is needed in extrapolating results, standards, and management systems from one range type to another. The whole infrastructure of range inventory and range monitoring tools (particularly range condition and trend standards), which is taken for granted in the United States, is not available in Australia. The same principles probably apply but need to be adapted to Australian conditions. There is a dearth of range management training, at both research and operator level, in Australia.

Conservative range management practices need to be based on a knowledge of the phenology of range plants. The general lack of information on the growth and development of range plants (particularly shrubs and forbs) and their response to defoliation makes it difficult to devise soundly based grazing systems, and even to interpret the results of some grazing trials. For example, it is not always clear whether experimental results are due to rest periods or grazing periods. Plant physiologists have an important role to play in providing information in a form which can be used in devising management strategies.

EFFECTS OF WATER STRESS ON PLANT MORPHOGENESIS

By R. O. Slatyer¹

Abstract

Water stress has a profound effect on metabolism and morphogenesis, affecting many aspects of growth and development. At the cellular level, both cell division and cell enlargement are sensitive to stress. Both appear to be progressively inhibited as water deficits develop, but cell enlargement generally ceases before cell division, frequently at water potentials of the order of $\Psi = -5$ bars. Initiation of vegetative and floral primordia appears to be completely suppressed by quite small water deficits. Stem and root elongation and leaf and inflorescence development appear to parallel the behavior of individual cells. Stress may affect root and shoot development differently, root development being less influenced by internal levels of water potential and more influenced by local levels of soil water potential.

The transition from formation of vegetative to floral primordia in woody plants is sometimes hastened by water stress. In herbaceous plants there is no consistent pattern but, even when the ontogenetic stage at which flowering occurs is advanced, the date of flowering is generally delayed by the stress-induced retardation of most metabolic and morphogenic processes.

Additional key words: Water potential, growth, flowering

Introduction

Water stress affects the growth and development of plants in many ways and the mechanisms involved have been studied extensively, particularly by workers in subhumid and arid environments. However, despite this activity and the large amount of information which has accumu-

lated, it is still not possible to give a clear general account of the sequential effects of water stress on metabolism and morphogenesis.

In part, this is because plant water status is a highly dynamic parameter, strongly influenced by conditions in the soil and atmospheric microenvironment and also regulated to different degrees, in different situations and with different species, by physiological factors. It therefore constitutes a difficult parameter to examine experimentally.

Of greater importance, though, is the fact that both metabolism and morphogenesis are intimately related through feed back control mechanisms. Thus, a direct effect of dehydration on cell enlargement may indirectly influence protein synthesis by affecting the demand of the plant for the metabolites involved in cell division and enlargement. This leads to an end-product inhibition of protein synthesis. Since dehydration may also affect protein synthesis directly, it sometimes becomes extremely difficult to separate cause and effect relationships and to identify the sequence of metabolic and morphogenic events associated with stress effects. Furthermore, most factors which affect growth have repercussions throughout the whole plant. Thus, water stress not only directly affects such processes as nutrient uptake and photosynthesis, but the demand for mineral nutrients and assimilates is itself affected by growth rate.

Effect Of Water Deficits On Cellular Processes

Growth and development of a plant depend, in the simplest terms, on continuing cell division, and on the differentiation and expansion of individual cells until the characteristic form of the plant is realized. Associated with this (basically genetically determined) phenomenon is an interconnected web of metabolic events which involves the uptake of nutrients, the synthesis of metab-

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olites and structural materials, and the transport of substances within the plant body.

The manner in which water stress affects nucleic acid metabolism and protein synthesis is obscure but several generalizations can be made. It is known that water stress reduces the incorporation of amino acids into proteins, but amino acid synthesis does not appear to be unduly inhibited since amino acid pools tend to accumulate during stress periods (3). The synthesis of proteins from amino acids requires several steps, all of which are interwoven with nucleic acid metabolism and function. In the first place, transfer ribonucleic acid (RNA) is required to bring the amino acids to the ribosomes which are the sites of protein synthesis. Messenger RNA is then required to transcribe the amino acid sequences from the deoxynucleic acid (DNA) to the forming protein molecule. This leads to the accumulation of mono-ribosomes into polyribosomes specific for each protein. Water stress can, therefore, influence protein synthesis at one or more points in the overall sequence. Recent research has shown that polysome formation is markedly retarded by water stress (9). This may be a direct effect but there is

evidence that messenger RNA is itself inactivated by prolonged stress and that DNA may be affected.

Clearly, effects on these fundamental cellular processes must have profound effects on cellular development, even though the nature of the primary trigger for the sequence of events is still obscure. The key requirements for growth, cell division and cell enlargement are certainly affected by quite small water deficits.

At the root and shoot apex, both cell division and cell enlargement, and the initiation of new primordia appear to be completely suspended at water potentials of the order of $\Psi = -1$ to -5 bars. (9, 25).

The effect on primordial initiation appears to be superficially similar to that of dormancy, in the sense that initiation can be suspended without the potential for subsequent development being impaired, as long as the stress is not too severe or too protracted. Figure 1, from Gates (12), illustrates this point, by using apical development of lupine as experimental material. The virtual cessation of appearance of new primordia, when stress is imposed, followed by renewed develop-

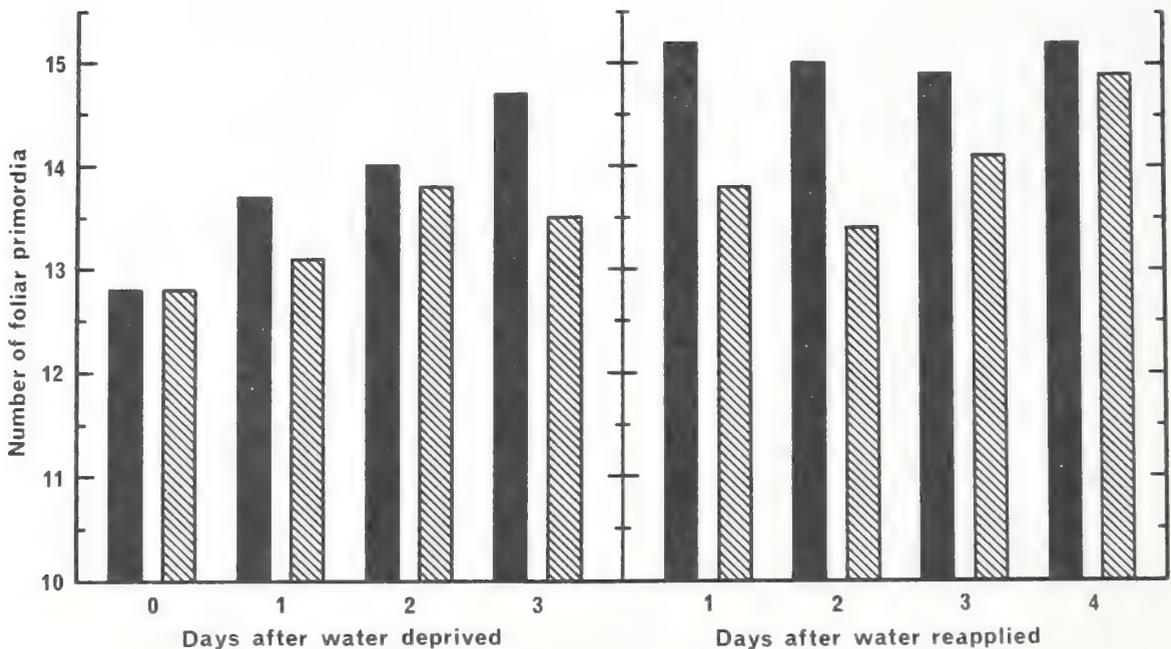


FIGURE 1.—Numbers of foliar primordia in lupine apices during water deprivation and upon rewatering (shaded columns), compared with well watered controls (solid columns) (after Gates (12)).

ment upon relief of stress, is a phenomenon that has been frequently cited (9, 10, 12, 30).

Renewed development upon rewatering may proceed at a more rapid rate than in the controls, sometimes enabling stressed plants to "catch up." This phenomenon, evident in figure 1, has also been demonstrated in the field. Morton and Watson (19), for example, showed that a crop of sugar beets, exposed to repeated cycles of water stress interspersed by irrigations, developed overall at the same rate as the well irrigated controls.

When stress is more severe or is prolonged, the total number of primordia formed is substantially reduced. In barley, for example, Husain and Aspinall (15) showed that total primordial number is significantly reduced by withholding water for several weeks (during which time the plant water potential dropped to levels corresponding approximately to permanent wilting). Even though initiation of primordia was resumed upon rewatering, their rate of appearance was insufficient to permit "catching up" to the well watered controls (fig. 2A). Similarly, in white pine (*Pinus strobus* L.) Zahner (37) reported that the number of needle primordia laid down in the terminal buds of late summer could be reduced by 40 percent

during summers in which mild droughts occurred at bud formation stage.

Cell division in organs that have been already initiated does not appear to be as sensitive as in the apical meristems, and may continue during stress, although at a progressively reduced rate, until quite severe conditions ($\Psi = -10$ to -20 bars) exist.

In the study on barley by Husain and Aspinall (15) for example, slow but persistent differentiation of pre-formed primordia continued during the stress period (fig. 2B). It has also been noted that the total number of cells in stressed leaves may be the same as in well-watered controls (29). Other corroborative evidence was obtained by Gardner and Nieman (8) from studies of DNA synthesis in stressed radish cotyledons. Although a marked reduction in the rate of increase of DNA occurred at small stress levels, some increases occurred even when severe stress ($\Psi = -15$ bars) was imposed. This phenomenon permits relatively rapid resumption of growth and development when stress is removed (fig. 2B).

The relative growth rates of plants measured following relief of water stress may be more rapid than those of control plants (9, 10, 36).

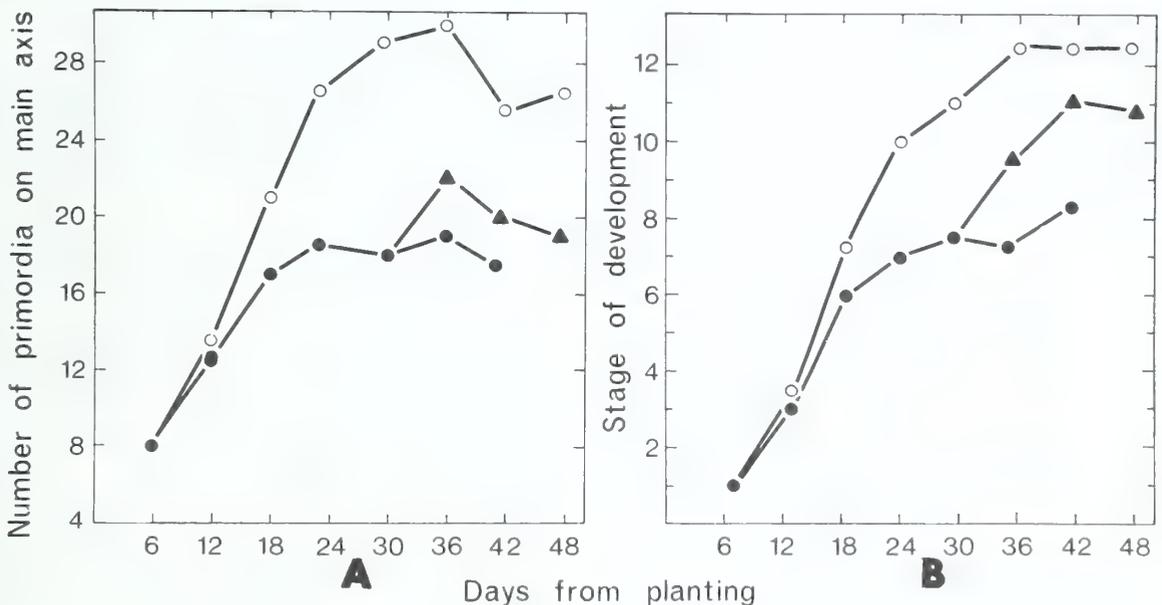


FIGURE 2.—Total number of primordia on main axis (A) and stage of development of main apex (B) of barley subjected to prolonged water stress. Plants watered throughout (○); not watered after day 0 (●); not watered between days 0 and 30 (Δ) (after Husain and Aspinall (15)).

This may be due in part to the availability of cells, already differentiated, which can rapidly expand, or it may be associated with a renewed supply of growth substances, or with other factors. However, higher relative growth rates are seldom sustained for long, so that compensation is seldom complete unless the stress period has been mild and brief. When it is severe, and total primordial number is permanently suppressed, complete compensation is clearly out of the question.

Cell enlargement in non-meristematic tissue may also proceed at stress levels which would stop enlargement at the root or shoot apex; but, in general, cell enlargement appears to be more sensitive to stress than cell division. In fact, reduced leaf and shoot elongation is frequently the first observable symptom of water deficits, and is a main cause of stunting which is perhaps the most common sign of water stress under field conditions.

The main difference between the long-term effect of reduced rates of cell enlargement and cell division is that cell enlargement is a plastic phenomenon, closely linked with the deposition of fairly rigid cell wall materials (23). In consequence, slower rates of enlargement are generally associated with smaller final cell size.

In some instances, leaf and stem elongation is rapidly resumed when stress is relieved. Hsiao et al. (14) suggested that this may be due to an effect of stress in increasing cell extensibility, although it may be frequently associated with both division and enlargement, rather than with enlargement alone. This is probably the explanation for Miller's (18) data with loblolly pine (*P. taeda* L.), which showed that in the 60 days following a 30-day stress period, needle elongation reached the same level as in the irrigated controls.

In some species, cell enlargement is so sensitive to water deficits that stem elongation or leaf enlargement can be inhibited by small diurnal water deficits that occur even with well watered plants on days of high radiation incidence or similar high evaporation-demand conditions (14, 32). A more general response is that of a progressive decline in rates of cell enlargement as water deficits develop, and enlargement generally ceases when turgor pressure levels are still at the level of several bars.

The relative effects on leaf and stem enlarge-

ment appear to differ with different species. In most cases stem elongation appears the more sensitive; the results of Lotan and Zahner (17) are typical. In a study of stem and needles elongation in red pine (*P. resinosa* Ait.), they found that elongation of internodes ceased several weeks earlier than that of needles, as stress was imposed. Also needles at the tops of shoots and on the uppermost branches were affected to a greater extent than needles lower on shoots or on lower branches. By comparison, in tomato, Slatyer (28) noted continued stem elongation at water potentials sufficient to cause pronounced leaf wilting.

The effect of water stress on the continued development of tissues which are already mature, or approaching maturity, resembles that of hastened senescence. One of the earliest signs of stress is the migration of phosphorus from older leaves to the stems and meristematic tissue (11, 36). This is closely followed by the movement of nitrogen, suggesting progressive protein hydrolysis and breakdown of normal cell function.

In summary, it seems that the effect of stress tends to be most pronounced in those tissues which are in rapid stages of development, a conclusion already reached by other workers (11, 31). The developing tissues appear to enter a rejuvenating phase on relief of stress and relative growth rates of such plants may be more rapid than those of controls. This rapid growth is aided by the continued slow cell division which has occurred during stress and perhaps by the availability of nutrients released from older tissues.

Relative Effects On Shoot And Root Development

Perhaps the most obvious effects of prolonged water stress on shoot development are those of reduced internode length and reduced leaf size. The effects on leaf size, on rate of leaf expansion, and on rate of appearance of new leaves have profound effects on total dry matter production, since the photosynthetic surface increases less rapidly and stomata tend to become nonfunctional in older leaves. Associated with this tendency for stomata to be less responsive and, in particular, to open less widely, is a progressive atrophication of the photosynthetic apparatus, so that older leaves tend to become less efficient

photosynthesisers. Continued growth clearly requires a flow of assimilates, so this tendency for reduction in photosynthesis leads to a negative feedback, and the overall metabolism tends to slow down.

In species with endogenously controlled and well defined seasonal growth patterns, such as many woody perennials, bud formation may be the primary control for the next season's growth. Water stress at this stage is clearly of profound importance and the dominance of this control mechanism has been clearly described by Clements (6). In a study of the shoot responses of young red pine (*P. resinosa*), Clements imposed three watering treatments during the bud formation stage, from late summer until early autumn, and two watering treatments in the subsequent spring. Size of apical buds, date of bud swell and bud burst in the spring, number of needle fascicles on new shoots, shoot length, and the spacing of the needle fascicles were closely related to the late summer-autumn treatments and relatively unaffected by the spring treatments (table 1). Most of these responses were also closely related to bud size.

Woody species without such strong control from prior bud formation, and other perennial species, do not appear to show much dependence of subsequent growth on stress during the previous season, except perhaps for the first spring growth flush. In such cases the pattern of shoot development is largely controlled by contemporary stress conditions.

TABLE 1.—Length and number of fascicles on shoots of *P. resinosa* exposed to differential watering treatments¹

Response	Treatment in	Treatment in 1964 ²	
	1963	Dry	Wet
Mean shoot length (cm.)	Wet	10.7 (± 1.2)	9.8 (± 1.5)
	Intermediate	11.0 (± 0.9)	8.0 (± 1.2)
	Dry	6.0 (± 0.7)	6.0 (± 0.8)
Number of fascicles on shoots	Wet	105.3 (± 8.0)	105.2 (± 8.9)
	Intermediate	94.6 (± 2.8)	93.6 (± 7.5)
	Dry	(± 7.6)	88.9 (± 6.0)

¹ From Clements (6).

² Figures in parentheses are standard error of mean.

The effects of water deficits on root development are less well known than on shoots. Although it is sometimes stated that root development is enhanced relative to shoot development during stress, there is little quantitative information on this point (25, 33, 34).

Two types of effects can be expected: (1) a reduction in rates of meristematic activity, and of root elongation, directly associated with the level of internal water deficit; and (2) an effect of suberization on the water and nutrient uptake properties of the root system as a whole.

Most research has shown a progressive reduction in rate of root elongation as water stress is imposed (21, 25). In some cases, root elongation ceases before shoot growth. In this regard, Newman's (21) work with flax shows a high dependence of rate of root extension on local soil water potential. Thus, roots in relatively moist soil may continue to elongate even though the plant as a whole is subject to severe internal water stress. In consequence continued exploration of the soil mass by root systems might be expected until the root zone is reduced to the same general level of water potential.

The effect of water stress on suberization can be expected to vary, depending upon the local rates of root extension. In rapidly growing roots a nonsuberized zone, several cm. long, may occur in some species, constituting a highly active and extensive absorbing surface. As rates of root elongation are reduced the rate of suberization exceeds the rate of elongation, and the nonsuberized zone is reduced, until it is effectively eliminated in nonelongating roots. This phenomenon, common under conditions of severe water stress, substantially reduces the effective surface area of the roots and their activity as absorbing organs.

On rewatering, the shoot and root responses differ. Shoot growth, as mentioned previously, tends to resume—sometimes more rapidly than before—with only a short recovery lag being observed. Photosynthesis in the shoot may be depressed for longer periods than cell division and enlargement but this may be due to delayed recovery of stomatal opening capacity rather than to lesions in the photosynthetic apparatus itself. The important point, though, is that as long as the stress does not cause permanent injury, shoot response is relatively rapid, and recurrent stress

periods do not appear to cause a progressive reduction in the capacity of the shoot to respond to rewatering.

Renewed root growth also requires the initiation of new primordia and renewed cell division and enlargement in the root meristem. By comparison with the shoot, however, renewed root growth often appears to be delayed, perhaps because of the need for a supply of fresh assimilates from the leaves. In consequence, if periods of stress recur before full rates of root elongation have resumed, a progressive decline in rates of root growth during each cycle may occur.

This phenomenon has been demonstrated by Kaufmann (16), in studies of root and shoot elongation in potted loblolly (*P. taeda*) and white (*P. strobus*) pine seedlings. Kaufmann imposed two watering regimes (5- and 7-day cycles), the most severe of which induced water potentials of the order of $\Psi = -16$ bars before rewatering. The control plants were watered daily. The relative responses of the shoots and roots to these treatments are shown (fig. 3). It is apparent that, although shoot growth is depressed in the water stress treatments, the amount of shoot growth in each cycle is maintained relatively constant. By comparison, a progressive decline occurred in the amount of root growth as the second and third stress cycles were imposed.

Although these experiments were conducted with woody perennial evergreen species, it seems likely that similar responses occur in annual and herbaceous species.

In Kaufmann's study, however, the entire root system was under stress. Under natural conditions, deeper roots may be in moist soil and Newman's work, cited earlier, suggests that such roots will continue to elongate even though roots in shallower, drier, soil may reflect the pattern just described.

Effect Of Water Stress On Reproductive Development

In focussing the general effects of water stress on to the specific area of reproductive development, there are two main stages to be considered. The first of these is the stage of floral initiation and inflorescence development when the potential fruit number is determined. The second is the

stage of anthesis and fertilization when this potential is realized, and fixed. This is followed by a third stage of fruit maturation during which fruit or seed weight progressively increases. This stage, of great importance to economic yield in many agricultural crops, is of reduced significance in browse species and will not be considered here.

It is extremely difficult to generalize as to the effects of water stress on floral development in different species because of the markedly different patterns which exist. Even so, it is desirable to bring out as many general features as possible.

The first stage to be considered is that of floral induction. The key question is whether the transition from the production of vegetative to floral primordia is affected by water stress and, if so, in which direction?

A change in environmental conditions is sometimes thought to induce initiation of floral primordia (26) and water stress has been regarded as one such stimulus (27). However, in many determinate annual herbs and grasses, the number of vegetative primordia formed before the appearance of the first floral primordium does not appear to be greatly affected by water stress. In tobacco, for example, Hopkinson (13) showed that water stress could lead to the laying down of additional vegetative primordia before floral initiation occurred, but the maximum number observed did not exceed five. In barley, Nicholls and May (22) found no effect of stress on the number of vegetative primordia laid down.

On the other hand, in sorghum, Whiteman and Wilson (35) found that, as onset of stress approached the normal time of floral initiation, mean leaf number could be reduced up to three. These workers considered that the leaf number at which floral initiation commenced depended on the interaction between the amount of vegetative development necessary to allow the formation of a floral stimulus, and the extent to which stress may suspend development. With stress imposed well ahead of the normal time of floral initiation, there was insufficient vegetative development so that, on rewatering, leaf formation was resumed, and the number of vegetative primordia formed was unaffected.

By comparison, when stress was imposed closer to the normal time of floral initiation, there was

sufficient vegetative development to permit formation and translocation of the floral stimulus and, upon rewatering, floral initiation occurred with the first primordia appearing at a lower leaf number.

More pronounced effects have been observed in species in which flowering can be induced by a

single inductive cycle: In studies of *Lobium temulentum* L., *Pharbitis nil* (L.) and Choisy, and *Xanthium strumarium* L. Aspinall and Husain (2) found that stress during the inductive cycle could completely prevent flowering.

Additional experiments with *P. nil* showed that stress directly before the inductive period could

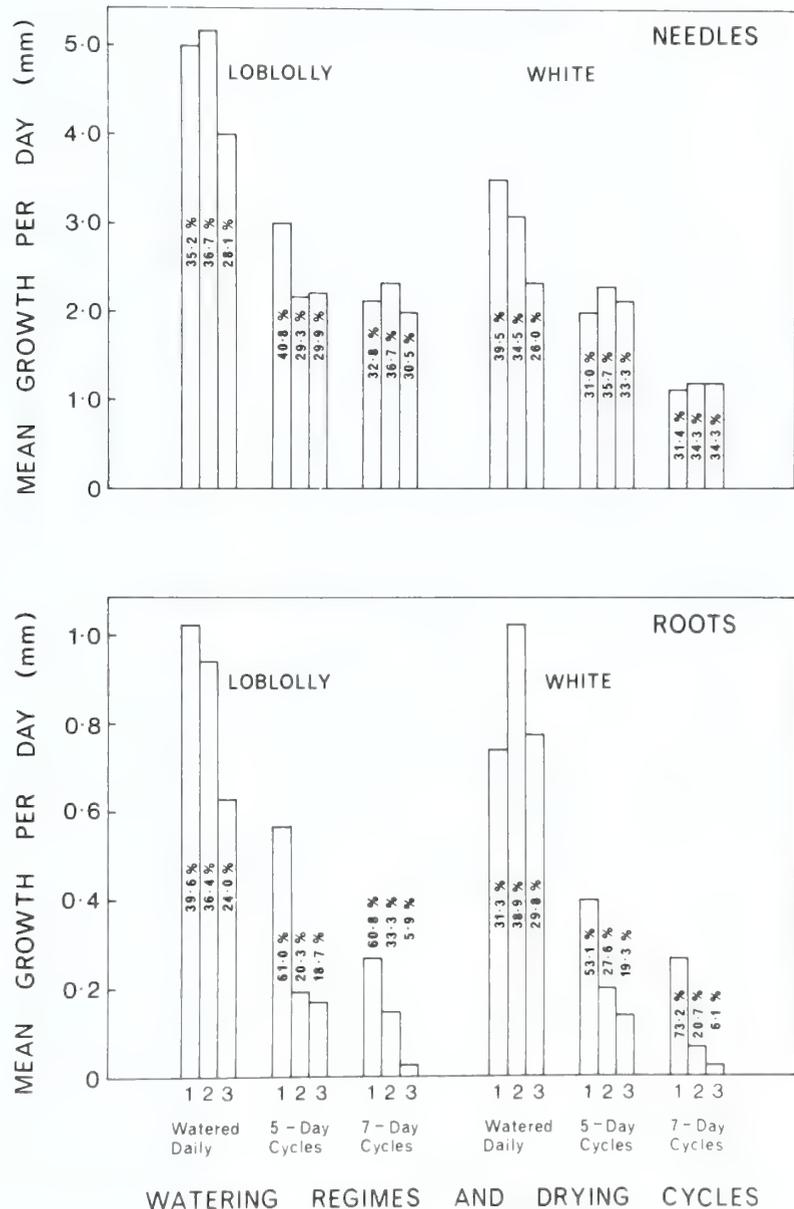


FIGURE 3.—Mean daily growth of needles (upper box) and roots (lower box) of loblolly and white pine seedlings during each of three drying cycles in three watering regimes. Percentages in histogram bars refer to growth per drying cycle as a percentage of total growth during three cycles (after Kaufmann (16)).

also suppress flowering, but stress after the inductive period was without effect. It was of interest that none of the treatments (down to $\Psi = -6$ bars) suppressed vegetative growth, expressed either as node number or internode length (figure 4). In *X. strumarium*, there was little suppression of flowering when stress was relieved before the inductive cycle.

These studies suggest that floral induction can be suppressed by water stress, at least in the species under study and possibly in other species if stress is sustained during the induction period.

The effect of water stress on transmission of the floral stimulus from the leaves to the apex has also been studied by Aspinall and Husain. Using *L. temulentum* and *X. strumarium* they established that, if stress was imposed at the end of the inductive cycle, and the leaves removed when stress was relieved, flowering was prevented. If defoliation were delayed until 24 hours after stress was relieved, a significant flowering response was observed, and a progressive increase in response occurred during this 24-hour period. These results suggest that the floral stimulus is not translocated out of the leaf while stress exists but that, once formed, it is not destroyed by stress (even though flower development is suppressed compared with the controls), and when stress is

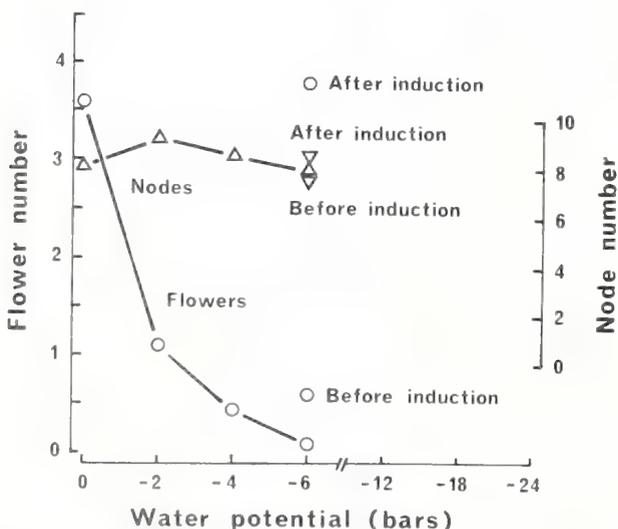


FIGURE 4.—Flowering response and node production in *Pharbitis nil* plants, subjected to osmotic stress during a 16-hour dark inductive period. (After Aspinall and Husain, (2).)

relieved it is translocated to the apex. This is in line with known effects of water stress on translocation of assimilates, even though translocation of the floral stimulus may be independent of assimilate transport (7).

It must be appreciated that, in the field, photo-inductive conditions continue for long periods, but water stress is also likely to be protracted. Also, variable degrees of stress may affect the formation and translocation of the floral stimulus differently than primordial initiation. If primordial initiation is the more sensitive, flowering can be expected to occur at a lower node number; if less sensitive, at a higher node number.

In either case, though, an associated effect of water stress will almost always be a delay in date of flowering, regardless of whether it occurs at a younger ontogenetic stage. In the study of Nicholls and May (22), stress did not affect the number of vegetative primordia formed in barley, before the first spikelet primordia appeared, but the appearance of the first double ridges was delayed several days by even mild stress. Rate of initiation of floral primordia became progressively slower in the stressed plants. Upon rewatering, the initiation rate in the "mild" ($\Psi = -5$ bars) stress treatments increased rapidly so that when stamens were initiated, total spikelet number was almost the same as in the controls. By comparison, in the "severe" ($\Psi = -15$ bars) stress treatment, total spikelet number was at a much lower level at the time when development of the spike was concluded.

Whiteman and Wilson (35) conducted experiments with grain sorghum in which the timing and duration of stress was varied around the stage of floral initiation, but in which all treatments constituted "severe" stress (wilted for one week or more). They found that development of the inflorescence could be suspended during stress yet could be resumed on rewatering and result in a flowering head not significantly different from that of control plants.

In one experiment in which severe stress was imposed for periods of about 1 week, on three occasions during the normal time of floral initiation, initiation was totally suspended but was resumed upon rewatering. The time at which inflorescence development was completed was de-

layed for approximately 10 days, as was the time to commencement of flowering.

In another experiment (35), stresses were imposed at about the conclusion of floral initiation and persisted for 14, 21, and 28 days. Floral initiation occurred in all treatments at about the same time as in the controls but there was no elongation of the inflorescence in the stressed plants until rewatering. From then on, development proceeded more or less at the same rate as in the controls and emergence of flowers took place at intervals of 10, 24, and 30 days after the controls, periods corresponding fairly closely to the durations of stress.

From the stage of spikelet initiation to fertilization of the ovules, a number of other processes, associated with the development of the inflorescence, are likely to be sensitive to water deficits, and thus cause a reduction in the number of fertile flowers formed (27).

The effects have been attributed, in some cases, to specific interference with the sexual development of the spikelets, such as meiosis in the gametes, but the availability of mineral nutrients and carbohydrates during the preflowering phase can also influence floral development and may be an important means by which water stress effects are mediated.

If it is severe, stress at anthesis can reduce fertilization and fruit set, but mild stresses do not appear to have a marked effect. Since stress is frequently associated with arid atmospheric conditions, it is sometimes suggested that it dehydrates pollen grains. However, it also seems possible that germination of the pollen, or growth of the pollen tube from the stigma to the ovule, may be impaired.

The relative sensitivity of different species to stress at the preflowering and flowering stages appears to vary somewhat, but comparable stress treatments have seldom been imposed and internal water deficits have seldom been measured, so detailed comparisons are not possible. Clearly, though, species which flower over an extended period have an advantage in avoiding stress effects on reproductive development.

In woody perennial plants the switch from initiation of vegetation to floral primordia frequently appears to be enhanced by water stress

and the intensity of flowering may be substantially increased (1, 5, 20, 27).

In other cases, particularly in those species which form overwintering buds, high water status during the period of bud development appears to enhance subsequent post-winter flowering intensity and may advance flowering dates slightly (4).

Evergreen xermorphic shrubs, characteristic of arid regions, may flower at almost any time of the year. Preece (24), established that *Acacia aneura* F. Muell. can flower in each season of the year in western New South Wales. Furthermore, with supplementary irrigation, the same shrubs may flower several times in one year. His studies did not estimate the period between floral induction and flowering, but it appears that any watering treatment which induces a marked vegetative growth flush leads to flowering in a period of 1 to 2 months. This pattern may well be reflected in other arid species, particularly those growing in areas with relatively warm winters and without definite seasonal rainfall patterns.

On the other hand, many species may have a preferred flowering season, coinciding with the preferred period of vegetative growth. In *Acacia aneura*, for example, there appears to be a preferred period for growth and flowering in the spring and again in late summer.

The period from flowering to fruit maturation may be as short as a few days for some ephemeral species and longer than a year for some woody perennials. In the former case, water stress during fruit development is seldom a problem, since the species are well adapted to mature fruit during a drying cycle. However, in other species, water stress may frequently affect seed size, viability and some aspects of seed dormancy. Seed size, in particular, appears to be positively correlated with successful seedling growth, so water stress can have long term indirect effects through this means.

Conclusions

The preceding discussion on the effects of water stress on morphogenesis in three loosely grouped types of plants—annuals, perennial grasses, and woody perennials are summarized as follows:

The effect of water stress on annuals is likely to result in reduced leaf size and internode length,

and a general stunting of the tops of the plants. Root growth is also likely to be suppressed more or less in proportion to shoot growth. Flowering and fruit set will probably occur at much the same ontogenetic stage as well watered species, but are likely to be delayed in time. Both seed number and seed size are likely to be reduced, and seed viability may also be reduced. If stress is more severe, continued growth and development is likely to be stopped and the plant will finally die unless rewatered.

In perennial grasses, a similar general effect on shoot development—of reduced leaf size and internode length—can be expected to occur. Root growth, however, will be controlled more by local levels of soil-water potential than by mean plant-water potential and can be expected to continue in moist soil. If stress is severe, shoot growth will stop but will be resumed upon rewatering. Reproductive development is likely to be delayed and floral initiation may not occur unless stress is mild or absent. If the stress is sufficiently severe to induce shoot dieback, new tillers will develop from basal buds when water is reapplied. The residual tussocks are extremely tolerant of water stress and will probably persist through lengthy drought periods if they are not damaged by grazing.

Woody evergreens tend to reflect the same pattern of stress response as perennial grasses in that shoot growth may cease while root development continues in moist soil. However, the pattern of shoot development can be influenced over lengthy periods in cases where growth is largely seasonal and is based in part on development of overwintering buds. In such cases water stress at the times of bud development has an important bearing on subsequent shoot development, both vegetative and reproductive. In general, the number of leaves and flowers will be controlled by water stress during bud development, but leaf size and shoot length may be more influenced by water stress during the postwinter period, as will the amount of fruit set and final seed size. In species without such strong seasonal control, contemporary water stress operates in much the same way as in herbaceous species.

Woody perennials also tend to be extremely drought tolerant. There may be some drought induced leaf shedding, but unless the stress is

almost lethal, leaf shedding tends to be greatest after water is reapplied and when new growth is commencing.

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DEVELOPMENT AND REVERSAL OF PLANT RESPONSES TO SALINITY AND WATER STRESS¹

By James W. O'Leary²

Abstract

As the osmotic pressure of the solution around plant roots increases, plants increase their internal osmotic pressure. This osmotic adjustment of plant cells is reversible. The water permeability of roots in osmotically adjusted plants is irreversibly decreased, and this allows water stress to develop in these plants. Fresh weight, dry weight, and leaf area are reduced by the increased osmotic pressure, as is leaf initiation. Upon removal of the osmotic stress, growth rates of the stressed plants return to normal, except that leaf expansion is still slightly suppressed. This is considered to be due to decreased extensibility of cell walls resulting from the increased osmotic pressure of the cells. Data support the conclusion that one of the major effects of increased osmotic pressure in the cells is an acceleration of cell aging.

Additional key words: Salinity, osmotic stress, water relations, water stress

Introduction

The equilibrium water status of a plant is dependent on the plant's environment. For a terrestrial vascular plant, that means the equilibrium plant-water potential will be equal to or less than the soil-water potential under most conditions (45). That is, the soil-water potential (Ψ_s) determines the maximum plant-water potential (Ψ_p) that can be developed. It is for this reason that considerable emphasis is placed on maintaining soil-water potential as high as is reasonably practical. The value of the soil-water poten-

tial depends almost exclusively on matric (τ) and osmotic pressures (π). This relationship can be indicated as:

$$\Psi_s = -\pi - \tau \quad (1)$$

As the water content of a soil decreases, both matric and osmotic pressures increase, and Ψ_s is lowered accordingly. Under nonsaline soil-water conditions, π is so small relative to τ that it usually is neglected, and equation 1 becomes:

$$\Psi_s = -\tau \quad (2)$$

As the salinity of the soil-water increases, π becomes more important. This is a matter of great concern because it makes possible the existence of low soil-water potentials, even at high soil-water content. For example, since there is such a close relationship between τ and soil-water content, measurements of water content or τ are the soil-water measurements typically employed. However, if the salt content of the soil-water was such that π_{soil} was 3 bars, then neither of those measurements would reveal the fact, and more important, the Ψ_s would be -3 bars even at field capacity. Under most conditions, the salinity of the soil-water gradually increases over time and may not be apparent until it has become quite high. Thus, it is important to include measurement of π_{soil} along with the other soil-water measurements, even if direct psychometric measurement of Ψ_s is made.

If π_{soil} affected plant growth only insofar as it reduces Ψ_s , that is, if it only acted in the same fashion as τ_{soil} , then there would be no need for concern, but if plant growth is reduced in some other way, then it is important. For many years, it was thought that π_{soil} and τ_{soil} acted in the same way in affecting plant growth, that is, they simply lowered Ψ_s , but that idea has been questioned (31). Why this idea has been questioned

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and how π_{soil} influences plant growth, other than through its effect on lowering Ψ_s , will be included in the discussion to follow.

Since Slatyer has reviewed the effects of water stress, primarily water stress resulting from increased τ_{soil} , I would like to confine my discussion to the effects of π_{soil} on plants, particularly as it affects leaf morphogenesis. To do this, I will discuss the response of plants to increased π_{soil} in terms of osmotic adjustment of the plant cells, changes in resistance to water movement, how these factors can lead to development of water stress in the leaves and its resultant effects on leaf growth, and how osmotic adjustment of the cells directly influences leaf initiation and growth in the absence of water stress. I also will discuss the reversibility of these changes. Unless specifically stated otherwise at points in the discussion, the plant to which I will be referring is the red kidney bean (*Phaseolus vulgaris* L.). Also, unless stated otherwise, I will be referring to osmotically adjusted plants that have been subjected to gradually increasing levels of NaCl in the root environment (2, 44). Seeds were germinated in paper towels, transferred to nutrient solution when 7 days old, and NaCl additions started on the ninth day. Salt additions were completed by the 15th day (44).

Osmotic Adjustment

For many years the effect of increased π_{soil} was considered to be the same as increased τ_{soil} . This viewpoint was implicit in development and acceptance of the concept of physiological drought. This view was popular in spite of the demonstration many years ago that, as π_{soil} increased, so did π_{plant} (36). This is illustrated by the data in table 1. Even though this demonstration of internal osmotic adjustment was confirmed several times in the following years, not until after the papers of Bernstein (2) and Slatyer (53) appeared, did the realization of plant osmotic adjustment become widespread. Slatyer (54) has reviewed the literature on this subject.

When the π_{plant} increases in response to increase in π_{soil} , there is not always a direct correspondence between the two. Sometimes the osmotic adjustment is less than complete (26, 27, 40); sometimes it is complete (53), and π_{plant} has even been found

TABLE 1.—Osmotic adjustment of corn roots in response to increased salinity of the soil solution¹
[π = osmotic pressure]

π of growth medium	π of root cells
(bars)	(bars)
1.21	4.59
1.99	5.48
3.38	6.61
4.96	7.51
7.22	8.19

¹ Adapted from McColl and Millar (36).

to increase more than the increase in π of the root medium (6). This osmotic adjustment occurs whether the increase in π of the root medium is slow or fast (39, 52), within limits. Furthermore, the adjustment occurs whether the solutes responsible for the increase in π of the root medium are permeating (11, 12) or nonpermeating (26, 52), and it occurs in both glycophytes (40, 53) and halophytes (5). In fact, π_{plant} even has been found to increase proportionally with decrease in soil moisture, under certain conditions (50). Thus, osmotic adjustment in plants is truly a response to decreased water potential in the rhizosphere and not simply a response to increased concentration of permeating solutes.

Some of the variation in degree of adjustment found by various investigators undoubtedly is due to the normal fluctuations in π exhibited by plants. That is, a normal or non-salinized plant will exhibit fluctuations in internal osmotic pressure, dependent on age and environmental conditions. Thus, a more reasonable indication of how much a plant osmotically adjusts, in response to alterations in π_{soil} , may be given by comparing the difference in π of salinized and control plants with the difference in π of the ambient solution around the roots of the respective plants. Such a comparison is illustrated in table 2. We increased the π of the nutrient solution, in which bean plants were growing, by 1 bar every 2 days. Every 2 days, plants growing in both salinized and nonsalinized solutions were sampled. The π of control plants growing in nonsalinized nutrient solution fluctuated between 5.8 and 7.7 bars over the 2-week period. The plants growing

TABLE 2.—*Osmotic adjustment of Phaseolus vulgaris L. plants growing in solutions subjected to increasing concentration of NaCl. π = osmotic pressure*

π of nutrient solution	π of plant in nonsalinized solution	π of plant in salinized solution	$\Delta\pi$ between plants
<i>Bars</i>	<i>Bars</i>	<i>Bars</i>	<i>Bars</i>
1	7.7	8.5	0.8
2	6.4	7.1	.7
3	6.2	8.5	2.3
4	6.8	8.9	2.1
4	6.9	8.3	1.4
4	6.6	9.5	2.9
4	6.6	10.5	3.9
4	5.8	9.7	3.9

in the salinized solutions exhibited fluctuations from 8.3 to 10.5 bars. However, within a week after the maximum salinity level had been reached, the plants apparently were fluctuating in concert so that the difference in π of the plants was the same as the difference in π of the growth solutions.

Even though there have been numerous reports of osmotic adjustment in plants accompanying increasing π in the growth medium, there are no reports of whether the adjustment is reversible. We have found that the osmotic adjustment is, in fact, reversible (fig. 1). The plants were subjected to an increasing NaCl concentration in the growth solution at a rate of 1 bar every 2 days. Plants were sampled every 2 days also. Just as there is a lag in adjustment as π is increased, so is there a lag as π of the growth solution is then decreased back to zero. Nevertheless, the adjustment was almost completely reversed within a day of return of the plants to nonsalinized solution.

Root Resistance In Osmotically Adjusted Plants

Despite osmotic adjustment that occurs in plants, which should maintain the water potential gradient from growth solution to leaves (3, 33), it often has been observed that salinity toxicity symptoms resemble drought symptoms (2, 4). That is, it appears that water transport to leaves

may be reduced in osmotically adjusted plants under certain conditions. How this might occur can be seen from consideration of the generalized flow equation:

$$J_w = L_p (\Delta\Psi) \quad (3)$$

where J_w = waterflow across the root ($\text{cm.}^3 \text{ cm.}^{-2} \text{ sec.}^{-1}$), L_p = hydraulic conductivity coefficient of the root surface ($\text{cm. sec.}^{-1} \text{ bar}^{-1}$), and $\Delta\Psi$ = the water potential gradient from the external solution to the interior of the root (bars). Reduced waterflow into the plant could occur under a constant $\Delta\Psi$ if L_p is reduced. It has been suggested many times that permeability of roots may be reduced by increased salinity or decreased water content in the root environment (27, 28, 30, 37).

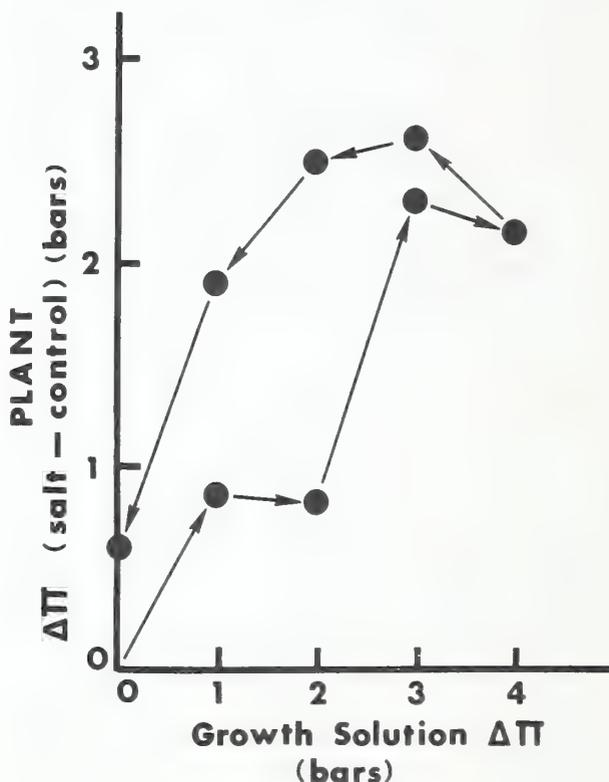


FIGURE 1.—Difference in osmotic pressure ($\Delta\pi$) between salinized and control plants vs. difference in osmotic pressure of nutrient solutions in which the plants were growing. Osmotic pressure of the growth solution was increased every 2 days and, upon reaching 4 bars, was then decreased every 2 days. On the alternate days, a plant was sampled from the adjusted solution and from the nonadjusted or control growth solution ($\pi=0.3$ bars, but called zero here).

It is not easy to determine from those studies, however, whether the permeability decrease occurs only in the presence of a high π in the external solution or whether there is a definite structural change in the roots that causes the reduced permeability. That is, when the roots are placed in water with a π of 0, is the permeability still lower in those plants that had grown in the higher salinity environment?

When we measured the pressure-induced water-flow through truncated root systems, we found that, even in distilled water, the waterflow through root systems of osmotically adjusted plants was considerably less than in nonosmotically adjusted plants (44, 47.)

Recently, we have attempted to estimate the average L_p for an entire root system. Using the same techniques reported previously (44), and measuring π and P (pressure in excess of atmospheric) of xylem sap and external solution under controlled fluctuating values of both P and π of external solution, we have obtained values for L_p of the entire root system. It is realized that permeability of the root surface as well as the reflection coefficient for various solutes, varies considerably along the length of the root, because of aging of the cells (1). Also, it is not easy to accurately determine the surface area of an entire root system. However, we have worked out the relationship between fresh weight and surface area, using measurements of surface area on individual excised roots of various sizes and ages, and we calculated surface area from fresh weight data. The details of this work have been prepared for publication elsewhere. Using this approach, we obtained an average L_p for the entire root surface of a red kidney bean (*Phaseolus vulgaris* L.) plant of 1.0×10^{-6} cm. sec.⁻¹ bar⁻¹.

This is not far from the value obtained by House and Findlay (23) for single corn roots. They calculated a value for L_p of 0.6×10^{-6} cm. sec.⁻¹ bar⁻¹, and Klepper (28) found an L_p of 0.38×10^{-6} cm. sec.⁻¹ bar⁻¹ for corn roots also. Klepper (28) also found that L_p of 0.38×10^{-6} cm. sec.⁻¹ bar⁻¹ for corn roots also. Klepper (28) also found that L_p decreased as π of the external solution increased. When bean plants were grown in solutions with 4 bars of added NaCl, the L_p for the root surface was reduced to 0.1×10^{-6} cm. sec.⁻¹ bar⁻¹, even when placed in

distilled water. That is, the permeability reduction was the result of a change in the roots themselves and not just a condition resulting from the high π of the environment.

Development Of Water Stress In Osmotically Adjusted Plants

Water stress in plants usually occurs when the capacity of the soil to deliver water to the plant becomes limiting, or when transpiration is occurring so rapidly that it outruns water absorption by the plant, even in soil containing adequate water. Whether or not transpiration rate exceeds absorption rate depends on the evaporative demand of the air and the resistance to water transport to the leaves. When evaporative demand is high, transpiration often exceeds water absorption, and water stress and wilting occur. In osmotically adjusted plants, increased root resistance makes such an event more probable since the evaporative demand of the air does not have to be so high for transpiration rate to exceed absorption rate. When this happens, the osmotically adjusted plant incurs a water deficit and suffers the same consequences as the wilted plant in a drying soil. These events are summarized in fig. 2.

As π_{soil} increases, the Ψ_{soil} is decreased, but π_{plant} usually increases also, and Ψ_{plant} decreases accordingly. This maintains the water potential gradient from soil to plant. However, the increased root resistance counteracts this tendency to absorb water and, when transpiration is high, this results in an imbalance between transpiration and absorption rate, and water stress results. This causes reduced leaf expansion which, in turn, results in less photosynthetic surface, and these two factors both contribute to reduced growth of the plant. Thus, under certain environmental conditions, the osmotically adjusted plant can suffer from water stress similar to that suffered by a plant in drying soil. This, in effect, might be considered a form of physiological drought.

Vegetative Growth In Osmotically Adjusted Plants

Bean plants (*Phaseolus vulgaris* L.), treated and allowed to adjust osmotically as before (44),

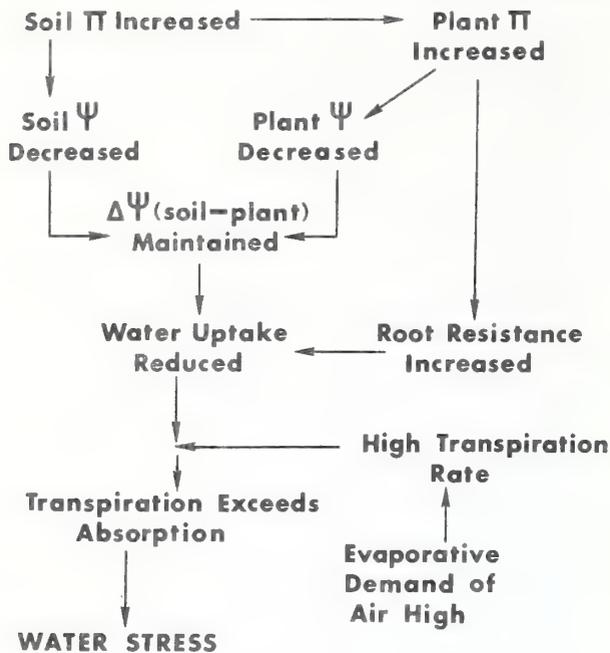


FIGURE 2.—Hypothesis to explain how osmotically adjusted plants can suffer from water stress under conditions of high evaporative demand. (ψ = water potential; π = osmotic pressure).

were used for analysis of the effect of osmotic stress on growth and development of the vegetative plant body. Five plants were harvested from both control and salt-treated groups of plants several times during the growing period. Fresh weight (fig. 3) and dry weight (fig. 4) both were affected immediately after receiving the increased salt concentration in the external solution. All parts of the plant were affected; that is, there was a general decrease in growth rate in the osmotically stressed plants. The rate of leaf initiation also was reduced (fig. 5). This is not in agreement with Livne and Levin (34), who indicated that 3 bars of NaCl added slowly (thus, presumably allowing osmotic adjustment to occur) to pea plants did not affect the rate of appearance of new leaves.

The leaf area of osmotically adjusted plants becomes drastically reduced also (38, 42, 47). This usually is the most noticeable effect of increased salinity in the root medium (42). Decreased leaf expansion usually is accompanied by increased leaf thickness, that is, the leaves are more succulent in the osmotically adjusted plants

(46), provided the plants are growing in an environment that does not promote development of water stress as indicated earlier. The following sequence of events probably occurs. In response to the elevated π of the root medium, plant cell π increases, water enters the cell in response to this increased π_{cell} but the cell wall does not yield normally, that is, the cell does not readily expand. This suggests to the writer that the increase in π_{cell} causes a decrease in cell wall extensibility. If this is so, then one should expect the turgor pressure to increase in the nonyielding, osmotically adjusted cells. Does that happen?

The literature indicates that such a situation has occurred many times, but little attention has been given to the increased turgor pressure. For example, Boyer (6) found that turgor pressure in cotton leaves subjected to an increase of 8 bars in the π of the external medium was double the turgor pressure in leaves of nonsalinized plants.

Gale and others (15) also found slightly higher turgor pressures in leaves of salt-treated cotton plants, and Meiri and Poljakoff-Mayber (39) found higher turgor pressures in leaves of bean plants subjected to increased salinity. This has consistently been observed in our laboratory as long as the environment of the plant does not favor high transpiration rates (43, 44, 46, 51). That this higher turgor pressure in osmotically adjusted plants is indicative of more rigid cell walls is supported by the observation that the dry weight per unit area of the leaf is increased considerably in the osmotically adjusted plants (46). This, of course, might indicate thicker cell walls if the cell number per unit leaf area was the same in each case, or it might indicate a greater number of cells per unit leaf area in the osmotically adjusted plants. Both conditions have been reported.

Nieman (42) reported that the number of cells per unit leaf area was the same in leaves from control and osmotically adjusted bean plants, while Meiri and Poljakoff-Mayber (38) reported that there are more cells per unit area in leaves from salt-treated bean plants.

We conducted experiments similar to those cited above, and the treatments were replicated in two different greenhouses (56). In one greenhouse, we obtained results that agreed with Nieman (42) and in the other we obtained results

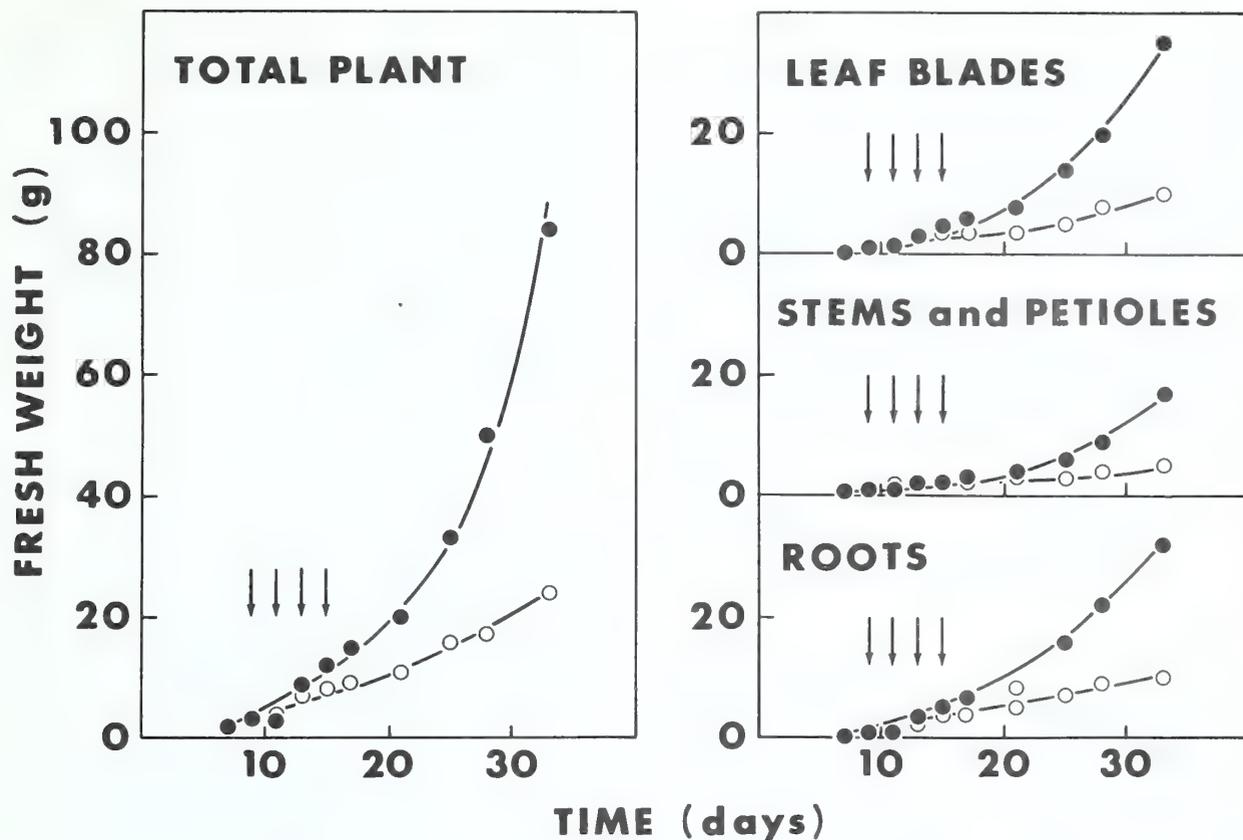


FIGURE 3.—Fresh weight of total plant and individual parts as affected by addition of NaCl to growth solution. Arrows indicate time of addition of each 24 meq. NaCl per liter of nutrient solution (each addition resulted in increase of solution π by 1 bar). Solid circles represent control plants, and open circles represent salt-treated plants. Each point is the average of 5 plants. Total NaCl added equalled 96 meq./liter, which was equivalent to a final osmotic pressure of 4 bars greater than the control solution.

that agreed with Meiri and Poljakoff-Mayber (38). It became clear to us that there are two extremely important considerations to be made in studies of this type. (1), The environment in which the leaves develop is important in determining how leaves respond to a given level of internal stress. (2), When comparing leaves on treated and nontreated plants, one must be extremely careful to compare the correct leaves. The first leaf initiated on each plant, for example, may not be physiologically similar. Differences in leaf thickness between salt-treated and control plants have not been found to be the same by all investigators (38, 42). We found that leaves present on the plant and expanding during the period of osmotic adjustment are not as thick as the corresponding leaves on control plants, but

leaves initiated subsequent to osmotic adjustment are thicker than corresponding leaves from control plants (46). We also found that there is normally a greater variation in thickness within a leaf and between leaves on control plants than on salt-treated plants (56). The salt-treated plants have smaller leaves with more uniform thickness. Thus, it makes a difference what part of what leaf happens to be selected for comparison. Bean leaf expansion is not a simple process (10, 61), and varying results among workers are likely, even under controlled-environmental conditions.

In summary, this writer feels that the increased turgor pressure and increased dry weight per unit leaf area are indicative of cells that have developed increased rigidity in the cell walls, in response to the increased π in the leaf cells. In-

creased osmotic pressure and leaf aging have been found to be accompanied by increased dry weight and decreased cell wall extensibility (29), and increased turgor pressure is found to follow as cell wall extensibility is reduced (9). Cell expansion is dependent upon both turgor and cell extensibility, and they are interdependent (18). Extensibility, thus, is a function of turgor pressure as well as other variables (35). Since cell wall growth is such a finely balanced sequence of events, and the specific molecular structure of the wall is due to this highly programmed sequence (41), any alteration of these events would be ex-

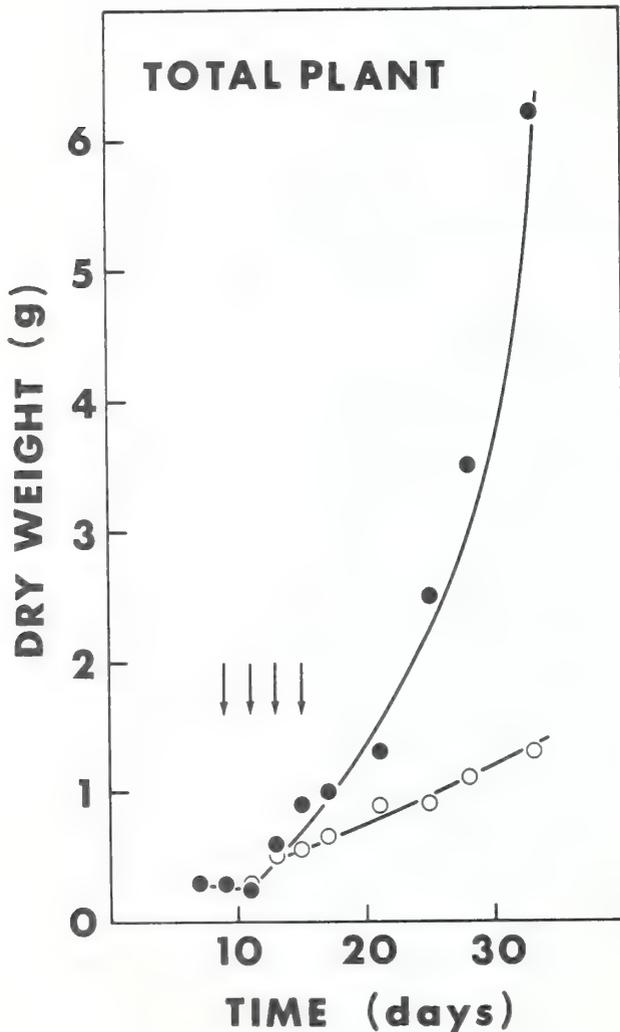


FIGURE 4.—Dry weight of total plant as affected by addition of NaCl to the growth solution. Symbols same as in figure 3.

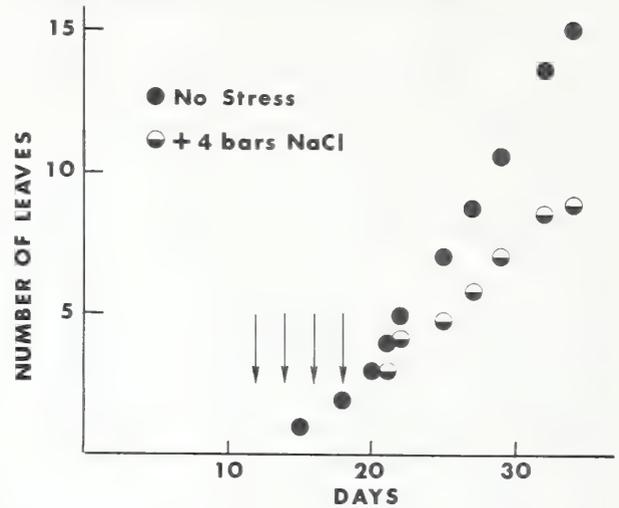


FIGURE 5.—Leaf initiation in bean plants as affected by addition of NaCl to the growth solution. Full circles are control plants and half-filled circles are salt-treated plants. Average of 8 plants for each point. Arrows have same meaning as in figures 3 and 4.

pected to affect the extensibility of the cell walls. Taylor (58) indicated that increased salinity frequently leads to thicker and heavier cell walls. Ordin (49) found that changes in π and turgor pressure in cells lead to alterations in types of cell wall polysaccharides that are formed, and this alteration of polysaccharide synthesis might explain the reduced cell extension in plants subjected to lowered water potentials (21). All of this information is compatible with the hypothesis that increased osmotic pressure in cells induces accelerated aging of the cells (46). This could be due to higher π of the leaf cells *per se* or decreased hormone delivery to the leaves, resulting from stress in the roots (25, 46).

Recovery From Salinity Stress

When plants subjected to water stress in drying soil are rewatered, they often exhibit growth rates that are higher than the control plants (13, 16, 17), and this may even result in the final size of the stressed plants being larger than the nonstressed plants (22). Rate of leaf expansion usually has been employed as the measurement of growth in those studies, and the increased rate of leaf expansion, upon rewatering, could be explained by the accumulation of sugars in cells

during the stress period (13). However, even dry matter production has been found to increase when stress was relieved (48), and there is a suggestion that grass plants may even be able to maintain a higher photosynthetic rate at a lower leaf turgor, after relief of water stress (59). It has been pointed out, however, that plants subjected to salinity stress do not show such behavior upon removal of the stress and, in fact, exhibit growth rates still lower than in nonstressed plants (31, 54). The data of Greenway (19) are used to support this conclusion. Meiri and others (40) also found that growth rates do not equal control plant growth rates when stress is relieved. When plants were alternated daily between saline and nonsaline conditions, however, they showed a burst of growth upon being placed in the nonsaline conditions, and this growth rate exceeded the growth rate in the control plants (60). Also, Strogonov (57) found that cotton plants subjected to salinity stress for a month and then returned to nonsaline conditions exhibited accelerated growth rates even 6 weeks later.

We subjected plants to four bars of added NaCl and then returned them to nonsaline conditions. Growth was measured 5 days and 10 days later. Fresh weight of plants returned to nonsaline conditions increased faster than fresh weight of the plants remaining in saline solution or of control plants (fig. 6). This was due to accelerated rates of fresh weight increase in both leaf blades and roots. Even though the rate of dry weight increase was accelerated considerably upon removal of the saline medium, it did not surpass the rate of control plants (fig. 7). It did, however, equal the growth rate of control plants. These increases did not occur until the second 5-day period. This is in good agreement with Greenway's (19) results, since his measurements of growth were taken 6 days after stress was relieved.

Conclusions

Much of the data discussed in this paper and elsewhere (46) support the conclusion that one of the primary effects of water stress and osmotic adjustment is in acceleration of the aging process in cells. The effects of osmotic and water stresses on hormone metabolism and the resultant effects

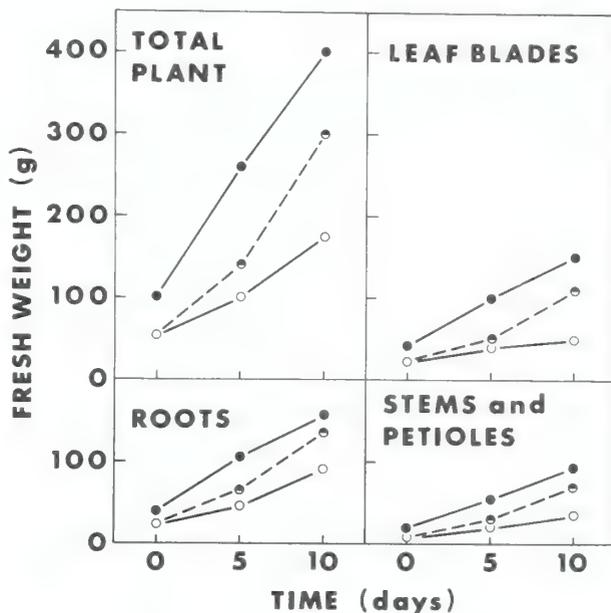


FIGURE 6.—Fresh weight of total plant and different plant parts as affected by growth in solutions with 4 bars added NaCl. Some of the plants were returned to nonsalinized solution after 2 weeks growth in the salinized solutions (Day 0). The solid circles represent control plants, the open circles represent plants grown continuously in solution with 4 bars added NaCl, and the half-filled circles represent plants removed from the salinized solution on Day 0. Each point is the average of 5 plants.

on senescence have been discussed by Itai and Vaadia (24, 25) and O'Leary (46). During the past decade, much evidence has been obtained showing the effects of stress on cellular metabolism. The most frequently observed disruptions in cell metabolism involve nucleic acid and protein metabolism. This, in turn, is reflected by chloroplast breakdown and other events that are characteristic of senescence. Much of the data is conflicting, and a discussion of the subject of stress and cell metabolism that is less than comprehensive in scope would be misleading and subject to misinterpretation. Thus, I offer no more than my subjective analysis of the enormous amount of data relating cell physiology and stress which is summed up in my general conclusion that water stress, salinity stress, and probably other forms of stress as well, act primarily to accelerate senescence in plants.

Of course, when environmental conditions are such that they cause a reduction in cell turgidity,

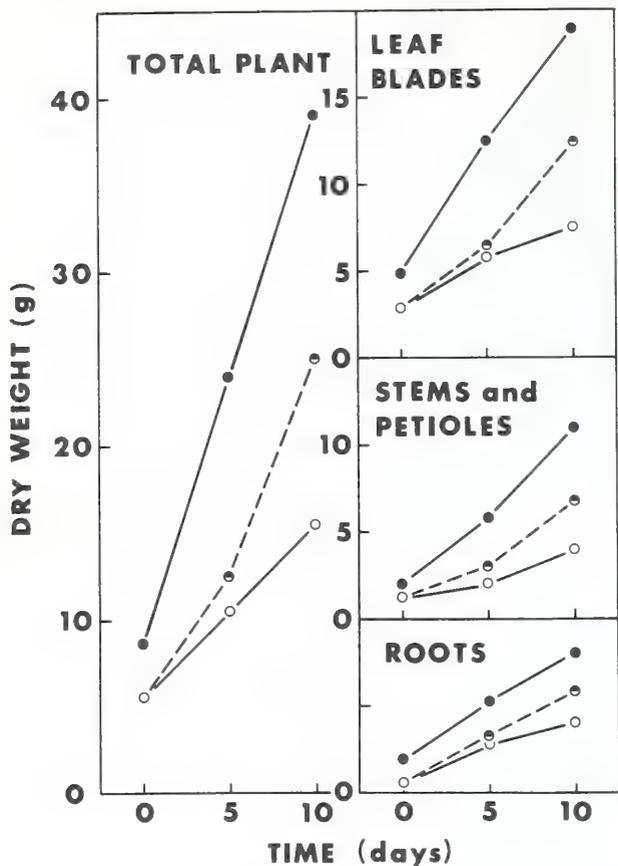


FIGURE 7.—Dry weight of bean plants and plant parts as affected by growth in salinized solutions for varying periods of time. Same conditions and symbols as in figure 6.

then this effect will predominate. The case for a minimum turgor pressure necessary for cell enlargement has been well established (7, 8). In the absence of reduced turgor, however, the growth reduction is due to something else. It is in these cases that I propose the acceleration of senescence to be of importance. Furthermore, the increased osmotic pressure in the osmotically adjusted plant probably is the cause of this effect. There already exists good data to support this hypothesis (14, 20).

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EFFECT OF TEMPERATURE ON MORPHOGENESIS¹

By Horton M. Laude²

Abstract

The influence of heat or cold on the form, function, and life cycle of range plants is reviewed. Particular attention is directed to those stress conditions of temperature which evoke impairment of function or visible injury. Investigations on nonrange species, especially the cereal grains, are included when the findings are deemed applicable to range vegetation. Several topics warranting further study with relation to range species are identified.

Additional key words: Temperature stress, temperature injury, critical stages

Introduction

Plant scientists recognize the importance of temperature in regulating the rate of physiological processes and in influencing growth and development. The application of temperature response specifically to the management of range resources has received less attention. The influence of temperature on the form, function, and growth of range species deserves consideration, both to identify the more important responses and to appraise their effect on the vegetation and its use.

Some limitations, however, deserve mention at the outset. A number of responses are best illustrated or have been studied on species other than those of rangelands. I have included these when the findings might be applicable to range. Furthermore, it must be remembered that temperature response is conditioned by the level of other factors of the environment. For example, temperature and moisture condition are closely associ-

ated, as are radiant energy and temperature, and others. I will, nevertheless, attempt to view temperature in situations in which it is the primary variable. Some difficulty will be encountered in stating the precise temperature of different tissues or organs of a plant, since authors in reporting experimentation often give only air temperatures surrounding the plant. And lastly, what levels of temperature deserve the greatest attention? An optimal temperature exists for a particular function or aspect of plant growth, but environments continually fluctuate in nature and plants experience temperatures above and below this optimum for the greater part of their life cycle. Near optimal temperatures do influence growth, but often produce little visible indication of their effect. Temperatures further removed from the optimal evoke more drastic responses, and visible symptoms become clearly apparent. There is merit, therefore, in considering those temperatures capable of producing definite stress and visible symptoms, and I have emphasized them in my selections from the literature. Some justification for this approach rests also on the fact that rangelands occupy sites subject to perhaps the most rigorous environment of any of man's major agricultural areas.

Temperature And Plant Form And Function

Although we recognize that cellular differences underlie changes in tissues and organs, most studies report responses at the tissue or organ level. Went and Sheps (38) enumerate examples of morphogenetic change induced by temperature. The responses they noted in different species are diverse and include number and size of floral parts, flower color, leaf shape, seed visibility, and germination.

Most studies have been conducted under some

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degree of environmental control. A noteworthy and extensive study of growth and development under essentially natural environments was conducted by Clausen, Keck, and Hiesey (4) in California. These investigators established transplant stations along a transect running at the same latitude from the coastal valleys to the high Sierras. Clonally propagated plant material was established at each station so that environmental effect could be measured on the same genotype. Photographs of typical response at each station depict marked alterations in size, form, and development. The primary transplant stations were at elevations of 30, 1,400 and 3,050 meters. Temperature differences were, of course, but one of the major environmental variables. However, this work depicts morphogenetic response of vegetation to an array of climatic conditions, many being typical of extended range areas in the southwestern United States, and serves to demonstrate admirably the magnitude of plant morphogenesis-environmental interaction.

Let us now consider some examples of response directly associated with temperature as the major variable. Fischer (7) produced variations of leaf shape in *Ranunculus hirtus* DC. by temperature treatment. At 10° C. the leaves developed three separate leaflets, while at 20° they were shallowly lobed, with thinner and larger laminae subtended by longer petioles. Taylor and McCall (35) found in winter and spring wheat that length of coleoptiles was increased by soil temperatures of 20° to 24° C., compared with cooler conditions of 12° to 16° C. Tillering was greater in the varieties grown at the cooler temperatures, being greatest when the soil was maintained at 16° C.

In grasses, the form of the plant is affected by the number and point of origin of tillers. Ryle (28) examined tillering in seven perennial grasses when grown overwinter in an unheated glasshouse, compared with plants in a glasshouse maintained at a minimum temperature of 15° C. By relating tillering to the number of available leaf axil sites, judged by the number of leaves produced on the main shoot, he found that the cooler environment enhanced tillering. A greater proportion of tillers developed from the lower axillary bud sites in the unheated glasshouse. Species differed in number and leaf axil position of their tillers. For example, S48 timothy pro-

duced fewer tillers particularly at the lower nodes than did the other species he studied.

Separate control of soil and air temperatures permitted Ketellapper (11) to grow *Phalaris tuberosa* L. at a constant air temperature of 20° or 30° C. with soil temperature being held at 20° or 30° C. In regrowth following clipping, he observed reduced tiller numbers with soil at 30° C. under both air temperatures. Again coolness is associated with greater tillering. Since the basal nodes and tiller buds of grasses may be at or slightly below the soil surface, soil temperatures would be directly involved.

Temperature is a consideration in practically all ecological and physiological research, but often its influence on conditions and processes has not been translated into precise effects on growth and development. We recognize that biochemical change precedes visible morphological change, but the sequence of events is seldom known. Schwabe (29) reviewed morphogenetic responses to climate and concluded that we have a morphogenetic jigsaw puzzle for which we have too few pieces to reveal an outline. Schwabe enumerated substances involved in morphogenetic control as including the nucleotides, enzymes, hormones and inhibitors, and substrate mass, and he envisions these as interacting simultaneously.

Langridge (16) reviewed the literature particularly of temperature extremes affecting the chemistry of growth processes in plants. The preponderance of this biochemical literature reports research with bacteria. It has been found as temperatures rise and growth ceases, that the addition of one or a few organic compounds will often lead to growth resumption. Glutamic acid, thiamin, and biotin have often been effective in stimulating growth after high-temperature growth cessation. Some investigators have reported similar growth stimulation after thermal inactivation in flowering plants, but the response has not been as striking as with microorganisms. Langridge discusses high temperature impairment of growth from the standpoints of gas availability (mainly CO₂), metabolite breakdown, temperature disruption or imbalance of reaction rates, inhibition of enzyme formation, and enzyme inactivation.

The influence of supra-optimal temperatures on nitrate reductase activity in young barley

seedlings has been reported recently (Onwueme et al., (25)). Activity of this enzyme was assayed during and following a heat stress of 43° C. for 24 hours under continuous light. This level of stress evoked pronounced change in the activity of the enzyme while producing no tissue necrosis in the seedlings. Nitrate reductase activity declined to approximately 30 percent of its initial value during 24 hours of heat stress. During the next 24 hours the plants were held at 24° C. and regained activity to near the prestress level. Irreversible damage to the enzyme was not indicated under the conditions of this experiment. Extracts from heat-stressed and control leaves were mixed in various proportions and gave additive activity, suggesting the absence of inhibitors in the extracts. It was recognized that moisture deficits can result in decreased enzyme activity. These authors determined that the water potential of stressed plants averaged 0.7 atmospheres lower than in the unstressed. However, when a water potential 2 atmospheres below that of freely watered plants was developed by withholding water, the nitrate reductase activity remained near 87 percent that of plants freely watered. Temperature, therefore, was viewed as being the primary factor inducing the reduced enzyme activity during the heat stress. These investigators further compared nitrate reductase activity in heat-hardened and unhardened seedlings, by subjecting both to heat stress. The rate of inactivation of the enzyme during stress did not differ significantly between hardened and unhardened plants, suggesting that the hardening treatments had not resulted in increased heat-stability of the enzyme. It was further determined that nitrate reductase activity decreased during darkness. Conceivably this might mean that under field conditions the reduced activity of the enzyme which starts during a hot afternoon could continue during the night. Heat the next day could impair further production of the enzyme and also result in further decrease in nitrate reductase activity. During a sequence of hot days, therefore, the activity of nitrate reductase may be depressed to low levels resulting in some degree of protein depletion. This line of reasoning may warrant further study.

Enzyme response to low temperature has been reviewed recently by Mayland and Cary (23) as

part of a broad consideration of frost and chilling injury. They view change in water structure around the protein molecule as instrumental in leading to protein denaturation. They noted that researchers have established temperature levels for some enzymes at which denaturation begins, but also that other enzymes are not inactivated by freezing and thawing. Obviously the degree of cold lability differs among enzymes. We might seek to determine which ones are most sensitive to temperature rise or decline, thus gaining an insight into what processes are first disrupted.

Temperature On Growth And Development

Some of the more visible responses associated with temperature, though reflecting change within cells, have been investigated from the standpoint of their effects on growth and development during or following the particular temperature condition. These involve rate of advance through the life cycle, changes from the vegetative to reproductive state, and growth interruptions.

Advance to maturity is often hastened by heat, this being especially noticeable in the annual grasses. Reduced vegetative growth coupled with earlier heading and maturity is frequently associated with fewer and smaller heads bearing smaller numbers of seeds. This is often observed in the field when both high temperatures and moisture deficiency prevail. *Bromus rubens* L., when in the two-leaf stage, was stressed for 5 hours at air-temperature of 54.4° C. (18). For a month following this stress, the treated plants were shorter and were slower to initiate new leaves and tillers. During subsequent growth under favorable environment, these effects slowly disappeared, but later a significant delay in date of heading was observed. Delay rather than acceleration in heading in this case was attributed to the severity of the stress used and to the particular ecotype studied. Some ecotypes responded to this magnitude of stress by earlier heading (6).

Differences among five species of forage legumes grown to flowering under controlled temperatures ranging from 32° C. day, and 27° night, to 15° C. day and 10° night were reported by Smith (31). Generally, flowering was delayed at the cooler temperatures. However, birdsfoot

trefoil flowered later at the warmest temperature than at intermediate levels. This delay in flowering was accompanied by greater dry weight accumulation. Birdsfoot trefoil, accordingly, did not follow the trend shown by the other species; namely, that of greater dry matter production at the lower temperatures.

Vernalization temperatures play a significant role in time of heading. Many species from temperate climates require a period of cool conditioning before floral induction. Following this "winter" requirement, which must be associated with short-day lengths in some species, the plant advances through floral initiation and development terminating in flowering. McKinney (24) reviewed the subject, noting studies on cool season crops for which vernalization temperatures from freezing to 10° C. are found effective in hastening flowering, and on warm season crops for which temperatures from 20° to 30° C. have been used, but often with less certainty of success. Most research has involved small grains, with less attention being directed to forage crops. Some of the morphological responses noted with rye and wheat when earliness is hastened are fewer leaves per culm, and fewer tillers, each bearing smaller numbers of seeds. Less rapid advance to maturity results in the opposite trend in these characters. In forage production, slower advance to maturity often would seem preferable to extend the period of vegetative growth. This may be accomplished either by warm temperatures nullifying the low-temperature effect or by inadequate vernalization. Lindsey and Peterson (21) demonstrated the reversal of thermal induction in Merion Kentucky bluegrass (*Poa pratensis* L.), a plant which requires both cold and short days followed by warm and long days to flower copiously. They found that a single day reaching 35° C. for a few hours reduced the percent of tillers heading after vernalization, and a period of 16 days reaching 35° C. prevented flowering in previously vernalized plants.

To gain the most vegetative growth from grasses, Peterson, Cooper, and Vose (26) suggested the use of nonflowering strains of herbage grasses. This they point out may be achieved in those species which have an obligatory requirement for cold and possibly for short day for floral induction, with flowering occurring later

under long, warm days. By growing these plants in regions where either the cold is inadequate or the subsequent daylength is too short, flowering is greatly depressed or even prevented. Seed production in such culture, of course, must be developed in regions other than those of forage production. Of the two limitations to flowering, inadequate cold or photoperiod, it is easier to employ photoperiod, since this varies seasonally depending on latitude while temperatures at any site are much more erratic. Still, inadequate low-temperature vernalization may be characteristic of some areas and may limit flowering. With range species, such manipulation of the vegetative-reproductive balance has not been attempted to the extent that it has been with cultivated pasture plants. Still, the same principles apply to the plants of both categories.

Morphological characters which might indicate the hardiness of a plant have long been sought with little success. Levitt (20) reviewed work reporting morphological features associated with frost hardiness. No single structural characteristic was consistently identified. Small cell size appeared to be the most reliable indicator, but this he considered only a secondary factor to which numerous exceptions were found.

During the development of hardiness to heat or cold, growth retardation consistently occurs as temperatures gradually rise or lower. Weiser (37) emphasized that in woody plants growth cessation is a prerequisite to the attainment of cold hardiness. Smith (30) reviewed low temperature responses of forage plants and noted that resistance to cold is reduced by conditions which stimulate growth. He cited work in Florida and Georgia showing less over-wintering ability in certain species following nitrogen applications. Fall applications of nitrogen, however, may be used to stimulate growth in the cool weather of autumn and early spring. Such is the case with annual grasses on the low foothills in California (19), where winterkilling is infrequent. In these regions, having day temperatures warm enough to promote some growth, vegetation fertilized with nitrogen appears less injured by frosty nights than does unfertilized vegetation.

Levitt (20) noted similarities in resistance to heat and to cold. This has been borne out in

studies which demonstrate that cold-resistant varieties often are heat-resistant as well (5). I have heat-hardened *Bromus catharticus* Vahl. and then found it more tolerant of cold stress than plants not heat-hardened. Likewise, cold-hardened plants have been found more heat-tolerant than plants not cold-hardened. This capacity may prove to be a meritorious attribute for range vegetation.

The ability of a plant to curtail growth during temperature stress and then to resume growth after the stress terminates probably deserves more attention than this behavior has received to date. Plants, for a short time, can survive extremes of temperature which are too severe to permit measurable growth. Between the maximum temperature permitting growth and that temperature producing mortality, the plant is in a state sometimes termed "rigor." Marinucci and Rivera (22) exposed seedlings of *Lupinus albus* L. to 52° C. for periods of 10 to 48 hours. They reported that growth was suspended for intervals from 2 to 22 days depending on the duration of the heat stress. Perhaps we should investigate the ability of range vegetation to enter temperature rigor and later to resume growth.

A more commonly observed growth cessation is that of dormancy in the perennial plant. A complex of factors contribute to winter or summer dormancy including temperature, moisture, and photoperiod. However, in different species these factors change in relative importance. An example of temperature playing a major role with photoperiod is found in the summer dormancy of *Poa scabrella* (Thurb.) Benth. ex Vasey (17). This species becomes dormant about June 1 at Davis, Calif., even when soil moisture is readily available. Investigation revealed that high temperatures coupled with the long day-lengths of that season triggered the onset of dormancy.

Disorders And Injuries From Heat And Cold

Factors of the physical environment are responsible for well over half of the disorders of plants, according to Treshow (36). Still these noninfectious factors can be most elusive. High

or low temperatures are associated with a diverse array of injuries. Treshow considered primarily woody species and vegetables, and listed among other conditions leaf chlorosis, leaf scorch, sunscald, stem cracks and lesions, and frost at flowering and fruiting. The literature treating grasses (including cereals) and legumes provides examples of these and an array of additional symptoms. Though these studies have seldom used range species, they are, in the opinion of this writer, applicable to range vegetation and are deserving of greater attention by range investigators.

Frischknecht (8) observed the breaking over of seedlings upon emergence, numbers of seedlings emerging as albinos, and frost heaving in studies of grasses fall or spring planted at high elevations in Utah. Many of the broken seedlings revealed etiolated frost banding near the soil surface, and few of these survived. Seedlings which emerged with little chlorophyll or as albinos usually died. It would be well to note any effects on later development in those seedlings which did survive. Suneson and Stevens (34) observed the later growth of frost-induced color-deficient seedlings of barley. Approximately 48 hours after seedlings at the two-leaf stage experienced a minimum night temperature of near -4° C., the leaves lost chlorophyll. Some survived by producing later leaves of normal color. However, survivors which had exhibited this early chlorosis were identified for comparison with plants from normal seedlings. At heading those from albino seedlings had decidedly fewer matured tillers and caryopses than plants which had not shown this albinism. Competitive ability of the albinos was greatly reduced.

Heat banding of leaves has been reported in the field in Russia by Bukharin (3) who noted that seedling leaves of wheat exhibited pale yellow constrictions where they contacted hot soils. Soil surface temperatures above 54.5° C. produced severe burns. The leaves bent or broke over at the points of heat constriction. Heat banding of barley leaves has been produced in a controlled environment (18). When 5-day-old seedlings were subjected to 54.4° C. for 4.75 hours a chlorotic band appeared at the constricted point of emergence of the first foliage leaf from the cole-

optile. After a few days these leaves broke over at the chlorotic band. Many workers have observed young tree seedlings that have been heat girdled at the soil surface. It is reasonable to assume that grass seedlings may be subject to similar injury.

The loss of seedlings following frost heaving of soil is well recognized in regions where slow freezing and thawing occurs at seasons of high soil moisture on heavy, fine-textured soils with poor drainage. Fall seedlings in the foothills of California often are severely heaved before spring. We know more about the conditions which produce soil heaving than we do about the action of heaving on the plants themselves. Too often the effects of heaving are noted at some considerable time following the stress. Portz (27) reported that the more prostrate varieties of alfalfa heaved less than an upright variety under overwintering field conditions in Illinois. He suggested that morphological and anatomical factors probably influence varietal differences, but these were not studied. Biswell and others (2) noted that taproots reaching depths of 0.9 to 1.2 meters in 1-year-old brush seedlings were broken by heaving at 10 to 15 centimeters below the soil surface. Reseeded legumes were more subject to heaving than reseeded grasses, and smilo (*Oryzopsis miliacea* (L.) Beuth and Hook ex Aschen. and Schweinf.) with finely branched roots was heaved more than hardinggrass (*Phalaris tuberosa* L.) with coarser roots.

Perhaps the most detailed measurements of frost heaving injury to specific plants is reported by Kinbacher (14) who studied hardinggrass, perennial ryegrass (*Lolium perenne* L.) and two winter wheats. By using a method to produce heaving in the laboratory (15), he was able to observe seedlings at definite times after known soil and plant movement. With this technique, stem and leaf breakage proved more frequent and lethal than root breakage. After heaving, plants were permitted to recover under favorable growth conditions in the greenhouse. Kinbacher found in this favorable recovery environment that if the break occurred below the soil surface but above the shoot apex, most plants failed to recover since subsequent leaf growth was unable

to emerge above the soil. If the break was in the roots and adventitious roots grew quickly, the plants survived. Generally perennial ryegrass seedlings were less injured than hardinggrass, but no explanation was given for this difference.

Ice cover of vegetation has been studied with regard to the overwintering of perennial forage plants. Injury under ice sheets has been attributed by various workers to accumulated carbon dioxide or other respiratory products, or to reduced oxygen. However, hardened plants appear able to survive for several weeks under ice. Beard (1) working with turf of Kentucky bluegrass and bentgrass (*Agrostis palustris* Huds.) reported that although both species tolerated a 5-cm. ice cover, or a 2.5-cm. ice cover over a 5-cm. snow layer for 51 days without reduction in survival, compacted slush covered with 5-cm. of ice for 6 days greatly reduced the survival of the bluegrass, with only 5 percent of the rhizomes or stolons recovering. He suggested that the compaction reduced air pockets in the sod, and recommended the control of trampling during slushy conditions. Were range species to react like the bluegrass, one might well consider the effect of animal treading on low herbaceous cover during alternate thawing and freezing when ice sheets may form.

Grasses are particularly sensitive to temperature stress at the flowering stage. Recognition of the meager temperature tolerance of the staminate parts of the flower has led plant breeders to employ heat or cold to emasculate grass florets. Emasculation by frost occurs in nature and has been studied particularly in cereals where considerable economic losses may be encountered. Suneson (33) reported that Ramona wheat yields at Davis, Calif., were reduced from 30 to 60 percent in 3 out of 12 successive years. Minimum night temperatures ranging from freezing down to -2° C. can produce this injury when occurring at precise stages of floral development. The pistillate organs remained receptive to pollen after the anthers of the same floret were rendered sterile as indicated by successful cross pollination. No doubt both frost and heat emasculation of range grasses occurs under natural conditions.

Temperature During Seed Maturation And Germination

Germination and vigorous seedling growth have long been important considerations in range reseeding. Temperature during seed maturation is known to influence germinability of seed upon maturity, and may have some influence on the resulting seedling. Massengale et al. (6) in Arizona produced seed of alfalfa from an irrigated stand at different periods between April and September. The temperature regimes varied considerably over these months. Reduction in number of racemes, flowers, pods, and seed per pod was most pronounced during growth periods having both the highest maximum and minimum temperatures. Seedlings grown from seed produced under the warmer temperature regimes tended to be less vigorous as judged by dry weight. Stearns (32) matured seed of bracted plantain (*Plantago aristata* Michx.) at 15.5° or 26.6° C. in growth chambers and then grew plants from this seed at either 15.5° or 26.6°. Growth was measured by cotyledon and leaf lengths, and revealed that seed matured at the higher temperature yielded larger and more vigorous seedlings than did seed produced at the lower temperature. Behavior obviously varies with the species studied.

The nature of change in seed when subjected to heat stress during maturation was studied by Khan and Laude (12), using barley. Plants were subjected to 4 hours of heat above 38°C, reaching a maximum of 54° for 2 hours. This stress was applied at maturation stages during the 30 days between awn emergence and seed maturity, and immediately upon maturity the seed was germinated. The same heat stress, which depressed germination when applied 7 to 10 days after awn emergence, improved germination if applied 20 to 22 days after awn emergence. At the younger stage, the seed had a high moisture content and was injured by the heat. At 3 weeks after awn emergence, the heat-stressed seed, compared to nonstressed samples, was found to have a thinner seed coat, more rapid rate of imbibition, and a lower content of water-soluble inhibitors. Whether or not range species would respond to heat stress during seed maturation as did this barley is not known, but such a study would be of

value in view of the considerable dormancy in fresh seed of many range plants.

As a concluding comment, I would urge not only more study of plant morphogenetic-environment interactions, but would encourage researchers to observe their plants to maturity even in investigations directed at early stages of development. I am convinced that we often miss important information by not considering the complete life cycle. Long ago Kidd and West (13) wrote on physiological predetermination. They were referring to the effect of environment early in development upon much later stages. Highkin and Lang (9) pursued this reasoning in studying the effect of germination temperature on the later growth of peas (*Pisum sativum* L.), and reported significant differences in growth rate, node of first flower, and seeds and pods per plant. Jones (10) added further support to the desirability of observing the complete life cycle. He subjected corn seedlings when just emerged to one hour of heat at 40°, 50°, or 60°C. Not only were the heat-treated plants shorter at maturity, but he found considerable pollen sterility in tassels that appeared otherwise normal. Important behavior may be associated with conditions prevailing long before we observe the response.

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PLANT ENVIRONMENT STUDIES WITH CONTROLLED SOIL TEMPERATURE FIELD PLOTS¹

By A. Morris Decker²

Abstract

The effects of soil temperature on plant growth and development of forage species were investigated. Use of equipment and facilities to modify soil temperature in the field is described and discussed. Tiller initiation, leaf growth, crown development, root growth, plant reserves, mineral uptake, and plant persistence were all markedly affected by variations in soil temperature. The use of this facility serves as a bridge between field studies with no environmental control and the growth chamber where climatic factors are rigidly controlled but are unlike the natural field environment.

Additional key words: Plant climate, soil temperature, forage, mineral nutrition, tillering, persistence

Introduction And Literature Review

Soil temperature affects plant growth directly and indirectly through chemical, physical, and biological activities. In the field, specific effects of soil temperature are difficult to determine because of wide soil differences and because of the close relationship of soil to air temperature which directly affects plants.

Seed germination and early growth are intimately related to soil temperature but, as plants grow, aerial environments play a greater role. Sosebee and Herbel (56) reported reduced survival of 11 of 14 range species at high soil temperatures even when soil moisture was maintained at field capacity. According to Daubenmire

(19), root temperatures closely approach those of the immediate environment. Thus, the root system of a single plant in the field may be subjected to wide ranges in temperature.

Morphology of plants can be modified by soil temperatures. Dickson (25) found subcrown internode elongation of wheat and relative growth rate of the coleoptile was slower than the culm growing point as soil temperatures increased. The initiation and growth of new roots in cool-season grasses is highest in spring and fall when soil temperatures are cool and least in midsummer when they are high (10, 11, 28, 63, 64). Saper and Mitchell (54) found that high temperature along with reduced light intensity decreased nodal roots of ryegrass.

Tillering of cool-season species decreases with high temperatures. Taylor and Templeton (66) reported maximum tillering of orchardgrass in spring and fall with a marked drop during summer. Mitchell (46) found increased tillering of ryegrass at lower temperatures, but at equal leaf-appearance age differences were not significant. Similarly, in smooth bromegrass (24, 49) and tall fescue (53, 68) low temperatures favor tiller production. Others reported that plant age, light conditions, and so forth, may, at times, play a greater role than temperature (6, 41, 44). Optimum temperature for tillering differs with genotype (47, 75). Hiesey (29) concluded, after studying 33 clones of *Poa*, that field behavior of unknown clones could be predicted from growth chamber response.

Tiller development was shown by Robson (53) to be closely associated with leaf and leaf axil bud development. Both leaf initiation and elongation are affected by temperature (38, 62, 67). Treharne and others (70) found that fully expanded leaves maintained high apparent photosynthesis (PR) for 15 to 20 days but declined rapidly

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after that time. The relative change of PR with leaf age was unaffected by the temperature.

Low light intensities reduce tillering (5, 22, 41, 73) and effects of temperature on tillering cannot be considered in isolation from such factors. Templeton and others (68) found tillering to be influenced by photoperiod, temperature, and age of plant. Mitchell (45, 46) found greater tillering with high light intensity at equivalent leaf stages.

Peters (50) and Knieval and Smith (33) found the time of tiller initiation to be critical in its growth and survival. Summer tillers produced significantly more secondary tillers than did winter tillers. Lambert (35, 36, 37) found the majority of orchardgrass and timothy seed heads were produced by autumn initiated tillers and production of floral tillers was influenced by plant density and tiller competition. He stated that aerial competition reduced the number of ears while edaphic competition affected the number of tillers per plant. Anslow (4) found that leaf removal at progressively younger stages restricted the growth of grass and that this effect was buffered by a higher net assimilation rate per area of leaf in a sward of predominantly young leaves. Part of the higher net photosynthesis could result from improved illumination of the younger leaves after removal of the older tissue but, as he pointed out, the rates of assimilation by foliage may depend on the demands created by the plant, and it is here that environment plays a big role. Reviews by Langer (39) and Black (8) gave excellent summaries of light effects on tillering.

Tied in closely with tiller, root, and crown growth is the carbohydrate status of the plant. Here, environmental factors and management play major roles. Researchers, looking at this problem, have credited carbohydrate level at a critical growth stage as a major factor in production and stand persistence (5, 9, 10, 12, 17, 65, 75). Davidson and Milthorpe (21) suggested that carbohydrates form only part of a labile pool supplying energy for regrowth and that nitrogen compounds are involved. Carlson (16) concluded from studies with ladino clover that carbohydrate reserves are chiefly used as a respiratory substrate and the degree to which they provide actual regrowth metabolites is yet unknown.

Sheard (58) suggested that high plant production requires carbohydrates for energy and readily available protein for synthesis of new protoplasm; if either is lacking regrowth will be slowed. Darrow (18) found root weights of bluegrass grown at 35° C. to be about half those at 15° or 25°. Top growth and rhizome numbers were also less. Higher concentrations of water soluble carbohydrates are generally found in cool-season species grown at low temperature (2, 7, 9, 20, 23, 59, 65). Temperature appears to particularly influence fructosans, the principle nonstructural polysaccharide of these grasses.

Soil temperatures can affect nutrient uptake by plants. Power and others (51) reported lower N and P uptake by barley at higher soil temperature, provided samples were taken at a specific stage of development. Smith (60) found low K content in plants grown at low temperature regimes. Walker (71) reported that, for different elements, the uptake by corn seedlings peaked at different soil temperatures, and Ca deficiency was present at soil temperatures above 27° C. He also found alternating soil temperatures to be more influential than those held constant. Apparently soil temperature influences growth most during the light period when plants are photosynthesizing (72). Hunsigi and Ketcheson (31) reported P uptake by corn to be initially high at 24° and 32° C but, with a subsequent reduction in the number of lateral roots, P uptake declined at these temperatures. Sharma and others (57) reported P appeared to interfere with the translocation of Zn at 15°.

Optimum soil temperatures can indeed be found for specific species as pointed out by Walker (71) and, since it has been demonstrated that changes in field soil temperatures are possible by mulching, irrigation, and so forth (1, 3, 27), more knowledge is needed regarding the optimum soil temperature for plants.

Much research dealing with soil temperature and plant responses has been conducted in growth chambers. These have proved valuable in the study of specific responses to single or multiple environmental factor variations. However, observed plant responses in growth chambers are not always comparable with those seen in the field. Complete simulation of ambient environ-

ment is most difficult as pointed out and discussed by Thomas and Ronningen (69).

In order to observe plants in the field while maintaining some control over the soil environment, researchers have installed controlled temperature tanks outside (14, 28). Mack and Evans (42) and MacLeod and Decker (43) have used heat exchangers to modify soil temperatures in the field. This paper deals with use of the Maryland facility to study soil temperature effects on perennial forage species (43).

Materials And Methods

The Maryland plant-climate facility is located in an open field on a Sassafras silt loam soil. A schematic is shown in figure 1. It consists of a chilled water source, three tempering tanks equipped with electric heaters, zone valves, and circulating pumps. Tempered water circulates

from tempering tanks to heat exchangers placed at a soil depth of 9 cm. to provide three replications for each temperature plot (1.83 by 4.57 m.). In and out temperature changes were usually less than 3° C., and controls were set to bracket target temperatures of 10°, 21°, and 32°. A fourth treatment was ambient temperature. Shading was used in some studies to vary light intensity, and individual plot irrigators were available. Field layout with shades and irrigators is shown in figure 2.

Average soil temperature 8 cm. under a sod at College Park, Md., April 1, approximates 10°C. This temperature was essentially maintained throughout the growing season at the 10° C treatment. It took about one week to reach an equilibrium temperature of 21° or 32° in the spring, and a similar time to cool the soil to 10° in midsummer. Typical temperature differentials

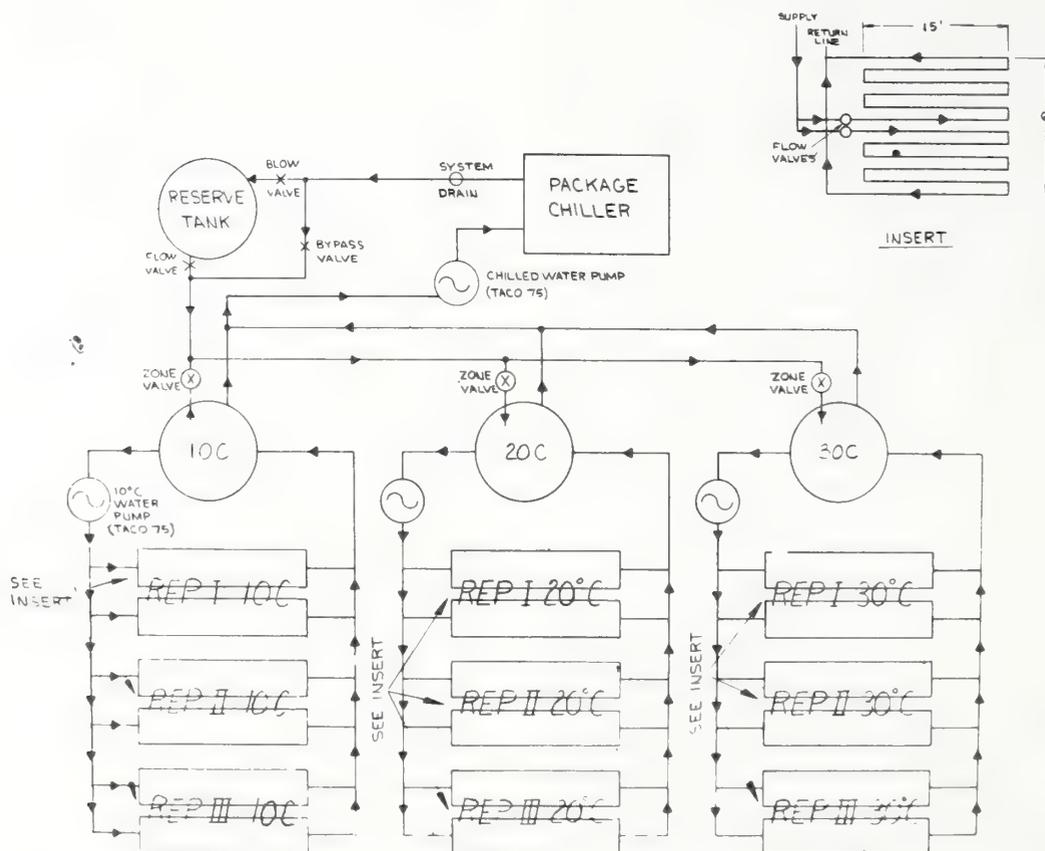


FIGURE 1.—Schematic of field plot soil temperature control system (43)

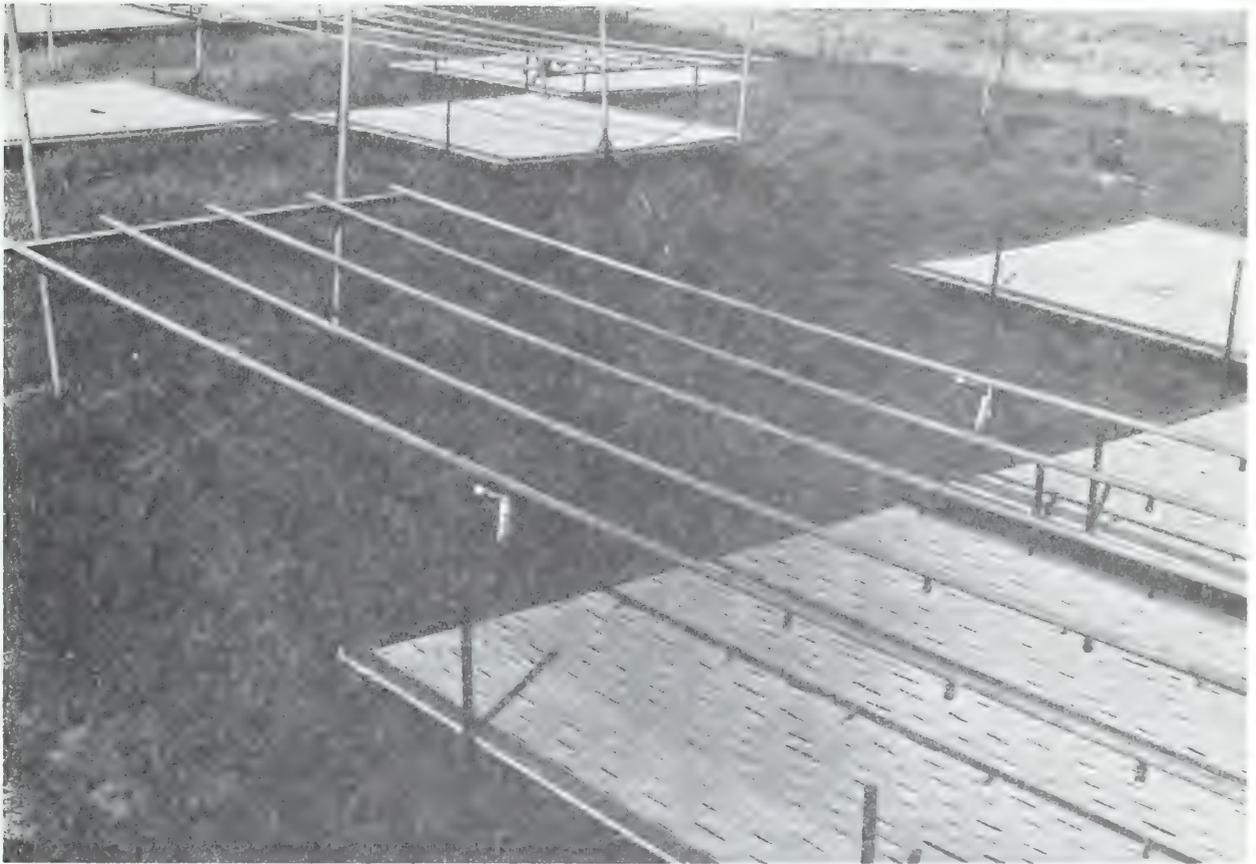


FIGURE 2.—Field layout showing movable shades and irrigators in operation. Thermocouple at 30 cm. is shaded for obtaining air temperature. Thermocouple at 7.6 cm. is within the grass canopy.

during a growing season are presented (fig. 3). One week after equipment was activated, soil temperature differences were well defined even though target temperatures were not exact. On April 19 at 0600, there was no difference between the ambient and 10° temperature profiles (fig. 4). By afternoon, they began to separate, and the weekly average showed a difference of 3° C at 8 cm. Profiles for the 21° and 32° temperatures were well defined. In mid-July, when air temperatures often reached the high 30's, temperature profiles were skewed to the right at the soil surface. Plots were irrigated differentially in an attempt to maintain uniform soil moisture as measured by soil tensiometers placed near the surface. This required more frequent irrigation of warm temperature plots.

This report deals with experiments conducted in these plots from 1964 through 1970. A small

part of the data will be presented and discussed in terms of similarities and differences with greenhouse and growth chamber studies.

The first major consideration was to determine the degree of environmental control possible and the magnitude of plant responses. With this in mind the facility was uniformly seeded to 'Potamac' orchardgrass (*Dactylis glomerata* L.). The design was a randomized split plot with three replications. Whole plots were four soil temperatures, sub-plots were full sunlight vs. shade (65 percent in 1964 and 75 percent in 1965), sub-sub-plots were 28 vs. 84 kg. N/ha, and sub-sub-sub-plots were stubble heights of 3.5 vs. 8.5 cm. Dry matter, tiller number, persistence, and chemical composition data were obtained.

Because of marked shifts in maturity and persistence, 'S-37' orchardgrass (late maturing) and 'Climax' timothy (*Phleum pratense* L.) (similar

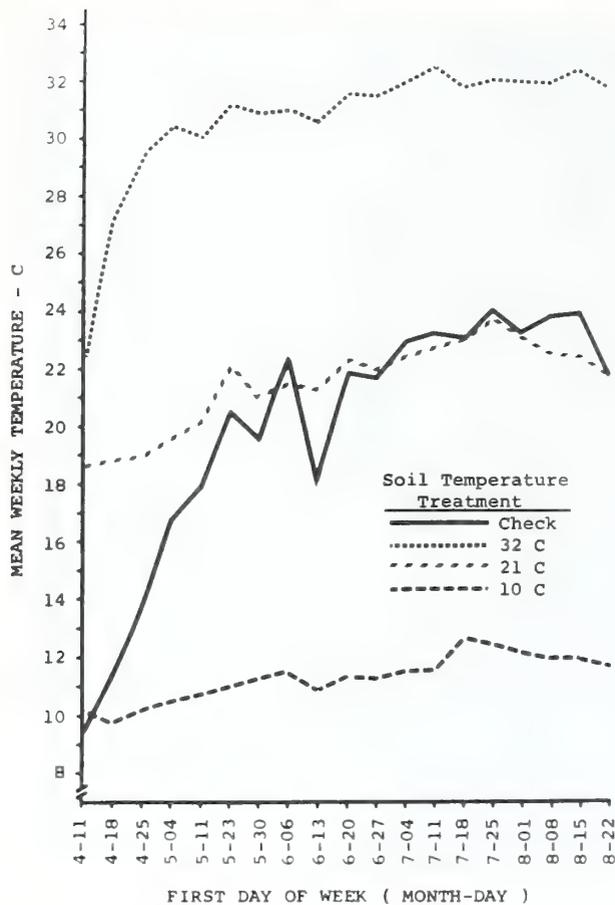


FIGURE 3.—Example of mean weekly temperature 8 cm. below the soil surface under an orchardgrass sod (1965).

to S-37 in maturity but more temperature sensitive) were added to 1966-68 studies. Light, nitrogen, and stubble height differentials were eliminated.

In 1968, red clover plants (*Trifolium pratense* L.) from a Maryland strain selected for longevity (MD. Syn-1) and from 'Dollard' were started in the greenhouse from seed. Uniform plants were placed in plastic pots and clipped three times before being moved to the field. Plants were placed systematically in solid timothy sward and harvested each time the latter was cut. The next spring similar red clover plants and clonal propagules from a single Climax timothy plant were placed on 18-cm. centers in bare soil in contrast to the timothy sward used in 1968. Each species was placed in a separate section of each tempera-

ture plot. Thus, competition was minimal and between plants of the same species. All plants were harvested on the same date. At the end of each season surviving plants were removed and crown root development determined.

Results And Discussion

The effects of soil temperature, light intensity, nitrogen fertilization, and stubble height at harvest upon total forage yields and tiller production of Potomac orchardgrass are presented in table 1. Since there were few significant interactions, and effects were generally additive, only main-effect means are shown. Lowest yields were obtained at high soil temperature, low light, low N fertilization, and high stubble. Tiller production was greatest at the coolest soil temperature, full sun, low nitrogen, and high stubble. Although tiller production at 10° C. was significantly higher than at all other temperatures, dry matter yields were similar for all except 32°. Similar results have been reported by others (33, 46, 58, 66).

TABLE 1.—Effects of soil temperature, shading, nitrogen level, and stubble height on forage yields and tiller production of Potomac orchardgrass

Main effects	Dry matter per plot		Tillers per 0.05m. ² , 1964
	1964 (100 g.)	1965 (100 g.)	
Soil temperature:			
Ambient	2.81 a	6.19 a	130 b
32° C.	2.25 b	4.51 b	120 b
21° C.	2.88 a	5.77 a	139 b
10° C.	2.76 a	5.62 a	204 a
Shaded	2.53 h	4.21 h	128 h
Full sun	2.82 g	7.21 g	169 g
High N (84 kg./ha.)	3.02 r	6.31 r	128 s
Low N (28 kg./ha.)	2.33 s	5.11 s	169 r
High stubble (8.9 cm.)	2.37 y	4.95 y	169 x
Low stubble (3.8 cm.)	2.98 x	6.46 x	128 y
CV, percent	39.7	9.1	18.5

¹ Values within each year and each main effect, followed by the same letter, are from the same statistical population at the 5-percent level of significance.

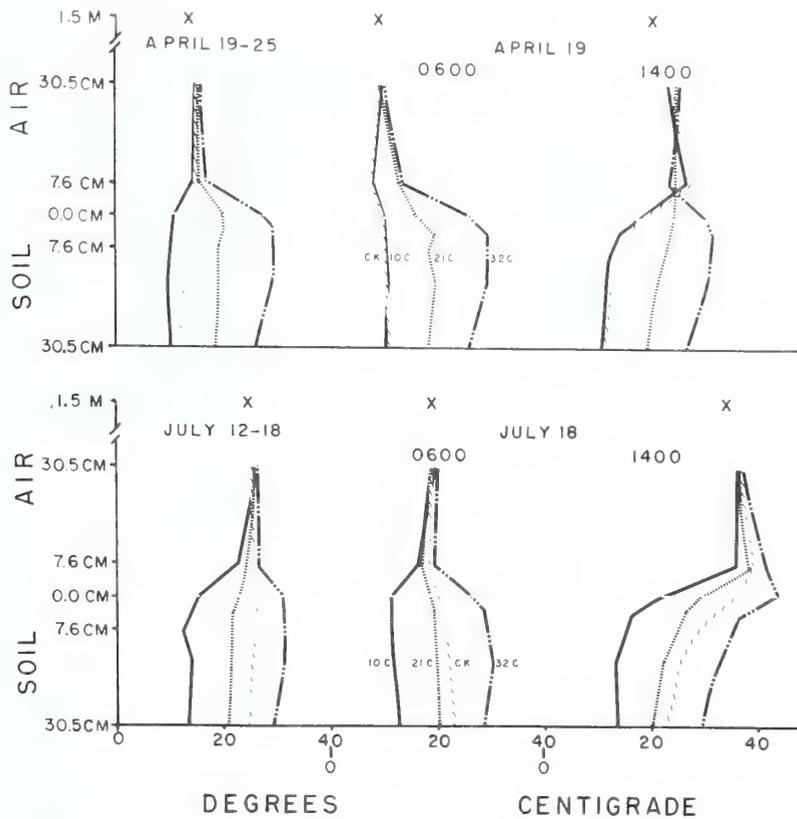


FIGURE 4.—Examples of mean weekly temperature profiles for early spring and midsummer, along with diurnal variations, under an orchardgrass sod (1965).

The maturity of Potomac orchardgrass in this first experiment was shifted as much as 2 weeks by combinations of soil temperature, light intensity, and nitrogen fertilization. For this and other reasons S-37, a late-maturing orchardgrass, and Climax timothy were added to the next experiment (table 2).

In 1966, Potomac at 32° C. started heading April 20. Within 7 days, heads appeared on Potomac at 21° and S-37 at 32°. By May 26, all Potomac plants at 32°, 90 percent at 21° and 85 to 90 percent at ambient had flowered, but at 10° plants were still in the late joint to early head stages. S-37 at 32° was similar to Potomac at 21°. A few heads were emerging from Climax sheaths at 32°, but at cooler soil temperatures this species was either in the early joint or vegetative growth stages. This response was repeated each spring and is similar to reports of others (44, 62, 67). Ridley and Laude (52) reported

temperatures near the stolon apex of white clover to have a greater influence on flowering than temperatures in the vicinity of expanded leaves. Likewise, temperatures in the crown area of grasses in this study had a major effect on tiller, crown, and root growth.

Forage yields from the second study were highest for Potomac followed by S-37 and then Climax but these differences were not always significant (table 2). Climax produced 86 percent as much forage as Potomac when grown at 10° but only 56 percent as much when grown at 32°. The pattern was similar between Potomac and S-37, but differences were smaller. Varieties originating in cooler regions were less tolerant of high soil temperatures, and timothy was more sensitive than orchardgrass. This resembles findings of Watschke and others (74), where bluegrasses originating in warmer regions were better adapted to high soil temperatures. Duncan and

TABLE 2.—*Dry matter yields per plot from three forage grasses grown at four soil temperatures*

Soil temperature	Species	Dry matter yield per plot ¹		
		1966	1967	1968
Ambient		100 g.	100 g.	100 g.
	Potomac	6.56 cd	10.04 ab	8.62 bc
	S-37	6.54 cd	9.76 abc	7.39 ef
	Climax	4.70 ef	8.31 e	7.09 f
	Av.	5.93 C	9.38 AB	7.70 B
32° C.	Potomac	4.82 e	6.82 f	7.16 ef
	S-37	4.51 f	5.99 f	5.62 g
	Climax	2.52 g	4.17 g	3.86 h
	Av.	3.83 D	5.66 C	5.55 C
21° C.	Potomac	7.01 bc	8.97 cde	8.45 bcd
	S-37	6.65 c	8.61 de	7.43 def
	Climax	5.96 d	8.76 de	7.23 ef
	Av.	6.61 B	8.77 B	7.70 B
10° C.	Potomac	7.61 ab	10.45 a	9.68 a
	S-37	7.68 a	9.82 abc	9.30 ab
	Climax	6.56 cd	9.28 bcd	8.16 cde
	Av.	7.28 A	9.86 A	9.05 A
Average:	Potomac	6.50 X	9.07 X	8.48 X
	S-37	6.25 X	8.54 Y	7.44 Y
	Climax	4.78 Y	7.63 Z	6.58 Z
CV, percent		17.1	5.8	21.3

¹ Values within each column with the same letter are from the same statistical population at 5-percent level of significance. Capital letters are used for main effects.

Hesketh (26) found that high altitude maize races had a lower net photosynthetic rate at high vs. low soil temperatures.

Tillering patterns of the three entries were similar in the first two experiments. Although data were taken at each harvest over a 3-year period, only three dates for 1966 are presented since they are representative (table 3). In the spring of each year, differences between varieties were small, and as the season progressed, numbers declined for each entry. These reductions occurred after only one month of increased soil temperature. At the end of the summer, orchardgrass had greater tiller numbers than timothy with S-37 having the most. Species differences were small at 10°, but by mid-August, Climax at

32° had significantly fewer tillers than either orchardgrass. As air temperatures dropped in September, new tillers were initiated on all species at all temperatures, but total numbers remained low at 32°. This is similar to the pattern reported by Taylor and Templeton (66) where plants tillered profusely during autumn and early spring, then declined rapidly in May and June, with greatly reduced tillering during midsummer. Tiller numbers for the ambient and 21° plots were similar just as the temperature profiles were similar (figs. 3 and 4). Many have reported increased tillering with lower temperature regimes (2, 6, 12, 20, 24, 61, 62, 66).

In ambient and 32°C. plots, tiller initiation and development slowed considerably during mid-

summer, while at cooler soil temperatures initiation continued throughout each growing month. New tillers per unit area were determined at each harvest, and the accumulation of these are shown in figure 5. The first count was made May 11, following the second forage harvest. Until this date air-temperatures were relatively cool, and at 10° C. soil temperature tiller initiation was much slower than at higher soil temperatures. In early summer, as air temperatures increased, tiller initiation was most rapid at 10°. Throughout much of the summer, there was little difference between 10° and 21°, but because of the large number in spring, accumulation of new tillers was largest at 21°. Where high soil temperatures were avoided, large numbers of tillers were initiated

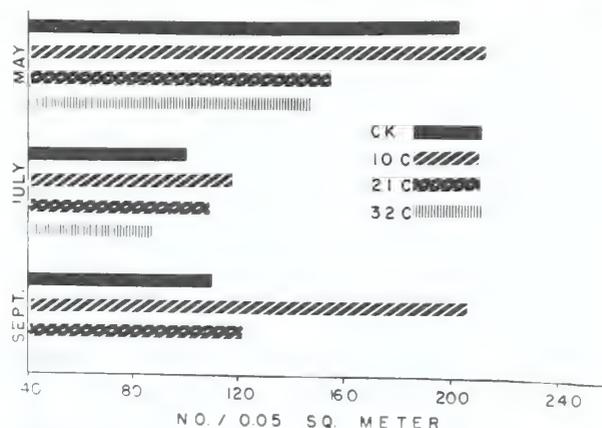


FIGURE 5.—Accumulation of new tillers on Climax timothy during the summer as influenced by soil temperature.

TABLE 3.—Total live tiller numbers for three forage grasses grown at four soil temperatures, 1966

Soil temperature	Species	Tillers per 0.05 m. ² ¹		
		May 4	Aug. 16	Sept. 23
Ambient	Potomac	337 ab	142 bc	129 b
	S-37	332 ab	118 bc	128 bc
	Climax	302 abc	125 bc	102 bed
	Av.	324 AB	128 B	120 B
32° C.	Potomac	171 f	99 c	89 d
	S-37	214 de	132 bc	87 d
	Climax	196 ef	41 d	76 d
	Av.	194 C	91 C	84 C
21° C.	Potomac	289 abc	147 b	120 bc
	S-37	252 cd	152 ab	125 bc
	Climax	279 bed	126 bc	101 cd
	Av.	273 B	142 AB	115 B
10° C.	Potomac	299 abc	165 ab	182 a
	S-37	352 a	198 a	180 a
	Climax	355 a	148 b	182 a
	Av.	335 A	170 A	181 A
Average:	Potomac	274 X	138 X	130 X
	S-37	287 X	150 X	130 X
	Climax	284 X	110 Y	115 Y
CV, percent		12.2	18.0	10.8

¹ Values within each column with the same letter are from the same statistical population at the 5-percent level of significance. Capital letters are used for main effects.

and a high percentage of these survived even in midsummer with high air temperatures.

Crown and root weights were taken on representative plants at the end of each season, but only 1966 crown and root data are presented (table 4). Orchardgrass produced significantly more crown and root growth than timothy. Average crown development significantly increased with cooler soil temperatures, with little difference between ambient and 21°. Orchardgrass did relatively better than timothy at higher soil temperatures.

Soil temperature markedly affected crown and root development and plant survival of red clover placed in a solid timothy stand (fig. 6). All MD Syn-1 plants survived and produced significant growth at all but 32°, where growth was as high

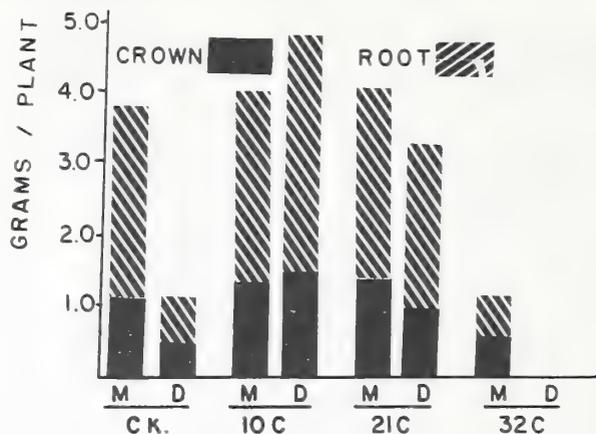


FIGURE 6.—Crown and root production of Dollard (D) and Maryland Syn-1 (M) red clover grown in a solid timothy sod at four temperatures. (Note: No Dollard plants survived at 32° C.)

TABLE 4.—Effect of soil temperature on crown and root growth of three forage grasses grown at four soil temperatures, 1966

Soil temperature	Species	Dry matter per plant (100 g.) ¹		
		Crown	Root	Total
Ambient	Potomac	1.99 b-e	2.05 c	4.04 bcd
	S-37	2.43 abc	1.95 c	4.38 bc
	Climax	1.10 cde	1.08 cde	2.18 e
	Av.	1.84 B	1.70 B	3.54 B
32° C.	Potomac	.88 de	.73 de	1.61 e
	S-37	.92 de	.77 de	1.69 e
	Climax	.68 e	.63 e	1.31 e
	Av.	.83 D	.71 C	1.54 C
21° C.	Potomac	1.58 b-e	2.22 bc	3.80 cd
	S-37	1.89 b-e	1.84 cd	3.73 cd
	Climax	1.28 cde	1.25 cde	2.53 de
	Av.	1.58 C	1.77 B	3.35 B
10° C.	Potomac	2.89 ab	4.99 a	7.88 a
	S-37	3.54 a	5.00 a	8.54 a
	Climax	2.26 a-d	3.16 b	5.42 b
	Av.	2.89 A	4.38 A	7.27 A
Average:	Potomac	1.83 X	2.50 X	4.33 X
	S-37	2.19 X	2.39 X	4.58 X
	Climax	1.33 Y	1.53 Y	2.86 Y
CV, percent		42.7	28.5	21.0

¹ Values within each column with the same letter are from the same statistical population at the 5 percent level of significance. Capital letters are used for main effects.

as for Dollard at ambient. Dollard was superior to the MD. Syn-1 at 10°, but no plants survived at 32°.

In 1969, when spaced plants of red clover and timothy were placed in bare soil and in different sections of each temperature plot, performance was different than in 1968. Without strong competition from the timothy sward, all clover plants survived (table 5). At 32°, crown and root growth of Dollard changed very little throughout the season while the growth of MD. Syn-1 increased. Weights for both clovers increased at 21°, 10° and ambient soil temperatures, with MD. Syn-1 being superior in each case.

Crown and root growth of Climax increased most at 10°, followed by 21°, ambient, and then 32°. Preselected plants were dug at the end of each month. Half were placed in a dark growth chamber where etiolated growth was measured (13) and crown and root weights were determined on the remainder. Regrowth potential in-

creased markedly throughout the season at 10°, but dropped at 32°. It was relatively low at ambient and 21°, changing little during the season.

Tiller numbers per plant, although not shown here, followed a similar pattern to that shown for solid stands (table 3). Tiller and leaf growth were followed closely on both species throughout the season. A "leaf development" index was recorded twice each week on all plants using techniques suggested by Carlson (15) for clover and Higgins and others for grasses (30). Although there was a direct relationship between soil temperature and leaf development (lower temperature—higher index), correlations between indices and forage yields were extremely low and variable even when calculations were made within temperatures. Low temperatures stimulated greater leaf initiation, especially during hot summer weather, but this did not necessarily mean extra forage yields.

Findings in these studies as well as other research have established the fact that, with cool-season grasses, tiller development is enhanced by cool soil temperatures and high light and that associated with high tiller production is a correspondingly high level of soluble carbohydrates. However, Sheard (58) suggested that without a high level of nitrogenous compounds within the plant for rapid synthesis of new protoplasm along with the high carbohydrate level, maximum growth will not result.

Tillers of perennial grasses must be considered as parts of the whole with varying degrees of independence. This makes the grass plant, then, a system rather than an entity. It seems that the primary function of tillers is to perpetuate the species and not necessarily to produce more leaves, dry matter, and so forth, although this may occur. Plants respond to environment in a way that favors survival. Perenniality depends upon the perpetuation of a process, not an entity, and soil temperature plays a major role in this process.

Soil samples were taken at the end of each experiment to determine changes in soil aggregation and organic matter caused by differences in soil temperature. Some of these data are presented in table 6. In the spring of 1969, the surface soil (10 cm.) from all temperature treatment plots within a replication was thoroughly

TABLE 5.—Effect of soil temperature on crown and root growth of red clover and timothy and on etiolated growth of timothy, 1969

Soil temperature	Date	Dollard	MD. Syn-1	Climax	Etiolated ¹ growth of Climax
Ambient	7-14	3.51	2.89	8.68	0.68
	8-15	5.33	5.78	15.69	1.83
	9-22	6.09	9.40	11.54	1.69
Average		4.98	6.02	11.97	1.40
32° C.	7-14	4.94	3.70	6.83	1.08
	8-15	3.17	4.00	9.53	0.92
	9-22	4.32	6.30	9.59	0.89
Average		4.14	4.67	8.65	0.96
21° C.	7-14	3.73	3.72	8.19	1.06
	8-15	6.94	5.77	14.45	0.89
	9-22	8.43	11.96	22.29	1.67
Average		6.37	7.15	14.98	1.21
10° C.	7-14	4.56	7.36	10.73	1.09
	8-15	9.32	5.90	10.69	2.76
	9-22	9.31	9.58	29.68	4.20
Average		7.73	7.61	17.03	2.68

¹ Technique suggested by Burton (13).

TABLE 6.—*Effect of soil temperature on soil aggregation*

Soil temperature	1965 ^{1 2}	1968 ^{2 3}	1970 ^{2 4}
Ambient	45.5 ab	36.7 b	55.1 a
32° C.	39.8 b	22.2 c	42.0 b
21° C.	46.9 a	35.2 b	62.8 a
10° C.	50.0 a	56.0 a	64.8 a
CV, percent	17.0	15.6	5.8

¹ Orchardgrass grown for two seasons (average of nitrogen levels, shade and stubble height over two growing seasons).

² Values within each year with the same letter are from the same statistical population at the 5-percent level of significance.

³ Average of Potomac and S-37 orchardgrass plus Climax timothy grown for 3 years after 2 years of Potomac.

⁴ Average of creeping bentgrass grown at 10 fertility treatments for 2 years.

mixed and redistributed to that replication. Therefore, values for 1965 and 1970 are the result of two years of treatment while those for 1968 are the accumulative effect from two studies (1964–68). As expected, soil aggregation closely paralleled the pattern of root and crown growth. In each experiment, the soil at 10° was significantly higher in aggregation than at 32° with ambient and 21° being intermediate. Percentage of soil organic matter followed a similar pattern except sample variation was higher. With increased shade, there was a significant reduction in soil aggregation and organic matter.

Examples of mineral uptake by three forage grasses as influenced by soil temperature are presented in table 7. Percentage of total nitrogen in the harvested forage was slightly lower at 10° than at other temperatures which were similar. However, the NO₃—N was significantly reduced at that temperature. Similar results are reported elsewhere (34, 48, 76). Uptake of the nitrate ion is greatly accelerated by large amounts of available nitrate in the soil and by the presence of cations, such as K (32, 40, 55). Schneider and Clark (55) found significantly higher nitrate N where K was applied alone or with Ca, Mg, or both. Coupled with higher nitrate percentage in the forage was a corresponding increase in K. The reverse was true for P, Ca, and Mg. Thus, a

cation balance system (40, 55) appears to be operating and influenced by soil temperature.

Soil analysis at the end of 1967 showed a marked reduction in available K at cooler temperatures (20.4, 52.6, 19.0, and 12.2 kg./ha. of available K for ambient, 32°, 21° and 10°, respectively).³ The plots had been fertilized at the beginning of the growing season with 74 and 195 kg./ha. of P and K, respectively. Nitrogen was applied three times at a rate of 62 kg./ha. for a total of 196 kg. Percentage of K in the forage was lowest at 10° and highest at 32°, while the amount available in the soil at the end of the season was the reverse. This is understandable since almost twice as much top growth was removed from the 10° as from the 32° plots, thus percentages need to be considered in terms of yields.

Further studies on the temperature-plant-nutrient-interrelationships are needed. Walker's research (72) suggests growth ceilings with corn may be tied in with soil temperature and Ca transport. He also reported accumulations of boron at high soil temperatures (71, 72). Experiments are now underway in these temperature plots to see if Walker's laboratory findings can be duplicated in the field.

Summary

The equipment used in these studies made it possible to modify soil temperatures in the field to study plant-environment relationships. Although field soil temperatures were not maintained at the exact prescribed level, it was possible to maintain relatively uniform temperature differentials. Research to date suggests that such facilities can provide a useful bridge in relating growth-chamber data to field conditions.

Soil temperatures had a dramatic effect on the growth of grasses and legumes. Some of the more marked responses were with tiller initiation, seed head emergence, crown and root growth, forage yields, mineral uptake, and stand persistence.

Environmental conditions that encourage the initiation of new tillers in cool-season grasses are not necessarily the same as those that promote greatest forage yields.

³ Bandel, V. A., C. K. Stottlemeyer, and C. E. Rivard. Soil testing methods. University of Maryland Soil Testing Laboratory, Agron. Mimeo 34. 1969.

TABLE 7.—*Effect of soil temperature on the uptake of P, K, Ca, Mg, total and nitrate N by three forage grasses, final harvest, 1967*

Soil temperature	Species	P ¹	K ¹	Ca ¹	Mg ¹	Total nitrogen ¹	Nitrate nitrogen ¹
		<i>Percent</i>	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>
Ambient	Potomac	0.39 bc	1.0 de	0.48 cd	0.50 ab	3.98 ab	0.040 bc
	S-37	0.37 cd	1.2 de	0.56 a	0.53 a	4.05 ab	0.048 abc
	Climax	0.35 de	2.1 b	0.41 e	0.39 d	3.56 cd	0.045 abc
	Average	0.37 B	1.4 B	0.48 A	0.47 A	3.86 A	0.044 A
32° C.	Potomac	0.33 e	2.8 a	0.44 de	0.41 cd	3.82 bc	0.036 c
	S-37	0.33 e	3.0 a	0.41 e	0.36 e	3.84 bc	0.065 a
	Climax	0.27 f	2.7 a	0.30 f	0.30 e	3.60 cd	0.057 ab
	Average	0.31 C	2.8 A	0.38 B	0.36 B	3.75 A	0.052 A
21° C.	Potomac	0.39 bc	1.2 de	0.46 cde	0.52 ab	4.00 ab	0.039 bc
	S-37	0.40 bc	1.3 d	0.56 a	0.46 bc	4.16 a	0.050 abc
	Climax	0.35 de	1.9 bc	0.43 de	0.42 cd	3.66 cd	0.054 abc
	Average	0.38 B	1.5 B	0.49 A	0.47 A	3.94 A	0.048 A
10° C.	Potomac	0.42 b	0.9 e	0.50 bc	0.55 a	3.47 d	0.014 d
	S-37	0.46 a	1.0 de	0.54 ab	0.52 ab	3.59 cd	0.013 d
	Climax	0.34 de	1.7 c	0.43 de	0.36 d	3.18 e	0.012 d
	Average	0.41 A	1.2 B	0.49 A	0.47 A	3.41 B	0.013 B
Average	Potomac	0.38 X	1.5 Y	0.47 Y	0.50 X	3.82 X	0.032 Y
	S-37	0.39 X	1.6 Y	0.52 X	0.46 Y	3.91 X	0.044 X
	Climax	0.33 Y	2.1 X	0.39 Z	0.37 Z	3.50 Y	0.042 X
CV, percent	Average	5.4	11.8	6.9	7.9	4.3	26.4

¹ Values within each column with the same letter are from the same statistical population at the 5-percent level of significance. Capital letters are used for main effect.

Many findings from these soil temperature studies were similar to research conducted in controlled growth chambers and greenhouses while others were different. Modifications of light intensity, day length, and moisture on such plots may help us to understand some of the differences found and make such field facilities more useful in future studies.

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ENVIRONMENTAL CONTROL OF THE GROWTH AND DEVELOPMENT OF PERENNIAL HERBAGE SPECIES¹

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Abstract

Under temperate, humid conditions, radiant energy levels and temperature play a dominant role in regulating growth and development of perennial herbage species. Light intensity rather than photoperiod appears to be an important environmental variable during seedling development. High levels of radiant energy during this stage of development insure rapid seedling growth and development of an adequate root system, resulting in a strongly competitive plant.

Development of regenerative tissue (tillers) is favored by short photoperiods and cool temperatures. Leaf expansion is favored by long photoperiods and warm temperatures. Such responses coincide with the characteristic development of perennial, long-day plants. Development of tillers occurs during the fall and spring. During late spring and early summer, when environmental conditions provide long daylengths and warm temperatures, most of the photosynthetic energy is utilized for tiller elongation, ultimately leading to flowering. This growth pattern may principally account for the seasonal variations in yield observed for many perennial herbage species.

Additional key words: Photoperiod response, floral development, seedling growth, tillering, light intensity, temperature response.

Introduction

Net productivity of a herbage ecosystem is dependent largely on the number of harvests per growing season. Invariably, herbage yields de-

cline at each successive harvest from spring to fall. For example, alfalfa (*Medicago sativa* L.) yields in the southwestern U.S. are reported to decrease to a seasonal low during late summer followed by a slight increase during the autumn period (16). A similar midsummer decline in growth and productivity of herbage grass species has been observed (14). Although several environmental factors have been implicated in these yield responses, it is obvious that dry matter accumulation or harvestable yield is dependent on a complex of interacting physiological and environmental factors.

Adding to this complexity is the fact that many herbage species are perennials whose developmental physiology is considerably different from that of annual species. The diversion of photosynthate to storage tissues and activation of regenerative tissue are important characteristics of perennial species that have a bearing on the net productivity of a herbage community. Thus, the effects of specific environmental factors on plant response are different, depending on the stage of development of a perennial plant. Elucidation of the relationships of an environmental factor or combination of factors with the physiological processes involved in dry matter accumulation would be a major contribution toward realizing maximum net productivity of a herbage ecosystem.

Although radiant energy levels establish the ultimate net productivity of crop systems, under natural conditions the environmental control of plant growth and development involves other factors including temperature, water, and nutrients. The importance of each factor in limiting plant growth varies with the climatic conditions of the geographic region. Under temperate, humid conditions, light and temperature play the most dominant role. Here I will discuss some of the

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effects these two important environmental variables have on growth and development of perennial herbage species.

Seedling Development

If soil moisture is adequate, seed germination and seedling emergence are primarily affected by temperature. Generally, increases in temperature, within limits, increase the rate of germination and emergence. The optimum temperature appears to be species or even cultivar related (10). On the other hand, seedling growth has been shown to be closely related to light intensity and temperature. Bula et al. (4) noted that total dry weight of 14- or 28-day old alfalfa seedlings was essentially linearly related to light intensity over the range of 8,000 to 32,000 lux (fig. 1). Combinations of light intensity levels during the 15-hr. illumination period resulted in greater dry weight accumulation after 14 days of growth

than an exposure to 16,000 lux during the entire illumination period even though all these light treatments provided equal amounts of light energy.

Dry weight accumulation in red clover (*Trifolium pratense* L.) seedlings at the end of a 28-day growing period increased markedly when grown at 16,000 lux compared to 8,000 lux (2). Only a slight increase in seedling growth was noted when the red clover were grown at 32,000 compared with 16,000 lux (fig. 2). Length of the illumination period also had an effect on seedling growth and development. An 8-hr. illumination period resulted in relatively low growth rates at all three intensities. A 20-hr. illumination period resulted in growth rates approximately six times higher than those noted for the 8-hr. period.

The effects of light intensity and illumination period on red clover seedling development are illustrated in table 1. Less than 30 percent of the plants of 'Pennscott' red clover produced flower-

- 1 - 8-3hr, 16-3hr, 32-3hr, 16-3hr, 8-3hr
 2 - 8-5hr, 32-5hr, 8-5hr
 3 - 8-10hr, 32-5hr
 4 - 32-5hr, 8-10hr

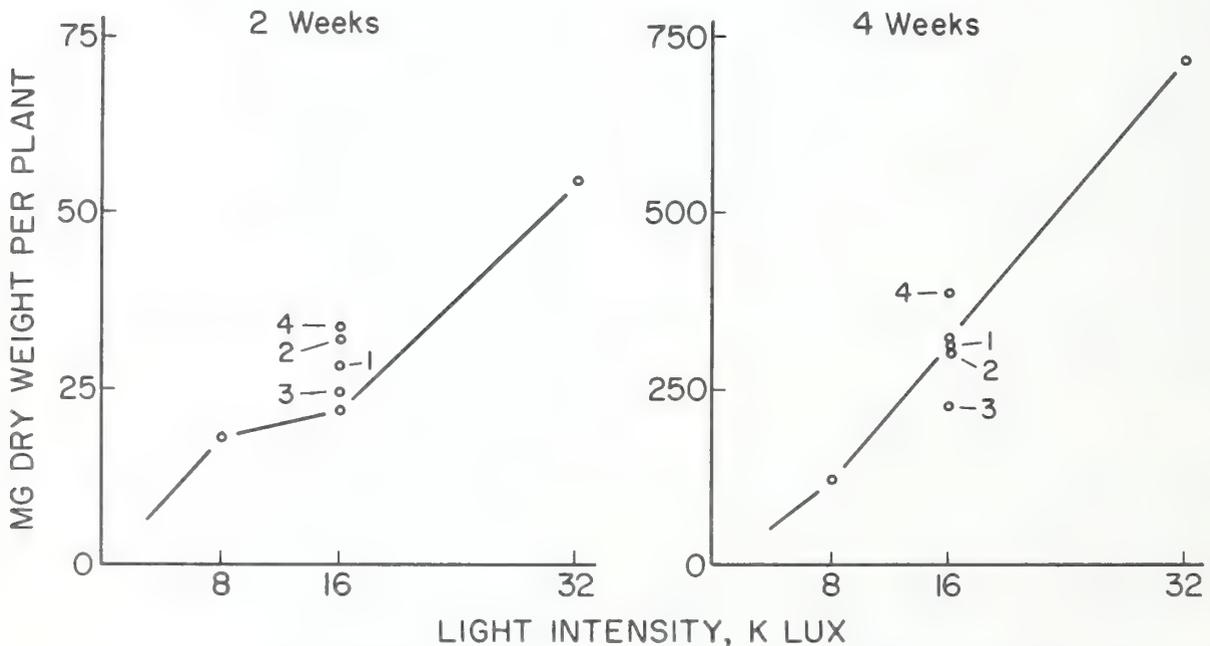


FIGURE 1.—Dry weight accumulation in alfalfa seedlings after 2- and 4-week growing periods under various light regimes.

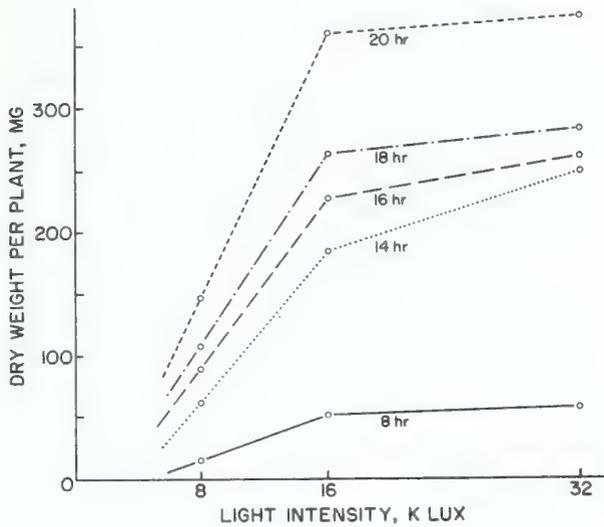


FIGURE 2.—Dry weight accumulation in red clover seedlings after a 4-week growing period at five illumination periods and three light levels, average of three cultivars (2).

ing stems when grown at a low light intensity. Increasing light intensity to 16,000 or 32,000 lux resulted in over 80 percent of the plant flowering, but only when grown under the long illumination periods. It is interesting to note that essentially the same percentage of plants of 'Dollard' red clover flowered under the three intensity levels. However, the percentage of flowering plants was considerably lower than noted for the Pennscott plants when grown at the higher intensities.

The relationship between light intensity and length of the illumination period in the plants of Pennscott red clover appears to be one of providing a maximal growth rate until the plants have developed sufficiently to respond to the flowering stimulus. However, a segment of the Dollard red clover plant population appears to have additional environmental requirements for floral development than simply seedling growth.

High light levels during the early stages of seedling growth favor development of the root system since root growth is reduced to a greater extent under low light conditions than is growth of aerial tissue. The ratio of aerial tissue to root tissue of 14-day-old alfalfa seedlings decreased from near 4.0 to slightly under 3.0 when grown

under light intensities of 8,000 and 16,000 lux, respectively (fig. 3). Likewise, Matches and others (13) reported that shading reduced dry weight of alfalfa root tissue to a greater extent than that of the aerial tissue.

Rapid seedling growth insures adequate root development which in turn increases competitive capacity of the seedling. Rhodes (15) reported that grasses with high competitive capacity (*Lolium* spp.) produced more root tissue during seedling development than species of low competitive capacity (*Dactylis* spp.). The time at which nodal roots emerged was suggested to be an important seedling characteristic determining the competitive capacity of several grass species. In view of the close association between root growth and light intensity, it is unfortunate that light levels under which these experiments were conducted were not defined. Since the experiments were conducted under greenhouse conditions, it would seem that light levels were low. It is not clear to what extent competitive capacity, as reflected by root growth characteristics, of the species evaluated may have been affected by low light intensity. However, these studies emphasize the importance of recognizing that vigorous root growth is essential for optimum seedling growth and development.

Temperature, being a major parameter of the natural environment and closely associated with radiation intensity, obviously has an important effect on seedling growth and development. A

TABLE 1.—Percentage of flowering plants of red clover cultivars grown at three light intensity levels and five illumination periods (2)

Cultivar	Illumination period (hours)				
	8	14	16	18	20
8,000 lux intensity					
Pennscott	0	0	0	27	28
Dollard	0	0	0	20	55
16,000 lux intensity					
Pennscott	0	0	0	36	83
Dollard	0	0	0	50	42
32,000 lux intensity					
Pennscott	0	0	10	45	82
Dollard	0	0	0	45	40

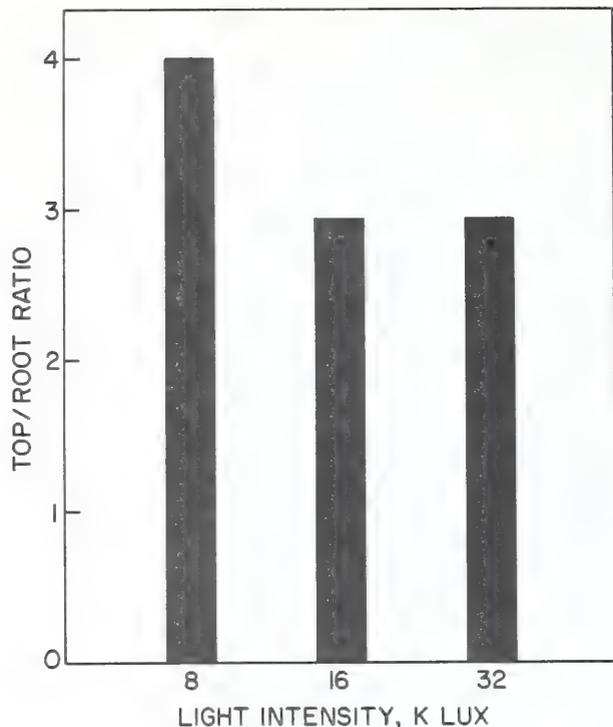


FIGURE 3.—Ratios of aerial/root tissue dry weights in alfalfa seedlings after a 2-week growing period at three light levels (4).

comparison of dry matter accumulation in seedlings of red clover, alfalfa (*Medicago sativa* L.), ladino clover (*Trifolium repens* L.), and birds-foot trefoil (*Lotus corniculatus* L.) grown at temperatures from 15° to 35° C. is shown in fig. 4. Plants were grown at 43,000 lux and 18-hr. photoperiod. Dry weights were determined at the end of a 3-week growing period following seedling emergence. A constant temperature of 15°, even at these relatively high light intensities, severely limited seedling growth and development. Over the range of 15° to 30°, dry matter accumulation increased proportionately to temperature. The optimum temperature for these legume species was near 30°. At 35°, red clover plants exhibited severe high temperature stress and would not have matured. Growth and seedling development of the other legume species was reasonably satisfactory at this high temperature.

Dry matter accumulations in bromegrass (*Bromus inermis* Leys.), orchardgrass (*Dactylis glomerata* L.), and timothy (*Phleum pratense*

L.) grown at temperatures from 15° to 35° are shown in figure 5. The grass plants were grown under environmental conditions analogous to those described for the legume species. The optimum temperature for the grass species was near 25°. Seedling growth of all three species was greatly reduced at 35° and in this respect resembled that reported for red clover.

Another interesting aspect of the temperature response of grasses and legumes was the comparative root growth. Ratios of aerial to root tissue weights are given in table 2. Plants grown at lower temperatures had the lowest ratios. Those species that were extremely sensitive to the high (35° C.) temperature had high stem to root ratios. Under the conditions of these experiments, cool temperatures favored the diversion of photosynthate to root growth. When the seedlings developed under temperatures that approached lethal levels, root growth was more severely retarded than top growth.

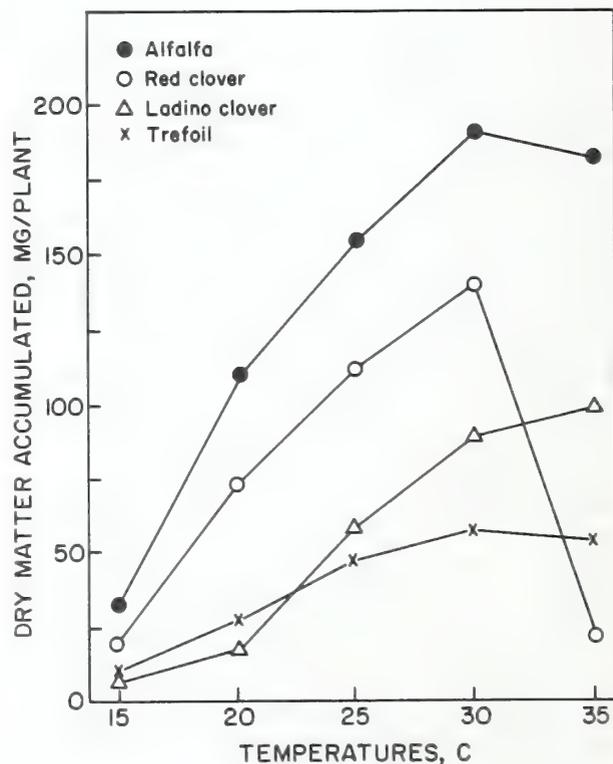


FIGURE 4.—Dry matter accumulation in legume seedlings grown for 2 weeks at temperatures ranging from 15° to 35° C.

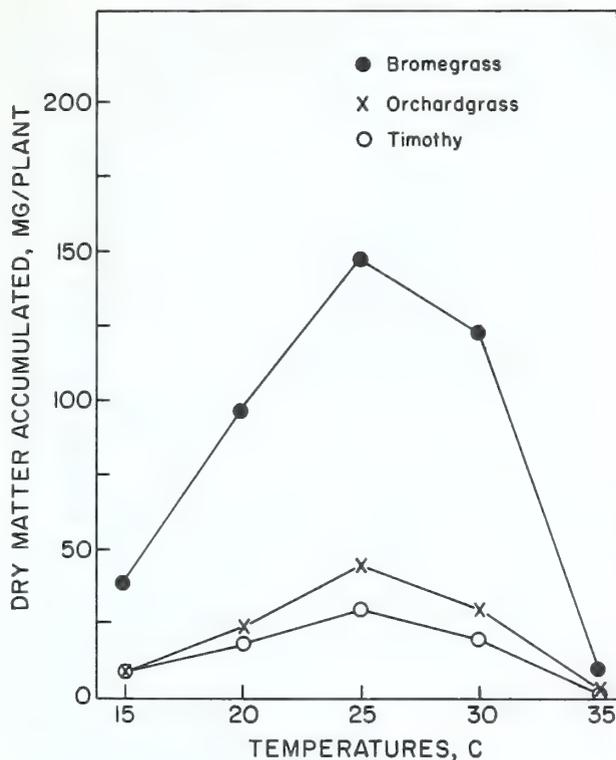


FIGURE 5.—Dry matter accumulation in grass seedlings grown for 3 weeks at temperatures ranging from 15° to 35° C.

Garza and others (9) found that growth of alfalfa seedlings, as measured by dry matter accumulation, was considerably higher at 30°C. and a light intensity of 43,000 lux than at the same temperature but at a light intensity of 11,000 lux (fig. 6). A temperature of 30° during the light and 15° during the dark period resulted in higher growth rates than constant temperatures

of 15° or 30°. This response was noted at both high and low light intensity. They concluded that temperature response was affected by light intensity and further that plant response changed with advancing age. However, low light intensity combined with high temperature was detrimental to growth of alfalfa at all stages of development.

Vegetative Development

As a seedling develops, buds near the soil surface are activated, leading to tiller formation and growth. Physiological and environmental responses of plants that have reached a stage of development where tiller production is relatively stable are different from responses of seedling plants. Tiller formation and development are of paramount importance in herbage production; consequently, extensive research has been conducted on this aspect of morphological development.

Tillers develop from activation of axillary buds or initiation of adventitious buds. Therefore, research has been primarily concerned with what physiological, environmental, or management factors are involved in the control of these buds and, more specifically, control of tiller development. This is particularly true of research on tiller development in perennial grasses where tillers arise from axillary buds. However, in the case of some legumes, tillers develop from adventitious buds arising from crown or root tissue.

Emphasis on developing alfalfa varieties with a creeping-rooted character has pointed to the need for a more complete understanding of adventitious bud formation in this species. Carlson

TABLE 2.—*Ratios of aerial/root tissue dry weights of legume and grass seedlings grown at five temperatures for 3 weeks*

Species	15° C.	20° C.	25° C.	30° C.	35° C.
Alfalfa	2.72	3.81	3.70	4.33	4.47
Red clover	2.53	3.03	3.00	4.20	¹ 7.03
Birdsfoot trefoil	1.74	3.73	5.00	5.08	4.70
Ladino clover	2.26	3.58	3.02	3.80	4.83
Bromegrass	1.33	1.34	1.30	1.98	¹ 7.30
Orchardgrass	1.94	2.40	2.67	3.39	¹ 6.36
Timothy	1.15	1.80	2.36	3.44	¹ 6.00

¹ Based on limited seedling growth and development.

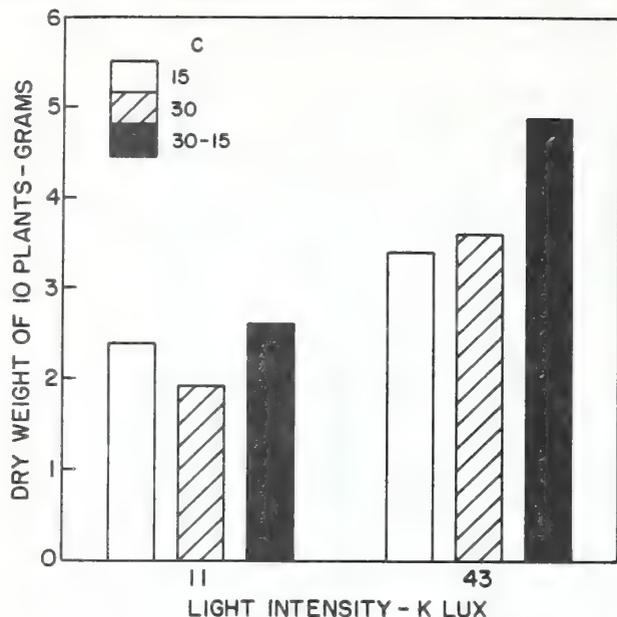


FIGURE 6.—Dry weights of alfalfa plants grown at two light levels and three temperatures, averaged over varieties and growing periods (9).

and others (5) found that the number of adventitious buds produced was greater when the plants were grown at warm temperatures (18° to 24°C.) and short day lengths (10 to 14 hr.) than when the plants were grown at cool temperatures (10° to 18°) and long day lengths (16 hr.). Specific clones were more responsive to day length than others suggesting an important genetic-environ-

mental interaction (table 3). Adventitious bud formation apparently was not related to root growth, root size, or carbohydrate content of the root tissue. Environmental conditions that reduced top growth, or defoliation, had a physiologically favorable effect on adventitious bud formation, suggesting a possible involvement of auxin or some analogous growth substance in the formation of these adventitious buds.

A further indication that endogenous growth substances may be involved in tiller development in alfalfa was reported by Cowett and Sprague (7). In their studies, number of stems per plant increased when the plants were treated with anti-auxin, triiodobenzoic acid, while an auxin, naphthaleneacetic acid, reduced stem number. Environmental conditions of light intensity, temperature, soil moisture, and fertility influenced the number of stems per plant primarily by affecting plant vigor. Plants exposed to full sunlight and grown at low plant densities had the highest number of stems per plant.

Vegetative growth of perennial herbage grasses consists almost entirely of leaf and sheath tissue. Thus, environmental effects on the vegetative development of herbage grasses involves the number of tillers per plant or unit area, rate of leaf appearance, and rate of leaf expansion. In an undisturbed condition, tiller number increases during the spring and fall seasons. During the summer period when stem elongation occurs, tiller

TABLE 3.—Adventitious bud formation in roots of creeping-rooted alfalfa clones grown at two temperatures and day lengths (5)

Temperature and day length	Number of buds ¹					Mean
	CHa ²	CHb	CMA	CMb	CLa	
Warm (18° to 24°)	--	--	--	--	--	20.2
Long (16 hr.)	31.0	1.3	7.3	22.0	1.7	12.6
Short (10 to 14 hr.)	38.3	33.7	9.7	49.7	7.0	27.7
Cool (10° to 18° C.)	--	--	--	--	--	5.1
Long (16 hr.)	6.3	1.0	1.0	2.0	1.3	2.3
Short (10 to 14 hr.)	6.7	11.0	2.3	16.7	3.0	7.9

¹ The value 1 was added to the observation of each pot to eliminate all zero observations for statistical purposes.

² The letter "a" refers to plants defoliated four times and "b" refers to plants defoliated three times during a 116-day period.

number remains stable. Removing tillers at various stages of development or heights has pronounced effects on tillering response. However, such management practices likely exert their influence on development of existing tiller initials rather than on tiller formation. Environmental factors would affect both tiller formation (activation of the axillary buds) as well as tiller development.

Templeton and others (19) found that the tiller number of fall fescue (*Festuca arundinacea* Schreb.) plants, growing in the field, increased throughout the winter even though weekly mean temperatures were near 0°. As mean weekly temperatures increased (mid-March) rate of tiller appearance increased markedly so that by mid-April the tiller number was approximately 3.5 times what it had been only 38 days earlier. Following this rapid tillering, the rate of tiller appearance decreased and remained low until early June.

Under controlled conditions, tillering was favored by a period of daily exposure to a temperature of 2°C (table 4). In all but one treatment combination, plants grown under an 8-hour photoperiod had a greater number of tillers than plants grown under a 16-hour photoperiod. Ryle (17) reported similar observations. In his studies, the number of tillers per plant of orchardgrass, meadow fescue (*Festuca pratensis* Huds.), and perennial ryegrass (*Lolium perene* L.) decreased as day length was increased from 8 to 24 hours

(table 5). The smaller number of tillers noted for plants grown under the long photoperiod was due to lack of axillary bud development at the lower nodes and to a longer time interval between the appearance of a leaf and the appearance of a tiller in its axil.

Literature on the influence of light intensity on tiller formation is somewhat contradictory. Horrocks and Washko (11) found that the number of tillers of both timothy (*Phleum pratense* L.) and reed canarygrass (*Phalaris arundinacea* L.) was greater on plants grown under shaded conditions compared to plants grown at full intensity (fig. 7). Full light intensity was 73 or 80 milliwatts cm.⁻² min.⁻¹. Reduction in number of tillers was most pronounced for the timothy plants. Others have reported that any change in the light regime that decreased energy available to the plants reduced their rate of tillering. Sato and Ito (18) reported that short days (8-hour photoperiods) and cool night temperatures (15°) were most favorable for tillering of orchardgrass. The ratio of dormant buds to total tillers per plant increased as temperatures under which the plants were grown increased. Sato and Ito suggested that tillering capacity is closely related to the nonstructural carbohydrate and nonprotein nitrogen content of the leaf-sheath and stem tissue. In their experiments, when growth of the shoot was reduced under lower temperatures and shorter day lengths, nonstructural carbohydrate and labile nitrogenous

TABLE 4.—Tiller number of tall fescue plants grown under controlled environments (19)

Age of plants when treatment began, weeks	Duration, weeks	Number of tillers grown under temperatures and photoperiods of—			
		23° C.		23° C. — 2° C. ¹	
		8 hr.	16 hr.	8 hr.	16 hr.
7	6	7.1	5.1	16.4	17.5
7	3	4.3	4.0	7.2	6.5
4	6	4.3	2.7	9.2	8.2
4	3	2.4	1.5	3.3	2.9
Mean		4.5	3.3	9.0	8.8

¹ Temperature was 23° C. during the 8-hour, high illumination period and 2° C. for 16 hours of darkness, or 8 hours of low illumination plus 8 hours of darkness.

TABLE 5.—Number of tillers per plant of three grasses grown at three day lengths (17)

Species	Number of tillers at day length of—		
	8 hr.	16 hr.	24 hr.
Orchardgrass	10.8	4.5	3.8
Meadow fescue	9.6	7.4	5.8
Perennial ryegrass	15.2	10.7	9.9
Mean	11.9	7.5	6.5

compounds accumulated and resulted in greater tillering capacity and a lower top/root ratio.

Although metabolic substrates are necessary for tiller development, as for any growth process, tillering is obviously a complex plant response reflecting much more than simply environmental control of substrate levels. More likely tillering of perennial herbage species is under control of

endogenous growth substances that in turn are regulated by the prevailing environment.

In contrast to tiller response, rate of leaf expansion was shown to be related in a positive manner to photoperiod. Ryle (17) found that leaf length of three grass species was markedly affected by photoperiodic conditions (table 6). The rate of leaf appearance (time interval between appearance of successive leaves) in these same species was somewhat higher at short photoperiods (8 hours) than long photoperiods (16 or 24 hours). Thus, development of leaf tissue (cell expansion) in perennial cool-season grasses appears to be favored by long day lengths while development of new leaves or tillers is favored by short photoperiods.

Such plant response coincides with the characteristic growth and development of long day plants. Development of regenerative tissue (tillers) occurs under short day conditions. When the environmental conditions provide long day lengths most of the photosynthetic energy is

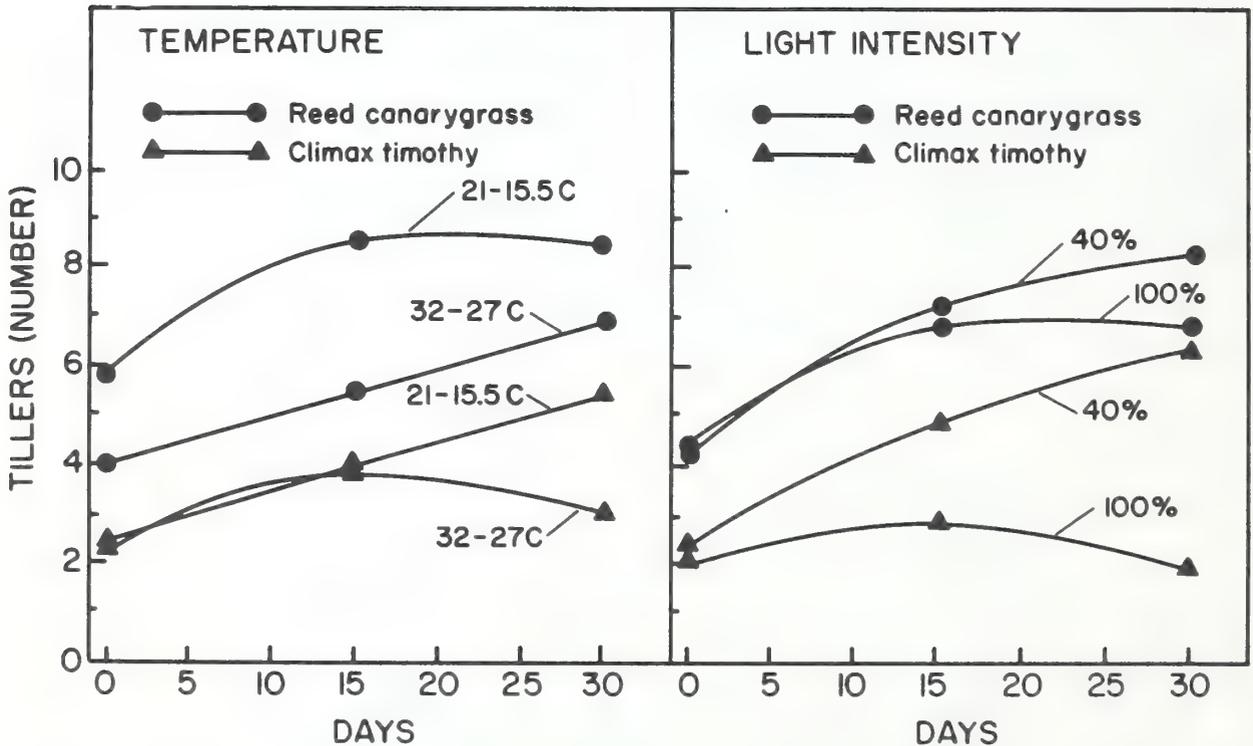


FIGURE 7.—Tiller numbers in timothy and reed canarygrass plants grown under different light intensities (100 percent equals 73 or 80 milliwatts $\text{cm}^{-2} \text{min}^{-1}$) and temperatures (11)

TABLE 6.—*Leaf lamina length (mm.) of three grass species grown at three day lengths (17)*

Species	Length of leaf lamina at day length of—		
	8 hr.	16 hr.	24 hr.
	<i>Mm.</i>	<i>Mm.</i>	<i>Mm.</i>
Orchardgrass	205	453	493
Meadow fescue	318	452	520
Perennial ryegrass	207	244	278
Mean	243	383	430

diverted to tiller development leading ultimately to flowering. Seasonal variations in dry matter yields coincide with tiller development. This photomorphogenic response, more than any other, may account for the seasonal variations in yield noted for many perennial herbage species, particularly cool-season grasses.

Floral Development

Recently, attention has been directed toward the significance of floral development and the associated increase in crop growth rate during this stage of development as well as the lower growth rates during the post-flowering period (6). This is particularly evident for seasonal yields of grass species, and research programs have been developed to alter these growth patterns (12). If floral development does indeed stimulate dry matter accumulation, understanding the role of environmental factors in floral development takes on added significance in herbage production.

Evans (8) and coworkers reported a comprehensive series of experiments on the flowering physiology of *Lolium temulentum* L. Their conclusions likely apply to other long day plants, particularly herbage grass species. Two aspects of floral development that need further elaboration pertain to the role of low temperature exposure and whether a juvenile stage of development exists in some herbage species. Bean (1) concludes that both tall and meadow fescue have a juvenile stage during which plants show a reduced response to inductive conditions. It is more difficult to document such a stage of development

in herbaceous species compared to deciduous species. At present, the existence of a juvenile stage remains an open question. It would be important to understand what physiological or environmental conditions are involved in the transition from a juvenile stage to a floral stage if one exists.

The role of low temperature in floral development has been associated with vernalization. Floral development of those species that have evolved ecotypes adapted to regions of subfreezing winter conditions appears to involve a low temperature requirement. An example of such natural selection can be found in red clover. Red clover has been described as a long-day plant but within some cultivars a segment of the population develops flowers very slowly or remains vegetative under conditions otherwise conducive to flowering.

Floral stem development of a Finnish variety 'Tammisto' was considerably later than that of Pennscott, a cultivar adapted to more temperate conditions (3). Plants grown under 16- or 20-hour photoperiods developed floral stems at essentially the same time. The cumulative percentage of floral plants of Pennscott went from 0 to 100 within a 4-week time span following the low temperature exposure compared to a 7-week time span for plants not exposed to low temperatures. Likewise, the cumulative percentage of floral plants of Tammisto went from 0 to 100 within a 6-week period following low temperature exposure compared with a 9-week period for plants not exposed to low temperatures.

An environmental regime that provided short photoperiods rather than long photoperiods during seedling development, followed by low temperature exposure, resulted in the most rapid floral development of the Tammisto plants. Apparently floral development of the Tammisto plants was adversely affected by exposure to long photoperiods prior to low temperature exposure. This effect was not noted for the Pennscott plants (fig. 8).

The environmental regime providing the most rapid rate of floral stem development was a 2-week period at 30° and 12-hour photoperiod during seedling development, followed by 2 weeks at 2° and 10-hour photoperiods, and then 30° and 20-hour photoperiods during the floral development period. Under these conditions, only

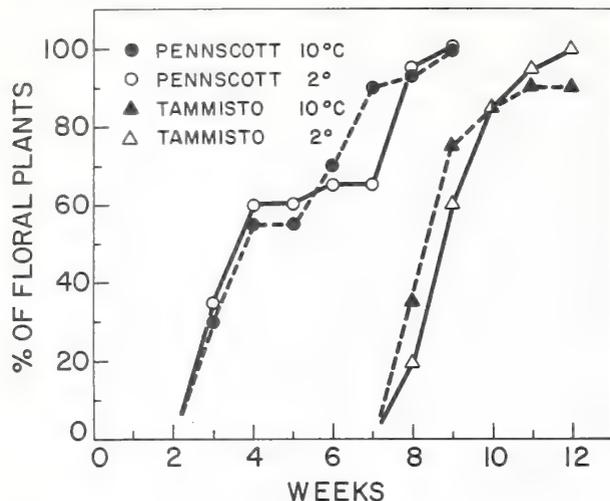


FIGURE 8.—Cumulative percentage of floral plants of Pennscoff and Tammisto red clovers grown under an environmental regime of 2 weeks at 30° C. and 20-hr. photoperiod, followed by 2 weeks at 30° and 12-hr. photoperiod, followed by 2 weeks at 2° or 10° and 10-hr. photoperiod, and grown out at 30° and 20-hr. photoperiod (3c).

about a week's delay was noted for development of an equivalent percentage of floral plants among the Tammisto and Pennscoff cultivars.

These observations and other reports suggest that the environmental requirements for floral development in many herbage species represent complex responses that warrant further study. In some ecotypes a particular environmental regime may enhance the subthreshold levels of floral stimulus rather than function as a requirement for development of the stimulus itself. Likewise, the physiological status of the plant including levels of non-structural carbohydrate in the aerial or root tissues may have an effect on expression of the floral stimulus. A response of this nature could, for example, be interpreted as depicting a juvenile stage of development when in reality it represents some other response.

Although most herbage species used in the temperate, humid regions are long day plants, the diversity of plant types within a species does not exclude floral response under day neutral or even short day conditions. The utilization of this

diversity by developing cultivars for unique environmental conditions will undoubtedly contribute toward increased productivity of the herbage ecosystem.

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MORPHOGENESIS AND MANAGEMENT OF WOODY PERENNIALS IN AUSTRALIA

By D. G. Wilcox¹

Abstract

The location and condition of shrub rangelands in Australia are described. The criteria for the germination and the establishment of *Atriplex* (saltbush) and *Kochia* (bluebush) species are reviewed. The significance of these genera to range forage is discussed in relation to grazing pressure and specific characteristics which determine their survival in the pastoral environment. *Acacia* shrublands are described with particular reference to *A. aneura* (mulga) and its requirements for germination, survival and maintenance. The productivity of these shrublands is reviewed.

Additional Key Words: Australian shrub rangelands, management, *Atriplex*, *Kochia*, *Acacia*, productivity

Introduction

Pastures in which shrubs are important in Australian rangelands lie in a region receiving between 150 and 500 mm. of annual rainfall, a large part of which falls in winter but which is always characteristically erratic in incidence. Most of these pastures lie south of an arbitrary winter-summer rainfall dominance line adapted from Perry (24) and J. McAlpine (private communication). An area of shrubby pasture in which *Acacia aneura* F. Muell. is important lies just to the north of this line, but in this region winter rainfall is still effective and comparatively reliable. Another area of shrubby pasture is found further north on the Barkly Tableland where *Chenopodium auricomum* Lindl. (northern

bluebush), is determined in its occurrence by seasonal flooding and is strongly limited by soil type (30). Shrubland distribution is shown in figure 1.

Perry (24) and Moore and others (21) described the shrubland pastures in Australia. Perry discussed the arid zone pastures falling within the categories of shrub steppe, acacia shrublands, and low arid woodlands (figs. 2 and 3). Moore described the semiarid woodlands, communities which lie between the arid zone and the mesophytic grazing and farming land where introduced pastures may be sown. Eucalyptus, acacia, and casuarina form an irregular overstory in these communities, above variable stands of low shrubs and grasses which change according to soil type and average annual rainfall.

Rainfall exerts an overwhelming influence upon the total production available in shrub communities, creating peaks and abysses of production coincident with rainfall variation. Perry (24) refers to the bare spaces which occur between shrubs in shrub steppe during frequent long, dry periods, and to the ephemeral nature of much of the ground layer in other communities. In prolonged dry periods the shrub components provide the only fodder available to grazing animals. The shrubland pastures of the Riverine Plain in New South Wales, described by Leigh and others (15, 16, 32, 33) in a number of papers, appear to differ from the remainder of shrubland zone since the associated *Danthonia*, *Stipa* and forbs present provide an almost stable alternative diet to shrubs in this 300 to 500 mm. rainfall region.

Moore (20) suggested that use of the Australian shrubland pastures has followed a pattern that was not always definable in precise sequence but which involved quite clear steps. Initially, the most palatable species were heavily grazed and even removed. This was followed by

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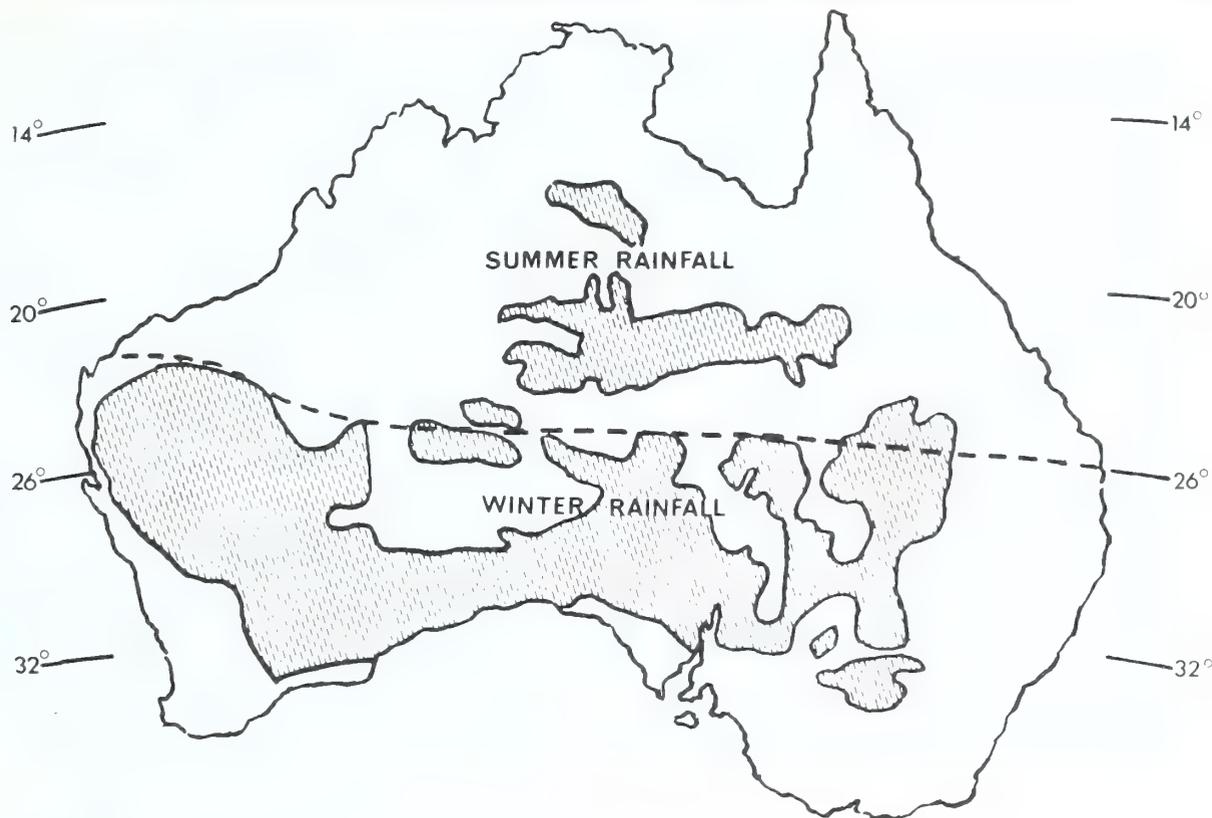


FIGURE 1.—Shrubland pasture distribution in Australia. Modified from Moore and others (21) and Perry (24).

an increase in unpalatable species, though their total expression was often tempered by drought. Where cover was completely destroyed, serious soil erosion took place. Complementary to this regression, additional stresses were placed upon the vegetation through the provision of watering points and fences, which restricted stock to specific areas. The explosion of the European wild rabbit into the rangelands of Eastern Australia in 1890 aggravated this situation, because they entirely removed the herbaceous vegetation which provided some protection for the remaining woody perennials. Through burrowing and ring-barking, rabbits contributed to the death of those plants which survived the effects of domestic livestock. Crocker and Skewes (6) described a number of paths by which specific pasture types degenerated from perennial woody shrubs to annual species in South Australia. Hall and others (9) described a dramatic sequence in vegetation decline in the natural shrubland pastures of north-

east South Australia. However, it is not clear whether these changes in species composition are the direct result of increased competition from undesirable species in the pasture, if they are due simply to reduced vigor, or to adverse changes in the total pasture environment induced by over-use by grazing animals.

In this setting of decline in condition of the shrub range, a number of studies have been undertaken which have aimed at determining the specific worth of particular pastures and their components; at investigating special aspects in the life cycles of pasture species; and at achieving an understanding of the interrelationships in grazed and ungrazed pastures. These are here described under the broad headings of halophytic (*Atriplex* and *Kochia*) pastures and of *Acacia*, particularly *A. aneura*, pastures. Very few, if any, of the investigations have developed to include the whole scope of the life history of pasture species and the impact of grazing upon the in-

ternal pressures in the pasture-animal ecosystem, where the animal has an immediate effect upon an admittedly mobile equilibrium in the arid pasture.

Halophytic Pastures

An understanding of the factors affecting germination and early seedling survival is prerequisite for the definition of management plans. Burbidge (2) defined the optimal germination criteria for *Atriplex vesicaria* Benth. and a number of *Kochia* species. She noted that as *A. vesicaria* germinated most readily at 15° C., and is significantly depressed at other temperatures, germination can only be expected with autumn rains, when in the interests of seedling survival, grazing should be restricted. However, Trumble (27) and Woodroffe (35) reported the survival and establishment of *Kochia sedifolia* F. Muell. seedlings at grazing rates as high as 0.5 sheep per hectare. *Kochia* species were shown by Burbidge to be more tolerant of hot conditions and to have a wider germination range. She also referred to

the effect of salt as a germination inhibitor in the bracteoles of *A. vesicaria*, which she presumed prevented germination with light falls of rain. However, Jones (12) working with *A. nummularia* Lindl., could obtain no increases in field germination after soaking seed and bracteoles in water to leach out salt. Trumble (27) found that *A. vesicaria* was adapted to a winter rainfall germination and summer growth pattern. He considered that this characteristic determined the species distribution.

Burbidge (2) showed that the germination of *A. vesicaria* was substantially decreased at depths greater than 1.25 cm. Winkworth (34) reported rapid drying out of some desert soils to more than 2.5 cm. within 24 hours which is of particular relevance here. It would suggest that prolonged and continuous rainfall is necessary for the germination and establishment of *Atriplex* spp., a condition found infrequently in Australian rangeland. It is suggested that management of degraded halophytic pastures will center upon the efficient use of excess rainfall years.



FIGURE 2.—*Acacia aneura*-low shrub-short grass-forb pasture in Western Australia. *A. aneura* in center and right rear, *Kochia* and *Solanum* spp. beneath the tall layer.



FIGURE 3.—Shrub steppe in Australia; *Kochia pyramidata* Benth., short grasses, and forbs.

Hall and others (9) drew attention to the changes which can be expected as a result of the overuse of shrubland pastures, particularly since characteristics such as the capacity to fruit readily, to have a high percentage of hard-seededness, and to have a high germinability are not possessed equally by all species. Along with differential palatability, these characteristics combine to produce striking changes in vegetation expression. Alterations in seedbed conditions under grazing also contribute to changes in pasture structure. Carrodus is quoted by Hall (9) as stating that water infiltration rate has a significant effect on the germination and establishment of *K. sedifolia*, though I. Noble (private communication) attributes a decline in the germination and establishment of this species to a drop in total soil nitrogen in the surface 1 cm. of soil. However, both these features may be symptomatic of a total decline in seedbed conditions brought about by incorrect grazing management.

Table 1 shows the pattern through time of the contributions made to pasture by different components in a halophytic community. The data are that from an *Atriplex-Kochia* community in a 200 to 250 mm. rainfall area in Western Aus-

tralia (Wilcox unpublished). Under conditions of low rainfall, the contribution of the ground flora is inadequate to maintain sheep even at the low stocking rate of one sheep to 10 or 12 hectares, common in these areas. Grazing animals must rely upon woody shrubs during these periods of stress.

Condon (5) and Ratcliffe (25) refer to the disappearance of extensive areas of valuable shrub species such as saltbush (*Atriplex*) and bluebush (*Kochia*) in western New South Wales and South Australia. Similar trends have been observed in Western Australia. These genera were considered to form the most important native pasture for sheep grazing, and their disappearance was considered to be responsible for a decline in productivity on the range. Osborn and others (23) in South Australia suggested that severe overuse of an *A. vesicaria* pasture by sheep resulted in complete removal of perennial cover in a zone immediately about a watering point. They recognized four zones of use extending away from the watering point till, at distances of about 1½ miles, dependent upon topography, a zone of little use characterized by moribund and senescent plants was reached.

They observed that intermittent but heavy use promoted the vigor of shrubs between the outermost and inner zones due to the effects of pruning and trampling which suppressed the weaker bushes.

Barker and Lange (1) point out that grazing pressure or dietary preference is not, per se, the only agency affecting drifts in vegetation structure in a halophytic community. They include resistance to use and brittleness as factors which should be considered in any application of the effects of morphological characteristics upon community structure. Lange's (14) piosphere concept, which he defines as a fundamental ecological condition imposed by grazing animals upon the natural pattern, was used by these authors in an analysis of change of vegetation around watering points. Annual species of *Atriplex* were found to reflect rapidly a changing environment, whereas changes in population of the perennial *A. vesicaria* were considered to be the product of long term effects of grazing and

not immediately indicative of any vegetation change.

Figure 4 (Wilcox unpublished) shows the order of changes which occurred in degraded saltbush communities after exclosure and under yearlong use. In a period of generally low rainfall from 1953 to 1960 when effective rain fell only on two occasions, a number of species remained relatively static, or even disappeared under grazing pressure. However, *A. paludosa* R.Br. is shown to be particularly labile and could be used as an indicator of range condition and as a detector of drifts in structure.

A number of workers have studied the effects of grazing on halophytic communities. Trumble (27) and Woodroffe (35) investigated the grazing of a *K. sedifolia* pasture in South Australia. In a pasture containing about 900 bushes per hectare, the green weight of bluebush fluctuated from 517 to 1,600 kg. per hectare, dependent upon rainfall. In a period of six years of low rainfall there was a downward trend in production in

TABLE 1.—Changes in relative contribution to pasture with time and season in exclosed and freely grazed saltbush association¹

[production in kg./ha., fresh wt.]

Date	Species ²						Total	Annual rainfall mm.
	Atpa	Atrh	Crsu	FRAN	Kopy	Ground		
October 1953	347	156	237	4	54	N/A ³	798	494
	<i>111</i>	<i>135</i>	<i>119</i>	--	8	N/A	<i>373</i>	
April 1954	208	78	86	3	36	6.8	417.8	137
	<i>114</i>	<i>102</i>	<i>43</i>	--	--	0.35	<i>259.35</i>	
April 1956	125	24	27	--	5	0.26	154.26	217
	<i>72</i>	<i>35</i>	<i>17</i>	--	--	Nil	<i>114</i>	
April 1957	154	18	17	--	3	0.02	192.02	152
	<i>121</i>	<i>54</i>	<i>11</i>	--	--	Nil	<i>186</i>	
April 1958	35	8	6	--	4	Nil	53	322
	<i>3</i>	<i>4</i>	--	--	--	Nil	<i>75</i>	
April 1959	85	24	14	--	4	Nil	127	196
	<i>46</i>	<i>22</i>	<i>7</i>	--	--	Nil	<i>75</i>	
May 1960	151	94	4	--	67	N/A ³	316	231
	<i>79</i>	<i>245</i>	<i>13</i>	22	--	N/A ³	<i>359</i>	

¹ Roman figures indicate exclosed; italicized figures indicate freely grazed.

² Species are indicated as follows: Atpa—*Atriplex paludosa*, Atrh—*Atriplex rhagodioides*, Crsu—*Cratystylis subspinescens*, FRAN—*Frankenia* sp., Kopy—*Kochia pyramidata*, and Ground—annual grasses and forbs.

³ N/A indicates data not available.

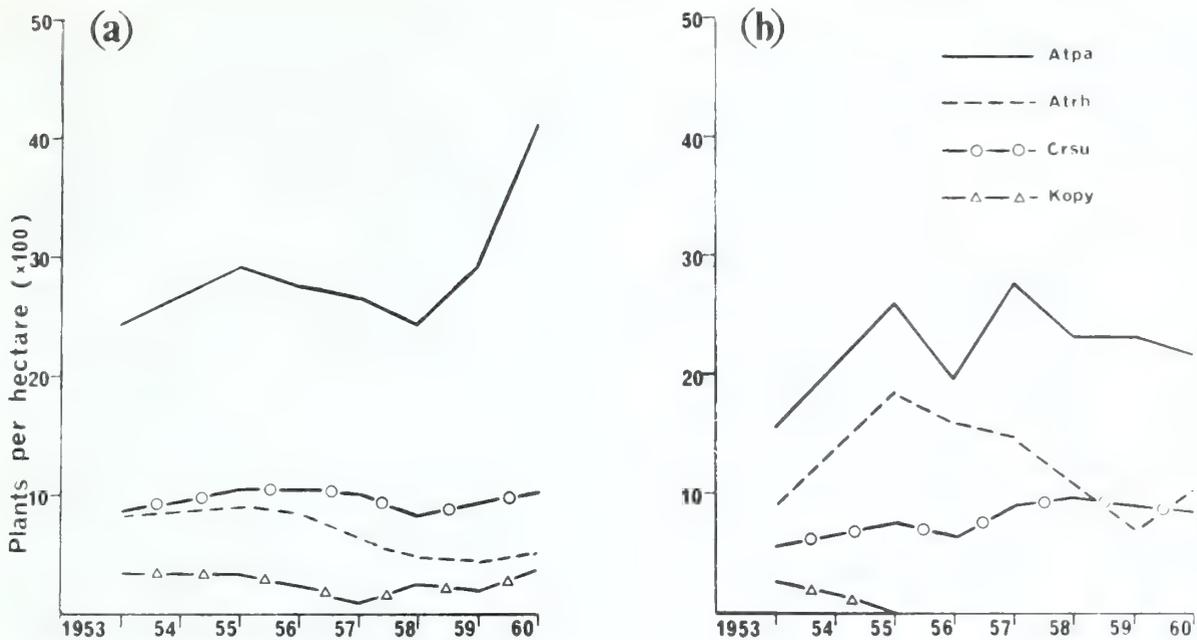


FIGURE 4.—Changes in species occurrence with (a) exclosure, and (b) open grazing in a halophytic community in Western Australia. Atpa—*Atriplex paludosa* R.Br.; Atrh—*Atriplex rhagodioides* F.Muell.; Crsu—*Cratystylis subspinescens* (F.Muell & Tate) S.Moore; and Kopy—*Kochia pyramidata* Benth.

pastures grazed at 0.4 and 0.5 sheep per hectare. However, this trend was reversed with increased rainfall as the heavily grazed plants produced more leaf and the number of plants per hectare increased. The enhanced production from the heavily grazed plots was considered to be due to an acceleration of the fertility cycle. Animals were important as circulators of nutrients which stimulated growth of mature plants and the development of young seedlings. They concluded that the productivity of shrub pastures may be considered as a function of grazing intensity and effective seasonal rainfall. However, Rixon (26) found that the rate of decomposition of residues on the soil surface in an *Atriplex* community in New South Wales was slow, and that the returns from animal residues were extremely small. The return of nutrients was of local significance where grazing pressure was high or where animals tended to congregate. Rixon suggested that the pattern of behavior of grazing animals was important in any consideration of nutrient recycling. He found a localized intensity of nutrient cycling beneath individual elements of the shrub cover.

Elimination of this plant cover could be expected to cause a significant reduction in the rate of nutrient cycling in the pasture, and a consequent reduction of potential productivity.

A series of investigations on halophytic shrub-grassland pastures in southwestern New South Wales has questioned the value of the shrub component in providing a source of basic diet or even of supplementary feed during periods of moisture stress.

Wilson and Leigh (32) compared the productivity of sheep grazing mixed *A. vesicaria*-grass pastures with that of sheep grazing *Danthonia-Stipa*, and mixed *Danthonia-Stipa*-forb pastures. At a stocking rate of 1.2 sheep per hectare, sheep grazing the shrub-grass pastures were superior in the first year only, and subsequently declined in condition due to death of the shrubs. On the grassy pastures the sheep were maintained indefinitely. At 2.4 sheep per hectare, both pastures failed. In a similar investigation, Leigh and others (15) studied the performance of merino sheep grazing a *Kochia aphylla* R.Br.-*Stipa-Danthonia* community at 1.6 sheep and at 0.9 sheep

per hectare. Even at the higher stocking rate, *K. aphylla* did not contribute more than 7 percent of the total forage taken. The major constituents of the diet were two compositae in winter, and *Danthonia* with an herbaceous chenopod in summer. It is significant that *Medicago polymorpha* L. was recorded as a principal constituent in autumn, a species found rarely in more arid environments and never in large quantities.

In a further study Wilson et al. (33) measured the performance of sheep grazing an *A. vesicaria*-*K. aphylla* community at 2.5, 1.2 and 0.6 sheep per hectare. In summer, sheep preferred the perennial grasses, annual grasses and forbs to the more abundant shrubs, but were inclined to take more shrub during autumn prior to the advent of winter rains. At the lowest stocking rate, animal production was maintained and there was no decline in shrub population, but at the higher levels of stocking the shrubs were almost completely, if not totally, removed. The authors noted the adverse effect of heavy or complete defoliation on *A. vesicaria* as it failed to recover during subsequent years. In a later paper, Leigh and Mulham (in press) suggest that this inability of *A. vesicaria* to persist after this type of use is due to the removal by grazing of potential growth sites which apparently occur only along the young stems. In contrast, Leigh and Wilson (16) report the *A. nummularia* is capable of producing new leaves along the main stems and branches following complete defoliation. These differences in morphology are obviously important in planning management strategies for pastures containing these shrub species.

Wilson (31) reviewed the role of browse in the nutrition of grazing animals and suggested that evaluations of browse should be made comparative to the alternative vegetation (table 1). There is an obvious need to define the pasture plants required for specific locations. In some places an ability to survive long periods of moisture stress may be an advantage, whereas in others high annual productivity may be more desirable.

Jones and others (13) reported a capacity in *A. nummularia* to produce 2.33 kg. dry wt. of material from a basal area of one square meter

in 500 days from establishment. They conclude from this, and from a further study with *A. vesicaria*, that the rangeland species of *Atriplex* are capable of high production and efficient growth in a favorable environment. This investigation, under plantation conditions, was not extended to the field situation where survival, durability, and resistance to water stress are important considerations in the arid zone.

Malcolm (18) worked with *Kochia brevifolia* R.Br. and a number of *Atriplex* species in a 750 mm. winter rainfall dominant region in Western Australia. He applied five handstripping regimes to the species and found that *K. brevifolia* produced most with heavy and moderate simulated stocking, while *Atriplex* responded better to light and moderate use. In a grazing situation, *K. brevifolia* declined under conditions of light use in autumn though it fluctuated less than *Atriplex* with variation in rainfall. Together the species produced about 600 kg. per hectare when the rainfall was about 380 mm. per annum. Yields were correlated in both species with rainfall which fell up to two years prior to grazing.

Hellmuth (10) reported an eco-physiological study on *Rhagodia baccata* (Labill.) Moq. in Western Australia in a 200 mm. annual rainfall area. He concluded that a sensitive hydroactive reaction by stomata once a "critical water deficit" was reached appeared to confer considerable drought resistance on this species. The species has a high heat resistance and capacity for positive continuous net assimilation. These characteristics, together with its ability to withstand water stress, make it particularly suited to the environment for grazing during moisture stress.

Considerations such as these are involved in the selection of plants worthy of promotion in an arid environment. While Leopold's (17) view that senescence or the ability to become deciduous in part has positive survival value for a species, this morphological feature is of negative value in the arid range situation. Jessup (11) referred to thorniness and unpalatability as aids to species survival in his description of halophytic communities in northwest South Australia, but these morphological characteristics have similarly no range value.

Acacia Communities

Figure 5 (Wilcox unpublished) shows the fluctuations in productivity which occurred in a mulga (*Acacia aneura*) community due to variations in annual rainfall effectiveness. As in the halophytic pastures, animals clearly must depend upon dietary sources other than herbage if they are to survive during periods of moisture stress.

Mulga communities have been exploited to provide a diet for sheep and cattle. Nichols (22) reported the successful feeding of large flocks of sheep on fallen mulga in Western Australia. Melville (19) described a number of *Acacia* species in Western Australia which can be fed to sheep once they are felled. He also drew attention to differences in the acceptability of mulga, a difference he ascribed to the level of ether ex-

tractable constituents in the phyllodes which may rise to 12 percent in unpalatable varieties.

In Queensland, Everist (8) suggested forms of mulga tree cutting which allow for the regrowth of the cut tree after rain. He also suggested the number of trees which should be left in the community to provide for regeneration. It should be noted in this discussion of *A. aneura* and associated tree forms that their value, particularly for sheep, only becomes apparent after they have been felled and the edible material becomes available. There has been no recorded work on the rate of mulga regrowth after lopping, nor any indication of the amount of lopping which could be permitted without erosion of the reserve of standing forage.

Rehabilitation of cut stands of mulga depends upon the successful colonization of the com-

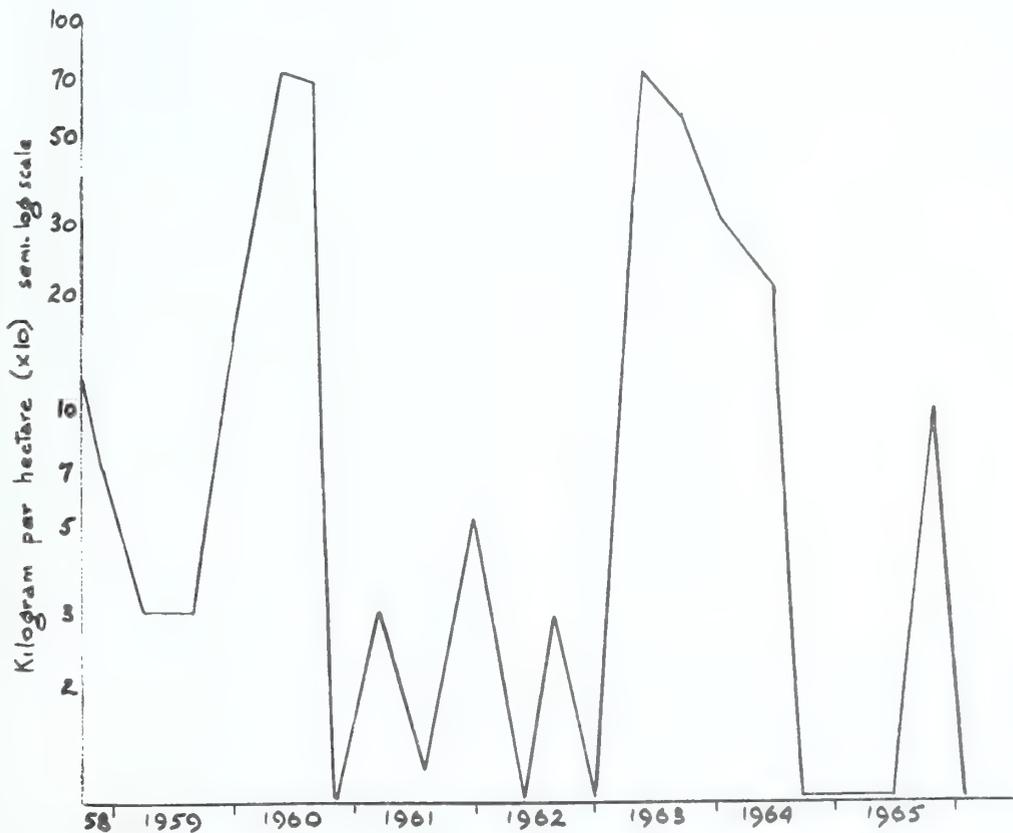


FIGURE 5.—Variation in ground species production in a mulga-short grass-forb community in Western Australia.

munity by seedlings and their subsequent survival. Very little has been published on this aspect of community morphogenesis in this pasture type. Some preliminary studies by Batianoff (private communication) on the germination of mulga suggest that germinability can be enhanced by various heat treatments. Since temperatures below 20°C. adversely affect germination, summer rains only are likely to be effective in promoting germination. It is suggested that pastures are likely to require some special treatments at these times if mulga re-establishment is desired. Davies (7) demonstrated cycles of flowering and seed set in mulga dependent upon a combination of summer and winter rains in succession. Seed production fails if rain is received in one season only. If maintenance of the seed supply is a consideration, grazing of mulga pastures should be restricted, in some areas, in a favorable rainfall year.

W. Burrows (private communication) pointed out that germination of mulga may occur even in average rainfall years where run-on water may create special sites favorable to germination. Burrows does not indicate, however, whether plants germinating under these conditions will survive with grazing. Hall et al. (9) refer to the susceptibility of seedling *Acacia aneura* and *Casuarina cristata* Miq. to grazing by rabbits, and indeed Moore (20) has indicated that the destruction of mulga pastures west of the Darling River in New South Wales is primarily due to the influence of these animals. There is no information on the effect of sheep grazing on the survival of mulga seedlings, although Chippendale and Jephcott (4) consider that cattle impose a heavy grazing pressure upon this community. They suggest that freedom from use for extended periods is required if seedlings are to mature, the vigor of the stand is to be maintained, and the seed supplies replenished.

For the most part, mulga trees, in the absence of lopping, provide a diet only through leaf and seed fall. Figure 6 (Wilcox unpublished) illustrates the fluctuations from this source through time. Leaf fall appears to follow periods of prolonged effective rain, as was suggested by Slatyer (private communication). At no time did seed fall exceed 2 kilograms per hectare. The fallen leaf contained an average of 8.5 percent crude protein

and 29.1 percent fibre, which is adequate for maintenance but not for reproduction in sheep. It is suggested that leaf value would deteriorate due to weathering and that its contribution to forage would decrease as it was consumed by termites (Watson private communication).

Beale (private communication) investigated the effects of thinning upon a mulga stand to 40, 160, and 640 trees per hectare. He showed that tree numbers have a significant effect on herbage and leaf production. In an analysis of all sites studied there was an inverse curvilinear relationship between grass and tree densities, and, by inference, of available forage production.

As Slatyer (private communication) has shown that 40 percent of the rainfall in excess of 2.5 mm intercepted by the crown of a mulga tree is channelled down the trunk to become available to the tree and not for the production of accessible forage, thinning of a mulga stand should be considered as a management technique which could enhance range site productivity. Tree removal, however, should not exceed the limits set by J. Marshall (private communication) beyond which landscape deterioration can be expected.

In Western Australia, Wilcox and Speck (29) and Wilcox (28) drew attention to the role of undershrubs in mulga communities since these can provide a durable source of pasture in periods of stress. Burrows and Beale (3) also emphasized the complex nature of mulga communities and the importance of microtopography as it influences species distribution. This is relevant to the range situation as species with different demands for survival may be found within one grazing area. Special management techniques for these shrubs associated with the ubiquitous mulga have yet to be devised.

C. W. E. Moore (private communication) referred to a complex interplay of factors in his discussion on the increase of woody species in western New South Wales. While it was possible for Moore to list a number of possible causes of change in range condition, it is much more difficult to determine which factors have the major effect, or to identify the significant interactions between them. *Eremophila mitchellii* Benth., *Dodonea attenuata* A. Cunn, and *Cassia nemophila* C. Cunn. ex Vogel are among some of the species which have converted the well-grassed woodlands

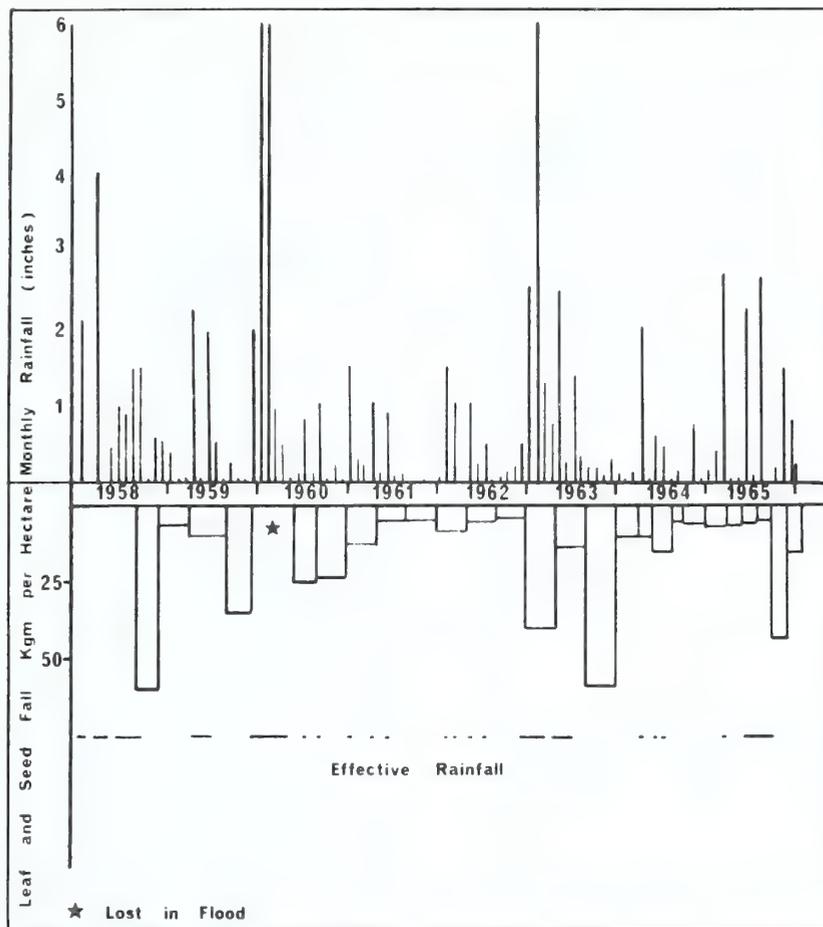


FIGURE 6.—Fluctuations in leaf fall from mulga trees in Western Australia.

to dense shrub woodlands with reduced productivity and increased run-off. In some cases, Moore considers this to be due to a reduction in competition as species such as palatable *Acacia cambagei* R. T. Baker and perennial grasses are preferentially removed, thereby reducing the competition which would normally obstruct the expansion of undesirable species. Overuse of the palatable *Casuarina cristata* and *Heterodendron oleifolium* Desf. during droughts is thought by Moore to have reduced the vigor of these species and to have allowed *Dodonea attenuata* to become established.

Summary

Specific morphological characters emphasized during the life of a woody perennial influence its survival in range land. Two factors affecting the

use of a species are palatability and accessibility since they modify, in turn, the chances of survival of a species and hence the vegetation structure and then the productivity of a particular range site. Apart from the work on the Riverine Plain, there is little in the Australian literature on woody perennials upon which to make judgments on the value of a species or a community. It is possible to extrapolate a form of management process from some of the particular studies performed on special plants in particular growth stages, but none of these procedures has been evaluated in the field where the whole complex of plant-animal interaction is expressed. With rainfall so variable in amount and incidence, field studies which aim at elucidating management schemes must necessarily be conducted over extended periods which would cover the gamut of rainfall expression.

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MORPHOGENESIS AND MANAGEMENT OF WOODY PERENNIALS IN THE UNITED STATES

By A. Perry Plummer¹

Woody perennial shrubs and small trees occur as an important part of the ground cover on over 300 million hectares in the United States. On millions of additional hectares, shrubs are important understory in the deciduous and conifer forests east of the Mississippi River and elsewhere. My emphasis is directed to rangeland aspects of woody vegetation of the West where shrubs are usually not understory.

Woody perennials occur over nearly the full gamut of climate and soils. They may be found at all altitudinal and latitudinal limits, except where the ground is permanently covered with snow. They are the prevailing cover in the hot deserts below sea level in the Salton Sea basin and in Death Valley, Calif. (5).

In various environments, this class of plants functions in many ways to serve mankind. They provide forage for millions of sheep, cattle, and wild animals and are important as a protective cover for these animals, especially when temperatures are extremely hot or cold. Without such protective shade, many small animals would be eliminated. Frequently, the shade of this class of plants also provides the microclimate for the growth of a great variety of understory herbs.

Woody perennials are unexcelled in the ability to grow in sterile and highly salt-impregnated land where they stabilize soils which would otherwise be completely barren and subject to wind and water erosion. In contrast, there are woody perennials which provide important cover in extremely wet, acid conditions. Characteristics that adapt shrubs for particular habitats result in a large variety of ecotypes and biotypes within species (11, 54). This may be more true for shrubs than for any other class of plants.

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A rationalization has grown up, at least in Western United States, that some woody plants are bad and others are good because of their differences in aggressiveness, forage value, susceptibility to fire, water consumption, and other attributes. No doubt there is a considerable bias at times, as to what may be a good or bad woody perennial. Some may be considered good in certain environments and bad in others.

An outstanding example of this is the widely occurring and variable big sagebrush (*Artemisia tridentata* Nutt.). On many spring and summer livestock ranges sagebrush is regarded as a competitive menace to grassland, and for this reason attempts are made to eliminate it. A large number of mechanical and herbicidal techniques have been devised for reducing it (38, 40, 45). In contrast, on many winter ranges for livestock and game, big sagebrush is the most important source of forage. Because of its high nutritive value and the fact that in this season it is palatable as well as highly productive, sagebrush has been recommended for seeding on extensive winter game ranges in Utah, and is one of the best shrubs available for this purpose. Special effort has been directed to aerial planting of sagebrush on large blocks of winter game range in Utah (45).

A great amount of emphasis has been given to encouraging replacement of woody perennials by herbaceous plants through management practices (39, 48), including artificial treatments and planting adapted species (43, 45). This is usually justifiable, but I have seen some elimination of woody perennials where I thought the judgments were misguided.

Uncontrolled grazing by livestock over the past century has been the major reason for a decline and loss of palatable elements of both woody and herbaceous species. However, major improvements have been obtained in some areas through

the application of managed grazing. Some of these have been helpful in restoration of browse as well as herbs (25, 26, 28, 38, 39, 48, 51).

Observations of grazing animals, as well as many chemical analyses and digestibility trials, show that woody perennials provide nutrients, such as protein and vitamins, which keep grazing animals healthy and vigorous through a considerable part of the year when herbaceous plants are dry and dormant and lack good nutritional qualities (12, 13, 14, 16, 19, 34, 51, 53). Hence, it is important on many ranges that woody perennials represent a fair degree of balance with herbs. Managing to maintain this balance is a major problem for the future.

Characterization Of Western Shrublands

Estimated hectares of the six major shrubland types in the Western United States, shrubs that characterize each type, and the approximate range in average annual precipitation for each area are shown below. These types are comprised of several species, and only the major ones are mentioned in this discussion or noted as follows:

NORTHERN DESERT SHRUBS:

Precipitation, 125–375 mm.; 100 million hectares

- Big sagebrush (*Artemisia tridentata* Nutt.)
- Black sagebrush (*A. arbuscula* Nutt. *nova* [A. Nels.] Conq.)
- Rubber rabbitbrush (*Chrysothamnus nauseosus* [Pall.] Britton)
- Small rabbitbrush (*C. viscidiflorus* [Hook.] Nutt.)
- Nevada ephedra (*Ephedra nevadensis* Wats.)
- Spiny sage (*A. spinescens* DC, Eaton)
- Blackbrush (*Coleogyne ramosissima*, Torr.)
- Fourwing saltbush (*Atriplex canescens* [Pursh.] Nutt.)
- Spiny hopsage (*Grayia spinosa* [Hook.] Moq.)
- Winterfat (*Eurotia lanata* [Pursh.] Moq.)

JUNIPER & PINYON

Precipitation 200–275 mm.; 36 million hectares

- Utah juniper (*Juniperus osteosperma* Torr. Little)
- Sierra juniper (*J. occidentalis* Hook.)
- Two-leaf pinyon pine (*Pinus edulis* Engelm.)

Single-leaf pinyon pine (*P. monophylla* Torr. & Frem.)

- Big sagebrush
- Black sagebrush
- Rubber rabbitbrush
- Cliffrose (*Cowania mexicana* D. Don)
- Antelope bitterbrush (*Purshia tridentata*, Pursh. DC)
- Green ephedra (*Ephedra viridis* Cov.)

MOUNTAIN BRUSH:

Precipitation 300–750 mm.; 6 million hectares

- Gambel oak (*Quercus gambelii* Nutt.)
- Big sagebrush
- Mountain snowberry (*Symphoricarpos oreophyllus* A. Gray)
- Black chokecherry (*Prunus virginiana melanocarpa* [A. Nels.] Sarg.)
- True mountain mahogany (*Cercocarpus montanus* Raf.)

SALT DESERT SHRUBS:

Precipitation, 100–350 mm.; 28 million hectares

- Black greasewood (*Sarcobatus vermiculatus* Hook.)
- Shadscale saltbush (*Atriplex confertifolia* Torr. & Frem)
- Gardner saltbush (*A. gardneri* Moq. D. Dietr.)
- Fourwing saltbush
- Spiny sagebrush
- Spiny hopsage
- Winterfat

CHAPARRAL:

Precipitation, 250–1,000 mm.; 12 million hectares

- Turbinella oak (*Quercus turbinella* Green) and other live oaks
- Buckbrush (*Ceanothus* spp. L.)
- Manzanita (*Arctostaphylos* spp. Adams.)
- Chamise (*Adenostoma fasciculatum* H. & A.)

SOUTHERN DESERT SHRUBS:

Precipitation, 200–750 mm.; 150 million hectares

- Velvet mesquite (*Prosopis juliflora* [Swartz.] DC.)
- Creosotebush (*Larrea divaricata* Cav.)
- Tarbrush (*Flourensia cernua* DC.)
- Saguaro (*Cereus giganteus* Engelm.)
- Joshua tree (*Yucca brevifolia* Engelm.)
- Blackbrush
- Fourwing saltbush

While ecotones between types may be quite distinct, in many places there is abundant inter-

mingling of species: Plant composition is influenced by both macro and micro climates as well as by differences in texture and chemistry of soils. Past grazing, clearing of the land for agriculture, and fire are also factors affecting composition.

Big sagebrush and its subspecies occur importantly over as much as one-half of the area of the northern desert shrub (4, 22). Major shrubs may grow intermixed or in alternates with each other or with salt desert shrubs. The alkalinity of the soil determines whether sagebrush or shrubby chenopods, such as black greasewood (*Sarcobatus vermiculatus* [Hook.] Torr.) or Gardner saltbush (*Atriplex gardneri* [Moq.] D. Dietr.), are dominant. This variation in species denotes the distinction between northern desert and salt desert shrublands.

The juniper-pinyon and mountain brush types intermingle importantly and extensively with each other, as well as with the northern desert type and, to some extent, with the salt desert shrub type. Freezing is frequent in all of these types through much of the dormant growth period in winter, but the severity varies greatly between localities. On their southern limits, all four types are transitional with the southern desert shrub and to some extent with the chaparral.

Chaparral is probably the most distinct of the six types, but its shrubs do occur widely in the other types. Nearly half of the chaparral type occurs in California. Other tracts exist in Arizona, New Mexico, Nevada, and southern Utah. The woody plants of this type are mostly broad-leaf evergreens which are highly prone to burning and which sprout vigorously when the above-ground parts are removed. As catastrophic floods often follow burning, an important research project by the Pacific Southwest Forest and Range Experiment Station of the Forest Service, U.S. D.A., is aimed at finding fire retardant plants which can be established as live firebreaks (36).

All of these types are tremendously important for production of livestock and game animals. The northern desert shrub, salt desert shrub, and juniper-pinyon are especially important for winter and spring-fall grazing for sheep and cattle. This is true not only for the browse these types provide but often more importantly for the grasses which are associated with them (28).

In the southern desert shrub and elsewhere where there is a prevalence of summer precipitation, warm season growing grasses, such as the galleta grasses (*Hilaria* spp.) and grama grasses (*Bouteloua* spp.), predominate (27, 30). The wheatgrasses (*Agropyron* spp.), wildryes (*Elymus* spp.), and bluegrasses (*Poa* spp.) prevail where most of the accumulated moisture for plant growth results from winter precipitation. Indian ricegrass (*Oryzopsis hymenoides* [Roem. and Schult.]), bottlebrush squirreltail (*Sitanion hystrix* [Nutt.] J. G. Smith var.), and needlegrasses (*Stipa* spp.) are common in both summer and spring growing areas.

Sagebrush and rubber rabbitbrush (*Chrysothamnus nauseosus* [Pall.] Britton); Utah juniper (*Juniperus osteosperma* [Torr.] Little); two-leaf pinyon (*Pinus edulis* Engelm.) and single-leaf pinyon (*P. monophylla* Torr. and Frem.); as well as velvet mesquite (*Prosopis julifolia* [Swartz] DC.); creosote bush (*Larrea divaricata* Cav.); and tar bush (*Flourensia cernua* DC.) have increased their prevalence and expanded their areas of occupancy on what were once primarily grasslands (8, 29, 30, 39, 41, 44). Some have considered that the increase of sagebrush and other shrubs, at a time when there was severe depletion of herbs, actually favored an increase of deer (32, 47).

Range Improvement

Treatment Methods

A good deal of what is being done to restore the range is experimental or in pilot programs. Restoration is essentially confined to experimental plantings where annual precipitation is not in excess of 250 mm. (7, 42, 43).

Improvement of all types involves techniques that reduce the undesirable competing plants which have gained control. After competition is reduced, desired species are planted. If the desirable native species released from competition are abundant enough, such planting may not be necessary.

Mechanical and chemical means and burning are all being used to reduce competition. Over most range areas, mechanical techniques are more widely accepted and used than spraying with selective herbicides. One of the favorite and

most effective techniques for rapid treatment of large areas is that of pulling a heavy anchor chain between crawler tractors to reduce the undesirable brush and trees. Adapted species are then aerially seeded and the area is chained again in the opposite direction to cover the seed and further reduce competition (45).

While anchor chaining has been found especially useful on rough and sloping lands, disk plows and undercutters are widely and effectively used on more level ranges. These methods are followed by drilling the seed of adapted species. Two pieces of rugged equipment in popular use are the brushland plow for eliminating competition and preparing the seedbed, and the range-land drill for planting. This equipment was designed after similar pieces used in Australia.

Controlled burning has been used quite extensively in the northern desert shrub type where big sagebrush prevails and where fire will carry. It is also being fairly widely applied in the chaparral (6, 31). After burning, adapted species are aerially seeded, and techniques similar to those described above are used to cover the seed. Spraying with either 2,4-D, 2,4,5-T, or a mixture of them is done to keep sprouting brush under control. These chemicals have been widely used to control undesirable shrubby plants. They have probably been most widely and successfully applied on big sagebrush, but experimental and pilot spraying programs are underway on several types of undesirable brush (30, 52).

Plant Species

Similar to overlapping occurrence of native shrubs between regional types, there is wide range in the adaption of species which can be utilized for artificially improving shrublands. More than one hundred species, including grasses, forbs, and shrubs, are in some degree of use on wildlands. It is of interest that most of the grasses are exotics, whereas the majority of shrubs are natives, and the forbs are about equally divided. I will remark only on the major species and will not allude to strains.

On ranges being improved for game, effort is made to achieve a reasonable balance of grasses, forbs, and shrubs. At present this is difficult because seed supplies of adapted shrubs and forbs

are inadequate. However, progress is being made in this area (45, 46).

Planting of forbs and shrubs has been principally confined to the juniper-pinyon, mountain brush, and northern desert shrub where effort is directed to improvement of game range. Where emphasis is on improvement of range for livestock, grasses are principally planted.

Grasses most seeded through the northern desert shrub, juniper-pinyon, and mountain brush are crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.), desert wheatgrass (*A. desertorum* [Fisch] Schult.), intermediate wheatgrass (*A. intermedium* [Host] Beauv.), pubescent wheatgrass (*A. trichophorum* [Link] Richt.), smooth brome (*Bromus inermis* Leyss.), Russian wildrye (*Elymus junceus* Fish), and hard fescue (*Festuca ovina duriuscula* [L.] Koch). These latter two grasses have exhibited greater value than any other for improving succulence on late fall, winter, and spring ranges.

Because of its marked adaption to alkaline soils, Russian wildrye has shown unusual adaptation to sites throughout the northern desert shrub for growing in association with the existing shrubby cover, such as shadscale saltbush (*A. confertifolia* [Torr. and Frem.] S. Wats.) and black greasewood. It will do well on areas receiving only 200 mm. precipitation or even where there is somewhat less. Tall wheatgrass (*A. elongatum* Host) has good adaption for planting in the more moist, salt desert shrublands as well as in basic soils of the aforementioned types, but this grass needs a minimum of 300 mm. precipitation or the presence of a water table a few feet from the surface (45).

Intermediate and pubescent wheatgrass are also widely used in the chaparral for suppressing regrowth of the sprouting species. In addition, Harding grass (*Phalaris tuberosa* var. *stenoptera* [Hack.] Hitchc.) and smilgrass (*Oryzopsis miliacea* [L.] Benth. and Hook.) are used. Soft chess (*Bromus mollis* L.), an annual, is sometimes planted to provide a quick competitive cover while perennials are becoming established (6).

In the southern desert shrub, Lehmann lovegrass (*Eragrostis lehmanniana* Nees.) is the most extensively planted grass (9). Boer lovegrass (*E. chloromelas* Steud.), weeping lovegrass (*E. curvula* [Schrud.] Nees.) (31), sideoats gramma

(*Bouteloua curtipendula* [Michx.] Torr.), vine-mesquite (*Panicum obtusum* HBK), and switchgrass (*P. virgatum* L.) are used in areas where precipitation may exceed 350 mm. (1, 27, 30).

Some native adapted forbs now being planted in the first three types listed on page 73 are pacific aster (*Aster chilensis adscendens* [Lindl.] Cronq.), arrowleaf balsamroot (*Balsamorhiza sagittata* [Pursh] Nutt.), blue flax (*Linum lewisii* Pursh), and sweetvetch (*Hedysarum boreale* Nutt.). Introduced forbs being fairly widely used are range types of alfalfa (*Medicago sativa* L.), chickpea milkvetch (*Astragalus cicer* L.), sicklepod milkvetch (*A. falcatus* L.), and small burnnett (*Sanguisorba minor* Scop.).

The shrubs in extended plantings are big sagebrush, rubber rabbitbrush, antelope bitterbrush (*Purshia tridentata* [Pursh.] DC.), Stansbury cliffrose (*Cowania mexicana stansburiana* [Torr.] Jeps.), wedgeleaf ceanothus (*Ceanothus cuneatus* [Hook] Nutt.), and winterfat (*Eurotia lanata* [Pursh.] Moq). Fourwing saltbush (*A. canescens* [Pursh.] Nutt.) and winterfat show good adaption within most types where soils are basic.

Aspects Of Morphogenesis

Throughout the shrublands of the West, striking differences are often seen in the morphology of individual shrubs from place to place and sometimes in the same place. Environmental factors such as climate, soils, light, and modifications of these by elevation and latitude, are important causes for differences, and are probably reasons for the occurrence of what we may call regional ecotypes.

The environmental factors exerting their influence on sites over extended periods of time were no doubt responsible for fixing climatic or regional ecotypes and sometimes subspecies and even species. Excellent consideration has been given to this aspect through reciprocal transplant studies by Clausen, Keck, and Hiesey (11). While most of their studies involved moving herbaceous species from one elevation or climate into another, shrubs were involved, and certainly the principles developed by these investigators have considerable application to woody plants. Similar, but limited, transplanting of shrubs from the

southern to the northern desert shrub type in Utah, and vice versa, supports their findings (44, 45).

Cropping And Grazing

The continuing and constant use made of plants over a period of time, as by grazing, has temporarily altered shrub form. Over a long period of time it is reasonable to expect that, through the process of natural selection, a population would evolve to better tolerate this use. I strongly suspect this has occurred in the past century of grazing by livestock.

Commonly seen in nature are shrubs which have been grazed in about the same way over a period of years. As a result, they frequently assume a definite hedged appearance similar to ornamental hedges around homes. Once shrubs of some species acquire a hedged form, they persist unusually well despite what appears to be heavy annual cropping of the new shoots that grow above the hedge line. This characteristic has been noted in antelope bitterbrush, true mountain mahogany (*Cercocarpus montanus* Raf.), blackbrush (*Coleogyne ramosissima* Torr.), fourwing saltbush, rubber rabbitbrush, and others. From observations, it appears evident that the persistence of these hedged plants is attributed to the presence of leaves within the strong interwoven branches. Since they are not available to grazing animals, they produce sufficient carbohydrate reserves to maintain vigor. New growth above the hedge line is stimulated by the removal of apical dominance (17, 33, 49).

Artificial cropping of five shrub species by Garison (21) in Oregon showed that all were stimulated to a considerable increased production of herbage when the twig ends were removed. This increased growth continued over a 4- to 5-year period of cropping. The shrubs were antelope bitterbrush, rubber rabbitbrush, curleaf mahogany (*Cercocarpus ledifolius* Nutt.), snowbrush ceanothus (*Ceanothus velutinus* Dougl.), and creambush rockspirea (*Holodiscus discolor* [Pursh.] Maxim.). Removal of the terminal buds resulted in production of two or more twigs from lateral dormant buds the next growing season. McKell and Willard (35) in Utah have recently found

similar response from clipping mountain snowberry (*Symphoricarpos oreophilus* A. Gray) and rubber rabbitbrush. In both of these investigations removal of 50 percent or more of the twigs resulted in greater production than lighter cropping, but removal of 25 to 30 percent of the twigs resulted in more production than no clipping.

Ferguson and Basile (20) found through a 4-year period that a November cropping back of the main branches of antelope bitterbrush to about a 1-meter height from double this height or more, resulted in a nine-fold increase of new twigs as compared to the checks. Somewhat in contrast, when 80 percent of twig growth of big sagebrush and three-tip sagebrush (*Artemisia tripartita* Rydb.) was removed in 8 months out of the year on the Snake River plains (57), there was some depression of growth at all months of clipping, as compared to nonclipped checks. The greatest depression was from clipping in the active growth period of July when carbohydrates were at their lowest point. It is interesting that sagebrush is probably more sensitive to heavy removal of foliage than most other shrubs. In some places, high removal of herbage has killed sagebrush, and in others it appears that heavy grazing has extended its lifespan.

Curlleaf mountain mahogany, a broadleaf winter evergreen, furnishes protective cover and forage to big game and livestock on large tracts of winter range in the mountain States. On extensive stands, it assumes a semitree form of growth so that most of the twigs and leaves are not available to grazing animals. When Ferguson and Basile (20), and later Thompson (56), cut back the heavy branches of curlleaf shrubs, no new twigs were produced, and all the shrubs died. Most shrubs—including curlleaf's deciduous counterpart, true mountain mahogany—are stimulated by similar treatment. However, Thompson discovered that a fairly good growth on curlleaf was induced from terminal spurs when one or more live limbs were left on the heavy branches. Regrowth was stimulated on the treelike form of the shrub when it was topped in the periods from April 20 to May 10 or from September 10 to 30. Not enough research has been done to determine why topping in other periods resulted in total mortality.

Genetic Phases

Heavy grazing over the past 125 years has reduced, and in some instances, markedly opened closed stands of shrubs and herbs on expansive areas in the West. Other human-related activities such as clearing and fire have had sharper and quicker effect, but the impacts of these have not been so continuous, nor have they affected such large areas.

The opening of closed communities of herbs and shrubs has provided habitats for establishment of new natural combinations of closely related species and ecotypes. Anderson (2, 3) calls this "the hybridization of the habitats."

Over thousands of years, climatic change and the natural erosion associated with it have also created conditions which have changed the structure of vegetation. Cottam (15) found that change from a cooler to a warmer climate, between 7,500 and 4,500 years ago in Utah, affected the structure of oakbrush. In this warm post-pluvial period, Gambel oak (*Quercus gambeli* Nutt.) and turbinella oak (*Q. turbinella* Greene) existed together in north central Utah. In a subsequent cooling period, turbinella oak receded to southern Utah to the warmer temperatures to which it was accustomed, and where it was more at home with its true chaparral associates. However, F₁ hybrids and some backcrosses that survived cooler temperatures show that it was present more than 260 miles north of where it now occurs. In its warmer climate of southern Utah and northern Arizona, where turbinella oak is associated with Gambel oak, similar hybrids and backcrosses are found in abundance, some of them of recent origin. These same crosses have been artificially made and validated by Cottam and his associates. Since established hybrids can spread and maintain themselves by root sprouting, they persist indefinitely. No doubt, some clumps are at least a few thousand years old. Stutz (55) similarly points out the good possibility that cliffrose and antelope bitterbrush were historically together in Montana and Idaho, and hybridizing as they do where they grow together in Utah. Cooling temperatures removed cliffrose, but the introgressed glandular characteristics in its leaves were retained in the more cold-tolerant bitterbrush.

We have seen abundant incidence of polyploidy

and introgressive hybridization between ecotypes. Wherever species of *Cercocarpus* occur together or have been together, the putative hybrids are found. Noteworthy intermediates are seen in leaf size and structure of the shrubs. This has been particularly noted in the hybridization of true mountain mahogany (*Cercocarpus montanus* Raf.), with curlleaf mahogany and littleleaf mahogany (*C. ledifolius* Nutt. var *intricatus* [S. Wats.] M. E. Jones). The hybrid, with fire tolerance transmitted from true mountain mahogany, occurs on fire scars from which curlleaf has been completely lost.

Big sagebrush subspecies with many ecotypes and biotypes present tremendously impressive variation. Rather than eliminate it, we need to select among ecotypes of this shrub for palatability. The differences in palatability are likely related to the chemistry and amount of essential oils in the various ecotypes. A simple two-dimensional phenolic extraction on chromatography paper proved useful for quickly segregating palatable from unpalatable ecotypes (23). While there is little likelihood that phenols making the patterns and colored spots on the paper are responsible for the palatability or the lack of it, excellent association was found between these and observed palatability. We suspect the phenols are indicative of the kinds and amounts of essential oils that are present which do affect palatability. This simple laboratory procedure was successfully utilized to quickly predetermine palatability of sagebrush ecotypes. The technique appears to have usefulness for other species of shrubs. Certainly, it is clear that introgressive hybridization, both sympatric and allopatric, has and is continuing to have a tremendous effect on the gene flow from ecotype to ecotype and from species to species where they are closely related throughout the West because of the openings that exist for establishment of progeny from Mother Nature's experiments.

The centers of diversification and origin of a number of the shrub genera and species are in the West. Consequently, there are more species and ecotypes of shrubs assembled here than probably anywhere else in the world. For this reason alone, there is a great amount of inherent variation in the germ plasm found nowhere else. This, along with habitat openings for establishment, in-

deed maximizes the chances for the creation of new shrubs. I am impressed that this potentially creative aspect is highly active. The fact that a great many natural hybrids between closely related species have been observed gives credence to this (18, 23, 24, 33, 37, 54). Some of these have become fairly well stabilized as in the reported instance of desert bitterbrush (*Purshia glandulosa* Curran) (55). Further successful exploratory hybridization between several closely related species substantiates what has been observed in nature (18).

Consequently, opportunities are abundant for important advances in discovering improved shrubs for a multiplicity of purposes. Not only is there rich opportunity to select from a large assortment of shrubs which nature has provided, but given guidance, the chances are unexcelled for improvement of shrubs through breeding. Indeed, much basic background is lacking in the area of morphogenesis, but the time has arrived for strong impetus in this research.

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MORPHOGENESIS AND MANAGEMENT OF PERENNIAL GRASSES IN AUSTRALIA

By D. M. Calder¹

Abstract

The essence of rangeland management must be to promote plant welfare. This can be done more effectively if we understand the genetic and environmental control of plant growth and development and the effect of utilization by the grazing animal. Perennial grasses play an important role in the rangelands of Australia. This paper discusses the main morphogenetic events in the life of a perennial grass, viz, germination and establishment; quantity and quality of vegetative growth; perennation; and flowering and seed production.

Additional key words: Arid zone grasses; growth and development; mitchell grasses; review; physiological ecology

Introduction

In 1969, C. Wayne Cook (*3*) said "It is recognized that the biological efficiency of the ecosystem is measured by responses of both plants and animals to management. However, once the nutritional requirements of the grazing animal have been provided by varying vegetation types, management becomes largely a matter of plant welfare."

You will find in this generalization, as in most, some points of debate, but the significant phrase in the present context is the last, viz, that management becomes largely a matter of plant welfare. I would go further and say that, because productivity of the ecosystem is largely a matter of the welfare of the primary producers, *management must promote plant welfare*—the condi-

tion of the range depends almost entirely on the condition of the plants which grow on it.

There are, obviously, many different kinds of range environments, but they are all characterized by extended periods which are unfavorable to plant growth. Consequently, plant recovery from heavy grazing is naturally slow; it is, indeed, unpredictable because of the variable nature of the climate. These points draw attention to the vulnerability and the sensitivity of range vegetation and to the basis for their slow recovery. From this it is clear that in the management of rangelands we need to be primarily concerned with plant welfare.

Enlightened management is attainable only if we have a thorough understanding of the ways in which the component species react under the particular conditions of climate, soil, and management to which they are exposed. Unlike the situation in areas of high production, management of rangelands is largely determined by and dependent upon the natural environment. In Australia, at present, it is impractical to change this by irrigation, fertilization, or other similar activities aimed at improving the environment. Since it is not possible to modify the environment to suit the plant, the plant must be adapted to the environment of which grazing is a part. We must, therefore, understand the morphological and physiological basis of plant adaptation as well as the biological limitations to the continued survival of species.

In this discussion, we consider how plant welfare is influenced by environmental conditions of climate, soil, and management in rangeland areas with very different floras and with very different histories. At the outset, I should confess to the paucity of information of Australian origin on this subject, and hence, my contribution will be more general in character and will include state-

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ments of problems and views which I hope will stimulate discussion. These statements will be based largely on the morphogenetic information available from perennial pasture species of the moist temperate regions of the world.

I propose to discuss the different morphological stages in the life cycle of perennial grasses using information which is available for grasses in general. The stages selected for discussion are: germination and establishment; quantity and quality of vegetative growth; perennation; flowering and seed production. In dealing with each of these, I will first outline the process and then discuss, where available, the results of research on Australian rangeland species. Where appropriate, this will be followed by speculation on the implications for adaptation and management.

Perennial Grasses In The Australian Rangelands

Two grassland communities (subformations) are recognized in the rangelands of Australia (9, 11), and these are each dominated by perennial grass species.

Arid Hummock Grassland

The dominant plants in the community belong to the genera *Triodia* and *Plectrachne*. It competes with *Acacia* shrubland as the most extensive community of arid Australia (22.6 percent) (9) and it occurs in both the winter and summer rainfall zones.

The dominant grasses form characteristic hummocks; some (for example, *Triodia longiceps* J. M. Black) extend to 6 m. in diameter and 1.8 m. high (11). Frequently the centers of these hummocks die out, leaving expanding rings of dense tillers. The leaves are generally harsh with pungent tips, and they are highly xeromorphic (1). Arid hummock grassland supports few stock (11) probably because of the extreme leaf xeromorphism and dense, pincushion growth form.

Arid Tussock Grassland

This grassland is much more restricted in its distribution, lying to the north and northeast of the arid zone and well within the summer rainfall areas. In it each plant forms a discrete tus-

sock some 20 cm. in diameter and 50 to 100 cm. tall. Often the ground between the tussocks is bare. There are several species of tussock grasses but nearly all belong to the genus *Astrebla* (mitchell grass) and in most areas few other species occur.

Unlike hummock grassland, the tussock grassland is very productive and has been estimated to support one half the livestock of arid Australia (11), despite the fact that it constitutes less than 10 percent of the rangeland area. Growth of these grasses is rapid following rain, and the grasses can be utilized for several months during the winter as standing hay. Some research on the growth and development of the mitchell grasses has recently been published (7) and has demonstrated the value of morphogenetic research as a basis from which sound management policies can be developed.

There are numerous perennial grasses which grow in the shrub and woodland communities of the Australian arid zone. Some of these provide fodder for grazing animals (9, 11). For example, in the northern, summer rainfall woodlands—which are dominated by *Eucalyptus* spp.—the genera of both the hummock and tussock grasslands are found in addition to species of *Heteropogon*, *Chrysopogon*, *Aristida*, *Sorghum*, *Themeda*, and *Setaria*. In the southern woodlands, characterized by erratic winter rainfall and dominated by eucalypts, *Callitris*, and *Casuarina*, the most important perennial grass genera are *Aristida*, *Stipa*, *Chloris*, *Neurachne*, *Eragrostis*, and *Enneapogon* with species of *Danthonia* and *Poa* growing where the annual rainfall rises to between 25 and 50 cm. (9).

In the saltbush shrub steppes, which achieve their maximum development in the southern, winter rainfall areas, *Danthonia*, *Stipa*, *Eragrostis*, and *Aristida* provide a winter and spring ground cover between the shrubs, provided the winter rains have been adequate. Where overgrazing and past cultivation have removed or greatly weakened the shrub cover, the land may become completely dominated by *Stipa*.

Eucalypt shrublands of the north are closely related to the summer rainfall woodlands described earlier, and the perennial grass genera found there are much the same. The *Acacia* shrublands form a different community and are widespread in the arid and semiarid zones occupying

almost 30 percent of Australia's arid lands. Their grass ground cover is well developed, in the north being dominated by *Astrelba* and in the south by *Danthonia*, *Enneapogon*, *Stipa*, and *Eragrostis*.

This short survey of the genera of Australian range grasses emphasizes the major division into summer rainfall northern types and winter rainfall southern types. Only the mitchell grasses form a grassland community of considerable economic importance. With the exception of the hummock grasses, the remaining genera are associated with woodland or shrubland communities and in these they provide important contributions to the fodder yield.

Germination And Establishment

Germination of the grass caryopsis involves first the imbibition of water, and this is followed by growth of the coleorhiza, a sheath of cells surrounding the radicle. The coleorhiza frequently develops cell outgrowths resembling root hairs, and, after a day or so, the radicle pushes through this sheath and down into the soil. Soon after emergence of the radicle, the coleoptile appears and through this grows the first leaf. With the appearance of this leaf the plant is potentially self supporting, and further growth ensures complete establishment.

The earliest stage of germination, the uptake of water, is reversible but once the morphogenetic events of root and shoot growth have started the plant is committed to growth and, at this stage, is particularly vulnerable to environmental extremes, especially drought.² Because of this vulnerability of the seedling, natural selection favors those species which germinate only after significant rains, that is, those species which have evolved germination control mechanisms.

Literature on germination and its control has grown massively over a number of decades. Certain conditions of moisture, temperature, aeration, and light are essential for the germination process, but even when these are provided and conditions are optimal, growth may not ensue be-

cause the seed is dormant (12). Several mechanisms by which dormancy can be achieved are given below.

1. Impermeable seed coats. These may be impermeable to water, oxygen, or both; germination is prevented until they are altered either biologically or mechanically.

2. Immature embryo. In these the embryo must undergo further growth and development after imbibition before germination appears.

3. Dry storage after-ripening. Fresh seed may fail to germinate until after a period of storage at ambient temperatures. This after-ripening is common in grasses and could be associated with gradual changes in the relative proportions of growth promoters and inhibitors.

4. Specific environmental requirement. Some seeds need prechilling or exposure to light before germination can take place. These conditions are necessary as a triggering mechanism to promote germination.

Seed dormancy exhibited by many Australian range grasses has been a deterrent to further work on their growth and development. Unpublished investigations³ on two species of *Stipa* demonstrate the presence of a growth inhibitor in the fresh seeds with properties similar to synthetic abscisic acid. On storage at room temperatures (between 20° and 25° C.), the levels of this inhibitor decline, and there is an associated increase of a growth promoter. In these two species, there appears to be a control mechanism which is based on the balance of growth regulators, both promoters and inhibitors. A water leachate from fresh seeds of these plants contains a strong growth inhibitor. Under natural conditions it is possible that germination control is exercised through a leaching process, inhibitor levels only being reduced to a low enough level after significant rains—rains which can support the continued growth necessary for full establishment. *Themeda australis* (R. Br.) Stapf. also contains an inhibitor in the fresh seed, but this has not been identified.

Early work on *Astrelba lappacea* (Lindl.) Domin. indicated that it also has a period of dor-

² During discussion, attention was drawn to the fact that some North American range grasses, for example, the introduced *Agropyron desertorum* (Fisch.) Schult., are capable of surviving dessication even after emergence of the radicle.

³ Lawlor, J., and Calder, D. M. Unpublished data on germination of *Stipa* spp. and *Themeda australis* (R. Br.) Stapf. 1971.

mancy after harvest (9). The percentage germination was low shortly after harvest and increased to a peak after one year. Also in this study it was shown that light conditions did not affect percentage germination. Working on four *Astrelba* species Jozwik and others (8) showed that there was little germination below 22° C. or above 38° C., and that, although a few seeds germinated rapidly at 38° (within 13 hours), the highest overall percentage germination was at the lower end of the temperature range. These germination tests were undertaken on older seeds which had presumably passed any postharvest dormancy. It is possible that the higher percentage germination at lower temperatures is a general phenomenon of warm and hot rangeland species. High-temperature inhibition of germination has a possible selective advantage in that it prevents germination in the hot season when there is a high evapotranspiration potential.

Interest in the germination of range grasses lies in the control mechanisms which have evolved and the way these fit the plants to the adverse environments. There is also a practical interest in germination control as a means of propagation for experimental work on the control of growth and development. A major problem in any experimental work with natural populations, particularly of range species, is the problem of low and erratic germination. From the standpoint of influencing range management or promoting plant welfare, germination is of little significance.

The period of establishment has, I believe, been completely ignored in studies on Australian rangeland perennial grasses. What characters do these plants possess which enable the vulnerable seedling to survive? Is root growth and penetration exceptionally rapid? Is leaf growth delayed? Information of this type is available for pasture grasses and, if available for range grasses, would be a major contribution to our understanding of the physiological and morphological basis of adaptation.

Vegetative Growth

In essence the grass seedling consists of an abbreviated axis giving rise to leaves, alternately on each side, as well as adventitious roots. As the

seedling develops, the axillary buds grow into tillers which, with their own adventitious root system, may ultimately become independent of the parent plant. Perennial herbage grasses achieve their perenniality through the continued production of tillers which in themselves may be quite short lived; they rarely survive more than 18 months, although in some perennial range grasses, tillers may survive for several years. In that they are groups of annual or biennial tillers, perennial grasses are morphologically and physiologically different from other perennial plants.

The form of the perennial grass is determined largely by the growth of the tillers. Those whose tillers grow within the sheath of the subtending leaf develop a tussock or bunchgrass form, while those whose tillers grow out through the sheath have a more lax form. In some grasses, underground rhizomes are produced and vertical leafy shoots grow from these. The life of a tiller ends normally with the production of the terminal inflorescence, although there is ample evidence to show that this is not the fate of all tillers. Many succumb to environmental or physiological conditions which cause their earlier death.

Herbage grasses and cereals have been used extensively in the study of both quantitative and qualitative growth, and it is fortunate that we have this information as a background for work on rangeland species. Much is known about the nature of tiller and root growth, the effect of the environment on morphogenesis including flowering and dormancy, and the effect of grazing and trampling on recovery and survival. In Australia at least, it is time that this type of investigation was extended to include the perennial range grasses.

A notable exception to the general lack of information on the growth of Australian range grasses is the recent work of Jozwik (7), Jozwik and others (8) Jozwik (unpublished),⁴ and Jozwik and others (unpublished),⁵ on the four species of *Astrelba*: *A. pectinata* (Lindl.) F. Muell., *A. lappacea* (Lindl.), *A. elymoides* Domin F. Muell., and *A. squarrosa* C. E. Hubbard.

⁴ F. X. Jozwik. Unpublished on *Astrelba* spp. 1970.

⁵ F. X. Jozwik and A. O. Nicholls. Growth and Development of *Astrelba pectinata* (Lindl.) F. Muell. ex Benth. under field conditions. Unpublished manuscript. 1971.

In a field study of *A. pectinata*⁵ at two sites in the summer rainfall region of northern Australia (rainfall was 267 mm. and 371 mm.), it was shown that previous seasons' tillers sprouted new shoots a few days after the first effective rain. The old vertical culms had from 5 to 9 nodes from which new shoots grew, with the lower nodes providing the stronger shoots. The maximum number of new tillers was reached some 20 to 30 days after the rain and then declined, perhaps as a result of competition. The underground rhizomes generally gave rise somewhat later to strong, sparingly branched, vertical shoots which eventually became the tallest tillers of all. Inflorescences were produced between 28 and 32 days after the start of growth.

The great value of this study as a contribution toward determining management policy is the finding that the base of previous season's vertical shoots are the sites for new tiller production and the bulk of the current season's growth. Grazing of *A. pectinata*, both during the short growth period and the ensuing dormant period, should aim to leave the lowermost part of the new vertical tillers from which the bulk of forage will be produced in the next growth period.

Controlled environment studies of the four *Astrebla* species (7) are the most significant of their type to have been undertaken on Australian arid zone perennial grasses. The studies showed that tiller number was not influenced significantly by photoperiods between 9 and 15 hours, although plants in the shorter photoperiods frequently had more tillers after 5 weeks of growth. Temperature generally had significant effects, with the optimum about 28°/23° C., although the differences tended to decline after 8 weeks. Species also differed from one another in their tillering potential. *A. lappacea* had the most tillers, followed by *A. pectinata*, *A. elymoides*, and *A. squarosa*. Different strains of *A. pectinata* varied significantly in tillering potentials.

Elongation of tillers was not significantly affected by photoperiod but, in general, elongation increased with temperature. Not all species reacted in the same way to temperature, and the time of rapid elongation was different in the different species. *A. squarosa* was generally short while *A. elymoides* was tall.

Axillary tiller production was not influenced

by photoperiod, but, again, temperature had a marked effect on the number of such tillers produced—the regime of 28°/23° C. stimulating the greatest number of tillers. Higher temperature also produced the greatest number of leaves per tiller.

The investigations on *Astrebla*, here reported in some detail, have provided some basic descriptive data on this very important genus. However, they raise a number of questions and point to the need for further physiological and phenological research with *Astrebla* and other range grasses. The three areas of research which require particular attention are (1), studies on dry weight accumulation and distribution; (2), the reaction of plants to defoliation; and (3), carbohydrate reserves and their effect on regrowth.

Williams (14), in an account of the physiology of wheat plant growth, described total dry weight changes with time as well as the dry weight changes of the component parts viz roots, stem, leaf sheath and leaves. With these data he was able to determine distribution indices, derived by expressing the increment in dry weight of the component part (root, stem, and so forth) for any harvest interval as a percentage of the total dry weight gain for the same interval. In Williams' paper, figure 8 shows that about 50 percent of plant assimilate was used in root growth over the first few days of germination. Most of this was, in fact, derived from the seed. By the 10th day, 75 percent of assimilate, an increasing proportion of which came from current photosynthesis, was used for leaf growth, and then this proportion gradually fell. The methods used by Williams have great potential for helping us to understand the nature of adaptation of range grasses. For instance, it would be valuable to determine the distribution indices of these grasses when grown at different temperatures or when subjected to different degrees of water stress. Information of this sort would help us determine the extent to which dry weight distribution is under developmental and environmental control. One might expect that the distribution index to root would be higher for a longer period in range grasses when compared with wheat, and leaves may never reach as high as 75 percent. An investigation along these lines would indicate the basic growth characteristics of the spe-

cies and the influence that environment has on grass morphology. It would reveal morphological aspects of adaptation.

Morphogenetic responses to defoliation are known for many herbage grasses, but little is known of range species. For instance, what is the effect of defoliation on *Astrelba*? Does it cause a cessation of root growth or a dieback of roots? Are all reserves mobilized to restore the lost leaf area? Is tillering affected, and if so, in what way? Is flowering promoted? These questions are easy to ask, but the answers are needed in order to determine the best management practices for promoting plant welfare.

Finally, in regard to carbohydrate reserves and regrowth, Whalley and Davidson (13) showed that in some summer-growing perennial grasses of semiarid Australia, available carbohydrates in the base of plants declined with the initial growth after rain and increased as the soil dried out so that the plant entered the dry period with carbohydrate reserves comparable to that of winter-dormant herbage grasses at the start of winter. Haydon (6) showed that both starch and sugars remain at a low level (2.0 percent and 1.1 percent, respectively) until flowering in *Astrelba lappacea* and then, in a 30-day period prior to drying off, these carbohydrates increase to 9.0 percent for starch and 2.0 percent for sugars. There appears to be no information available on the pattern of carbohydrate reserves in range grasses which have been grazed. In herbage grasses of temperate regions, reserves appear to be mobilized for the rapid production of new leaf (4).

The importance of morphogenetic information in determining management techniques appears to have fairly wide acceptance (3). The questions about plant welfare emerge clearly. Should the management system of vegetative plants allow for the development of a high leaf area during favorable growth periods in order to maximize productivity which can be utilized by the grazing animal? If this is desirable, then more intensive stock management with rotational grazing will be necessary. What effects would such a management procedure have on transpirational water loss? Does this management allow for subsequent recovery of the plants grazed during the dry season? None of these questions take into account

the added expense of more intensive management.

Perennation

Probably the main justification for dealing with perennial range grasses separately from the annuals is the capacity of perennials to survive extended periods of drought as established plants and to resume growth when favorable conditions return. Despite the considerable physiological and morphogenetic interest in these growth characteristics of perennial range grasses, we have little direct evidence on them in Australia.

Wareing (12) draws the distinction between imposed dormancy or quiescence and innate dormancy. In imposed dormancy, plant growth is arrested as a result of unfavorable environmental conditions—such as drought or excessively high temperatures—and resumes immediately on the return of favorable conditions. In innate dormancy, growth fails to occur even though external conditions appear to be favorable; growth resumes only after a certain amount of time passes or after a particular environmental or genetic trigger is released.

Jozwik⁶ and Jozwik and others (8) indicated the possibility that *Astrelba* is capable of imposed dormancy, although specific studies are needed to confirm this. In terms of plant adaptation, imposed dormancy is a reaction which fits plants to the arid rangeland environment since it allows them to exploit favorable conditions whenever they occur. However, this system of dormancy control carries the risk of growth, stimulated by rainfall, inadequate to allow the completion of either seed formation or resting bud formation.

The physiology of drought and high-temperature tolerance is worthy of investigation in this genus and in others because the perennating organs are frequently exposed to considerable water tension as well as very high temperatures.

With regard to the flowering of *Astrelba*, it would be interesting to know at what stage differentiation of the inflorescence takes place. Since inflorescences emerge 28 to 32 days after the first rains,⁷ initiation may occur at the end of the previous growth period or even during the

⁶ See footnote 4, p. 84.

⁷ See footnote 5, p. 84.

dormant period; if it occurred later than this, it could be inferred that the inflorescence has a very rapid rate of growth and differentiation.

Flowering

There have been many investigations into the control of flowering in grasses and, in general, the morphogenetic events associated with flowering are similar throughout the family. The apical meristem of the tiller undergoes a transformation and becomes completely involved with the production of the inflorescence which is thus terminal. After flowering, the tiller normally dies, although the plant as a whole might continue through the production of a new crop of tillers at the base of each flowering culm. There are, indeed, two ways in which a grass plant can achieve perenniality. On the one hand, not all the tillers might become reproductive at the same time—this would appear to be the situation in *Astrebla* where underground rhizomes with many potential meristematic sites provide a store of future tillers. On the other hand, axillary tillers from the base of flowering culms may grow out after flowering as a new crop of vegetative tillers.

It is quite clear from the review of Evans (5) that there are many forms of environmental response in the Gramineae. Some require long days, others short days, still others require other specific photoperiodic conditions for flowering, and a further group are insensitive to photoperiod. Similarly, some grasses have an inductive need for cold or short days before they are capable of responding to photoperiod. Still others may need to undergo a certain amount of vegetative growth before they will respond to any conditions which favor flowering (2). From all that is known, it is clear that while the morphogenetic events of flowering may be rather similar in all grasses, the environmental conditions which stimulate the flowering are many and appear to operate at different points of a pathway or even on different pathways leading to the final floral stimulus.

Jozwik (7), in his work on *Astrebla*, sheds little light on the environmental control of flowering in the genus except to show that, in general, the inflorescences emerged more rapidly

at shorter photoperiods (10 hours compared with 12 or 14 hours). He concludes that photoperiod plays a significant part in the development of inflorescences but appears to have little effect on the initiation of floral apices. Both field and laboratory experiments in which the apices were dissected would help to answer the questions posed by these results.

In discussing the results, Jozwik (7) claims that close regulation of flowering by photoperiod would be a distinct disadvantage in the Mitchell grasses. Moisture is the main climatic factor limiting their growth. Although growing periods commonly occur within a definite season, the date of onset of rain varies widely from year to year. In addition, adequate rainfalls can occur at any time of the year, and field observations suggest that flowering can take place at these times. Thus, it seems that selection has favored nonspecific flowering requirements just as it has favored nonspecific dormancy requirements, allowing the plant to take full advantage of favorable conditions when they occur. *Astrebla* appears to have an exploitive physiology and this could be the case for many of the perennial grasses of the Australian arid and semiarid areas.

Such a conclusion may not apply to all grasses. Some preliminary work we have undertaken on the control of flowering in *Danthonia caespitosa* Gandich. from the southern, predominantly winter-rainfall areas, suggests that a period of water stress acts as an inductive stimulus to flowering in long photoperiods. It is possible that such a response is linked with abscisic acid production. Like many grasses, *Danthonia* flowering is reduced by exposure to very high temperatures. This is a feature of likely adaptive significance in that it reduces seed formation in the hottest months of the year and protects the plant from the physiological strain of inflorescence and seed production at a time of year when water may be limited.

Conclusion

The major morphogenetic events which have been discussed briefly in this review are all relevant to understanding and promoting plant welfare which, I propose, is basic to the productivity and well-being of the range. It should be clear

that, while there is considerable information on the physiological and morphogenetic processes as a whole, we have little specific knowledge on Australian range grasses. There is ample scope here for research and the application of research findings.

In my view, the main demands for such research do not come from the need for increased productivity, but from the need for improving the condition of the range soil and vegetation. This is a matter of environmental protection, conservation, and promotion of landscape stability. In Australia, we are fortunate that a reasonable proportion of the rangeland is not badly degraded; nevertheless, improved management is urgently needed to stem the processes of degradation of the natural vegetation which in some areas are well advanced. This needs to be done while maintaining or improving existing productivity levels and should be based on a better understanding of the growth and development of range plants.

Astrebla is only one grass among many. The study of its biology and autecology has helped in formulating management practices in the regions where it dominates. We should be able to discuss with equal confidence the work on *Danthonia*, *Stipa*, *Eragrostis*, and other significant perennial grass species and, indeed, many other range plants.

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MORPHOGENESIS AND MANAGEMENT OF PERENNIAL GRASSES IN THE UNITED STATES

By D. N. Hyder¹

Abstract

Elevation of root and shoot primordia increases the susceptibility of perennial grasses to unfavorable conditions and treatments. All grass seedlings may exhibit some elevation of crowns, but elongation of the sub-coleoptile internode (mesocotyl) typically places the crown near the soil surface. Problems in seedling establishment and expansion by tillering might be solved by burying the crowns soon after emergence. The process of tillering from axillary buds on the crown can elevate successive tiller crowns and eventually can result in dead centers. Excessive elevation of crowns through the process of tillering might be prevented by mechanical or grazing treatments. Grasses have culmed or culmless vegetative shoots, some of which become reproductive. The time and amount of elevation of shoot apices and inflorescences affects resistance to grazing and the leaf replacement potential after defoliation. Thus, strategies for grazing management should consider morphogenetic characteristics.

Additional key words: Grass seedling morphology; vegetative shoot morphology

Introduction

Morphogenesis is defined as the structural changes during the development of an organism. These structural changes of plants suggest management practices and sometimes create management problems. Nevertheless, the subject of morphogenesis, as it relates to management, is scarcely developed beyond its importance in seed production. My objective is to describe some forms

of growth pertinent to grass management, particularly the ways in which the elevation of root and shoot primordia influences the susceptibility of perennial grasses to unfavorable conditions and treatments and affects the capacity of grasses for production of adventitious roots and leaves which are critically essential for plant survival and growth.

Root Morphogenesis

The grass root system consists of seminal (seed) roots and adventitious roots. The seminal-root system typically consists of one to five roots—the primary root (radicle) and two pairs of lateral roots, which arise in the same plane from the scutellar node. The scutellum, located adjacent to the endosperm of the seed, is the cotyledon (4). In addition, a single root may arise opposite the scutellum (4, 18). All seminal roots are slender and branched, and usually die in a few months (40).

The adventitious-root system consists of whorls of roots arising from the coleoptilar node and the nodes of shoots, and sometimes from culm internodes (4). Secondary shoots (tillers) are rooted less substantially than the seminal (primary) shoot, because they lack the seminal roots and their adventitious whorls consist of fewer roots (18). This rooting deficiency of tillers, among other factors, may cause declining yields of a seeded stand in the first two or three years. Yields of seeded stands on semiarid rangeland typically reach a maximum in one to three years. Yields of seeded stands on semiarid rangeland (24). Breeding and selection programs should include, among other things, emphasis on superior rooting characteristics, and management practices should be designed to minimize undesirable rooting phenomena.

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Since adventitious roots arise on the shoots, morphogenetic characteristics that cause excessive elevation of shoot primordia also may cause excessive elevation of adventitious-root primordia. Some of the important phenomena will be included in the topics on seedling morphogenesis and shoot morphogenesis.

Seedling Morphogenesis

Morphological Types Of Seedlings

For management purposes, we should recognize two types of grass seedlings (fig. 1): Type A typically has an elongated sub-coleoptile internode and a short coleoptile; whereas, Type B has a long coleoptile and no elongation in the sub-coleoptile internode. These seedling types elevate root and shoot primordia in different ways (32, 35, 36).

The terms mesocotyl and epicotyl have been repudiated from the terminology of parts of grass seedlings (4). Consequently, I call the first internode of the grass seedling (located below the divergence of the coleoptile) a sub-coleoptile internode, and the second internode (located above the divergence of, and inside, the coleoptile) an intra-coleoptile internode.

The coleoptile is the structure of grasses adapted specifically for seedling emergence. It protects the plumule bud within it while forcing its way upward through the soil. The seed of species having very short coleoptiles would need to be planted so shallow that they would be susceptible to the hazards of severe environmental fluctuations near the soil surface, unless the seedlings exhibited the characteristic of elongated sub-coleoptile internode. Thus, the reach of the coleoptile above planting depth is the total length

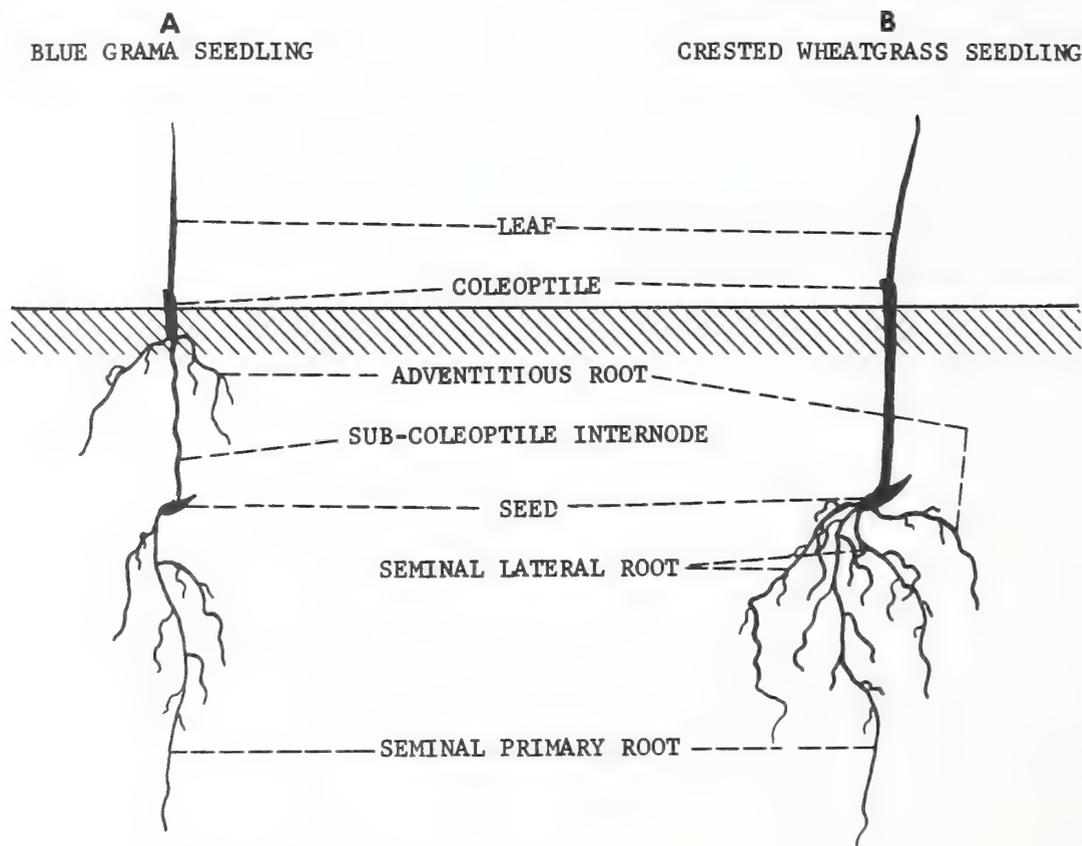


FIGURE 1.—Two types of grass seedlings: Type A, the blue grama seedling, has an elongated sub-coleoptile internode and a short coleoptile; and Type B, the crested wheatgrass seedling, lacks the elongated sub-coleoptile internode but has a long coleoptile.

of sub-coleoptile internode and coleoptile for Type A grass seedlings and that of the coleoptile alone for Type B seedlings.

Foliage leaves are poorly adapted to force a way upward through the soil above the reach of the coleoptile, because they have a long, soft region of meristematic tissue at the base. This leaf intercalary meristem kinks when the leaf blade encounters much resistance (25). By contrast, the narrow band of meristematic tissue located at the upper end of the sub-coleoptile internode (4) is well adapted to pushing short coleoptiles through the soil.

Elongation of the sub-coleoptile internode elevates the coleoptilar and higher nodes, from which adventitious roots develop. In short, the depth from soil surface to origin of adventitious roots is determined largely by the length of the coleoptile. Short coleoptiles place the origin of adventitious roots very near the soil surface (11) where they are susceptible to the hazards of extreme variations in microclimatic conditions (33). For example, blue grama (*Bouteloua gracilis* (H.B.K.) Lag.) initiates adventitious roots at an average depth of 2 mm. below the soil surface (25). Since Type B grass seedlings do not have elongated sub-coleoptile internodes, the lowermost adventitious roots may arise near planting depth from or near the coleoptilar node.

Both types of grass seedlings exhibit some typical variations (fig. 2). In fact Hoshikawa (21) defines 6 types of grass seedlings in terms of the presence or absence of (a) sub-coleoptile internode, (b) seminal lateral roots, and (c) adventitious roots from the sub-coleoptile internode. Adventitious roots commonly arise from the sub-coleoptile internode in species of *Panicum* and *Andropogon*, which have Type A seedlings. These internodal adventitious roots are adaptively advantageous for seedling survival because they arise at various depths in the soil. By contrast, blue grama depends on a single seminal root of short longevity (34, 40), and adventitious roots from the nodes of the coleoptile and plumule. Successful extension of adventitious roots from the crown of the primary shoot of blue grama requires 3 or 4 consecutive days of wet, cloudy weather when the seedlings are 3 to 7 weeks old. A typical variation in Type B seedlings is elongation in the intra-coleoptile internode (fig. 2),

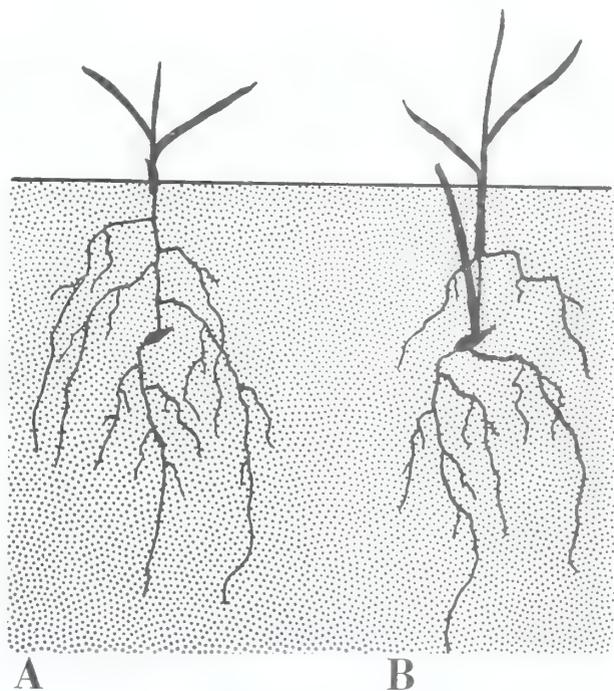


FIGURE 2.—Typical variations within seedling types: *A*, a Type A seedling has adventitious roots arising from the sub-coleoptile internode (left); *B*, a Type B seedling has an elongated intracoleoptile internode.

which increases in length with increase in planting depth and soil temperature (29). The first tiller may, nevertheless, arise from the coleoptilar node and establish its crown below the crown of the primary shoot (37). Intra-coleoptile internode elongation may include more than one internode. Consequently, whorls of adventitious roots can be found at two or more depths in the soil.

Elongation in either the sub-coleoptile or intra-coleoptile internode elevates the crown of the primary shoot above planting depth. The crown, a section of stem base in which the nodes are not appreciably separated by internode elongation, is the source of both tillers and adventitious roots. Therefore, its depth of placement in the soil is important to development of the plant (38). Vigorous tillering cannot continue unless each successive tiller can establish its own set of adventitious roots. The potential number of adventitious roots per tiller depends on the number of roots per whorl and the number of nodes in the crown.

Seeding Practices

Grass seedling morphogenesis directs attention to seeding practices that are important to germination, emergence, and establishment. Germination tends to increase with planting depth, depending on moisture supply and aeration in species which do not require light for germination. However, to assure good emergence, planting depth should not exceed the normal reach of the coleoptile grown in dark.

Plant establishment, excluding the effect of disease, is primarily a matter of the extension of adventitious roots. The urgency of adventitious roots depends on the number and longevity of seminal roots, which may remain active for several months in some species and for less than two months in others (40). The placement of crowns near the soil surface in the process of emergence may preclude the growth of adventitious roots at the crown and eliminate any chance of survival in semiarid conditions (25). Type A seedlings commonly place the crowns near the soil surface. In fact, the crowns can be elevated beyond the soil surface to near the surface of a sawdust or other opaque mulch layer. Subsequently, deterioration of the mulch can leave the crowns completely exposed.

Since excessive elevation of the crowns is undesirable, mulch layers applied immediately after seeding should be very shallow in depth or should admit enough light to the soil surface to stop the crowns below the soil surface. Mulching and cultivating practices are not common in grass seeding. But we surely have missed some important points of emphasis by failing to take a good look at seedling morphogenesis. Very thin moisture barriers on the soil surface, such as an asphalt emulsion mulch (3), might be very helpful in obtaining germination and emergence without excessive elevation of crowns. The thin moisture-barrier type mulch also would contribute to the initial extension of adventitious roots, but other practices should be evaluated. The natural elevation of crowns by some species exposes the seedlings to harsh conditions near the soil surface and causes high seedling mortalities. Perhaps most of all, we need cultivating equipment and experimental results on the effects of burying the crowns soon after emergence. Any mulching

applied after emergence might be beneficial, but cultivation is emphasized because soil is the most economical and durable material. Where establishment of grasses is difficult, such cultivation might be essential to good seeding success. Where establishment is not difficult, cultivation might nevertheless be beneficial to plant development and production because the process of tillering requires continuously favorable conditions for the extension of adventitious roots from the crowns of new tillers.

Shoot Morphogenesis

The Shoot Apex

The grass shoot apex is a prime object in management because it determines the course of subsequent growth and development. It can be destroyed, or it can be protected and influenced by management practices.

The shoot apex consists of an apical cone with an apical meristem at the summit. Cells at the extreme tip constitute the promeristem, from which the meristems giving rise to fundamental tissues are derived (14). Ridges arising alternately below the summit are the first external evidence of differentiation—that is, the formation of leaf primordia. A leaf primordium is at first a slight horizontal ridge that quickly encircles the apical cone. Three to six leaf primordia are common; but leaf formation lags to such an extent in some species that the number of leaf primordia gradually increases (14). As leaf growth begins, a leaf primordium expands very rapidly to form a shoulder below the shoot apex. Then the leaf arises vertically from the shoulder to enclose the shoot apex. Leaf growth is at first apical and marginal; however, cell division is restricted to the base of the leaf at an early time. Before the blade attains much length, a collar develops and separates the intercalary meristems of blade and sheath (13). Meristematic specialization proceeds to the interior of the axis where the intercalary meristem of the internode forms above the nodal plate with potential for an axillary bud.

At the time of transition to reproductive phase, the shoot apex elongates very rapidly and establishes a large number of leaf primordia (8, 14). Spikelet primordia, appearing as protrusions in

the axils of leaf primordia, often appear first at about the middle of the elongated shoot apex. Further differentiation proceeds upward and downward (34). The appearance of a spikelet primordium at the lowermost leaf ridge terminates the potential for initiation of new leaves on that shoot.

Environmental conditions before and during the time of floral induction determine the number or proportion of shoot apices that become reproductive, within genetic limitations. Environmental conditions during the time of floral differentiation and growth affect the size of the inflorescence—the number of spikelets. And environmental conditions during the time of anthesis and seed formation affect the number and size of caryopses. Since the shoot apex and its production of vegetative and reproductive structures is subject to the effects of management practices, the genetic limitations and environmental requirements of plants should be known. Perhaps, most of all, one should know the time of floral induction and floral differentiation (12, 15, 17, 19, 26, 28, 30).

Floral induction is interpreted as a biochemical process that may require a cold pretreatment (vernalization), a certain day length (long day or short day), and a certain sequence of day lengths (long before short or vice versa). On the other hand, some species flower independently of day length. Effects of day length are modified by temperature, and the entire process requires a minimal amount of vegetative development. Mature leaves are needed to feed the process, because assimilates are not exported from immature leaves (41). Thus, poor vegetative development or excessive defoliation at the season of floral induction will reduce reproductive development in most perennial grasses. Fertilization and other practices should be scheduled to coincide with a particular phase of development to attain described results.

The Phytomer

A shoot is built up by a succession of segments or phyton-units called phytomers (13, 16, 39). A phytomer includes the sequence of structures produced by the meristematic tissues contiguous to a leaf primordium. From top to bottom, a phytomer consists of blade, sheath, internode,

axillary bud (or potential thereof), and node; however, the node often is omitted from the description (13, 39). The potential for adventitious roots generally takes place near the nodal plate.

The elongation of blade, sheath, and internode appears predominantly as a 1, 2, 3 sequence; however, the internode may remain very short. One leaf follows closely, and is enclosed by the one immediately older. Thus, the process of vegetative growth is regular and indeterminate. An individual phytomer exhibits a determinate type of vegetative growth. If the blade is cut when immature, the undamaged intercalary meristem at the base continues to differentiate blade tissue. The leaf tip cannot rejuvenate. If a mature blade is removed, subsequent growth will be sheath and culm internode. However, the sheath and internode may remain unusually short when the blade of that phytomer is removed (1).

The growth of grass shoots can be defined and graphed, phytomer by phytomer, to illustrate rhythm of growth within and among phytomers as affected by environmental conditions or treatments (22).

The Crown

The term crown is used to mean any section of stem base in which two or more nodes remain close together. It includes the vertical section of a terminal rhizome, which has no special name; the proaxis of timothy (11); and, in fact, the basal part of essentially all grass shoots. The number of nodes in the crown indicates the number of basal leaves produced and the potential number of tillers and adventitious roots. Both the size and number of nodes in the crown determine the degree of elevation of tiller crowns therefrom. Where crowns are large, successive tiller crowns can be initiated at a much elevated position. Some species literally grow themselves out of the soil, eventually leaving dead centers. The most obvious example that I have seen is that of weeping lovegrass (*Eragrostis curvula* (Schrad.) Nees), but many species exhibit the same phenomena in a more subtle way. Tiller crowns may develop entirely above the soil surface. A deep accumulation of litter or dead stubble can contribute to crown elevation and can preclude the development of adventitious

roots and subsequent tillering from that portion. Furthermore, excessive crown elevation exposes plants to great damage from fire and grazing.

Russian wildrye (*Elymus junceus* Fisch.) exhibits an interesting elevation of crowns in late summer or fall. A vegetative shoot may be elevated a few centimeters by elongation of a stolon-like internode (27). This elevation exposes the shoot apices and rudimentary inflorescences to winter damage. However, close grazing in late summer and fall prevents the elevation and increases seed production.

We have yet to develop appropriate management practices to counter crown elevation, whether by seedlings or established plants. However, crown elevation by established grasses might be prevented or reduced by periodic burning, rotary hoeing, rotary beating, trampling and grazing by livestock, or other treatment. Both the frequency and season of treatment would be important. Treatment to prevent tillering from higher nodes and permit tillering from the lower nodes of the crown should increase tolerance for extreme weather conditions and minimize decline in productivity when considered over a number of years. The summer slump in rate of growth, also, might be reduced by forcing tillers to arise from greater depths in the soil.

The Vegetative Shoots

Rhizomes and stolons.—Nonphototropic branching at the base of a shoot produces stolons above ground or rhizomes below ground. Rhizomes provide advantages over stolons with reference to the elevation of root and shoot primordia. On the other hand, stolons contribute assimilates for their own growth more readily than rhizomes. Any branch depends on the parent shoot until it has mature leaves and adventitious roots (42).

The initiation of nonphototropic branches from axillary buds appears identical to that of phototropic branches (tillers). However, long days of summer generally favor rhizome and stolon growth, while tillers tend to arise in the spring and fall (13). Stolons generally are continuous, forming roots and tillers as they go. Rhizomes may be continuous or terminal. In the terminal type, the rhizome turns upward in the autumn

to become phototropic. However, defoliation in the summer can cause terminal rhizomes to turn upward and produce aerial shoots (1). In the truest sense, both stolons and rhizomes are vegetatively indeterminate. The transition from nonphototropic to phototropic growth by a terminal rhizome is, nevertheless, a continuation of growth by a single shoot apex.

Culmless vegetative shoots.—Phototropic vegetative shoots, also are of two types—culmless and culmed (22). Turfgrasses have been defined as perennial species capable of forming a dense sod (42). One other condition might be included; namely, they should produce culmless vegetative shoots. In culmless vegetative shoots, the persistent basal position of shoot apices and leaf intercalary meristems provides protection for the sources of further leaf expansion and of leaf replacement after defoliation. Culmless vegetative shoots are well adapted to frequent mowing and grazing. Leaf growth stops during unfavorable conditions; but cell division and expansion resumes in both apical and intercalary meristems upon the resumption of favorable conditions. Consequently, dead leaf tips are common on spring growth, and may be exhibited with any new surge of growth when exerted portions of immature leaves die back during a period of unfavorable conditions. Succession of the shoot apex to reproductive status, or death by any cause, terminates culmless vegetative shoots. Otherwise, they remain active and indeterminate in producing leaf tissue. Consequently, they cannot be called annual or biennial structures.

Culmed vegetative shoots.—By contrast, culmed vegetative shoots are characteristically annual structures, dying back to the base after the season of growth. The culmed type is at first culmless because internode elongation generally is much delayed compared to leaf growth. Subsequently, internode elongation elevates the shoot apex and leaf intercalary meristems as well. Cutting below the rise of the shoot apex stops leaf expansion and prevents leaf replacement except by the slower process of tillering from axillary buds of the crown.

The degree and timing of shoot apex elevation by culmed vegetative shoots affects resistance (tolerance) to grazing (5, 6), and the leaf replacement potential after defoliation (21). Any

harvest that removes a high proportion of shoot apices in early stages of culm elongation seriously reduces herbage production. Consequently, culmed vegetative shoots are better adapted to a periodic harvest, scheduled to coincide with advanced stages of growth when the axillary buds are better prepared to initiate new tillers. Under appropriate harvest regimes, grasses with culmed vegetative shoots tend to be more productive, but perhaps somewhat less nutritious, than those with culmless vegetative shoots. Additional consideration, however, must be given to the proportion of shoots becoming reproductive.

Reproductive shoots.—Reproductive shoots, also, begin growth in the form of culmless vegetative shoots. Depending on the fulfillment of minimal vegetative development and essential environmental conditions, some shoot apices differentiate to reproductive status. The percentage of shoots becoming reproductive is relevant to grass management because (a) both herbage and seed production tend to increase with the percentage, (b) forage quality and resistance to grazing tend to decrease with increase in the percentage, and (c) the growth form of reproductive shoots is better adapted to periodic harvest, after relatively long periods of growth, than to frequent harvest or continuous grazing. The reproductive-shoot percentage varies greatly among species, and from year to year and place to place within a species (5, 24). For many species, a thin stand has a higher percentage of reproductive shoots than a thick stand; and nitrogen fertilization generally increases that percentage (22).

With only a little culm elongation, many, if not all, leaves can be removed by cutting just above the rudimentary inflorescence. Subsequently, the culms remain obliged to grow, even though they may remain entirely leafless (7, 10, 23, 31). A harvest that cuts below the inflorescence and peduncle (the uppermost internode of the reproductive culm) stops further growth of that shoot and induces tillering at the base. This is the principle involved in the development of multiple-crop rotation schemes for grazing (20, 23).

Aborted reproductive shoots, those in which the peduncles and rudimentary inflorescences have been killed, soon reach maximum development. Although they are "blind" shoots, they lack

the shoot apex and indeterminate growth of the vegetative shoots. Aborted reproductive shoots often lose apical dominance over basal axillary buds and contribute new tillers at an earlier time than exhibited by ordinary reproductive shoots.

Grazing Management

Information about plant morphogenesis is needed to explain plant responses to range management. Such information can be used to define appropriate seasons or sequences of grazing, where an intensive degree of control over land and livestock can be attained. This assumption of intensive control omits the situation of poorly distributed grazing, for which rotation of deferred grazing and rest-rotation grazing can be used to prevent the destruction (sacrifice) of critical sites such as drainage systems. These conventional systems of grazing are discussed in other papers of this workshop.

Grazing is not only a means of harvesting but a treatment that affects subsequent herbage quantity and quality. At a given time and place, grazing might be conducted primarily to produce a strong tillering response, harvest a maximum quantity of nutrients per unit area, improve forage quality for subsequent grazing, manipulate botanical composition, protect and improve adjacent range, or create some other desirable effect. All good things cannot be produced on rangeland at one time or in one way. Thus, the point of emphasis in this section will be that information about plant morphogenesis can help define opportunities and alternatives for application in grazing management. The examples given are fundamental and illustrative. Their applicability depends on local opportunity, the degree of control over land and livestock, and perhaps other factors.

Let's consider first a very specific kind of treatment by grazing. Grasses such as squirrel-tail (*Sitanion hystrix* (Nutt.) J. G. Smith) and needle-and-thread (*Stipa comata* Trin. and Rupr.) have awns that cause mechanical injury to animals and confound the problem of grazing distribution. The inflorescences can be grazed safely while they are in the boot stage of development. Thereafter, leafy regrowth by vegetative shoots can be very desirable. The treatment can solve a problem, improve forage quality for a

later season of grazing, and provide more alternatives in management strategy.

The timely removal of shoot apices and seedheads of grasses with culmed vegetative shoots promotes tillering and reduces summer dormancy. Grazing practices for timothy (*Phleum pratense* L.) have been defined in terms of shoot morphogenesis (20). Timothy has culmed vegetative shoots and prominent crowns or proaxes (11). Grazing is started when the leaves from the crowns are well developed, but is stopped when the young seedheads are 5 to 8 cm. above the ground. Grazing is started again when the seedheads are exerting from the uppermost leaf sheath, and when new tillers are beginning to show; but this time the shoots are grazed down closely. The pasture can be mowed after the second grazing to stop all first-crop shoots, if uniformly close grazing is not attained. Thereafter, the next crop of shoots develops basal leafiness quickly, especially when properly fertilized and watered; and the sequence of graze, rest, graze is repeated. Three crops of shoots and six periods of grazing can be attained in a season. This morphogenetic basis for rotation grazing is appropriate for many species.

Growing seasons on semiarid rangelands are generally short. Thus, limited regrowth opportunities must be defined carefully. Native and introduced species may be integrated to improve forage production and utilization. For example, the introduced species crested wheatgrass (*Agropyron desertorum* (Fisch.) Schult.) can be used to advantage with big bluegrass (*Poa ampla* Merr.) and bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. & Smith) (23, 24).

Big bluegrass has culmless vegetative shoots and an intermediate percentage of shoots becoming reproductive. Growth begins in March; leaf heights are up about 12 cm. in early April; and reproductive shoots head out in early May. The main problem is weak rooting and extensive pull-up. Thick stands are needed for high productivity, low percentage of reproductive shoots, and greater resistance to pullup. The very early growth, good regrowth from culmless vegetative shoots, and good palatability of cured herbage suggest a spring-fall pattern of grazing. Pasturing can be scheduled in April to utilize and stop further development of reproductive shoots.

Thereafter, the culmless vegetative shoots produce, in May and June, a good amount of leafy regrowth that can be grazed in late summer and fall.

Crested wheatgrass, which is about 3 weeks behind big bluegrass, has culmed vegetative shoots and a large percentage of reproductive shoots. A primary undesirable feature is the growth of stiff culms that become unpalatable and interfere with subsequent grazing. For good forage quality and palatability, the first crop should be harvested in May and June. The reproductive culms have 5 to 7 phytomers. The first elongated internode, which generally remains less than 1 cm. in length, matures, enlarges, and accumulates carbohydrates at an early time. When four leaf blades are showing, the rudimentary seedhead is still near the soil surface. Close clipping or grazing at that time removes the leaf blades and causes the culms to arise without leaf replacement (7). When five leaf blades are showing and the seedheads are up in the boot stage, all meristematic tissues can be removed. Thereafter, regrowth is composed of new tillers from axillary buds. Greatest production of good quality forage can be obtained by grazing to produce one crop of shoots under the semiarid conditions of the sagebrush-bunchgrass range. Pasturing should begin when the seedheads are high in the boot and continue to full and uniform utilization by July. Earliest satisfactory grazing can be obtained by grazing to produce two crops of shoots. Pasturing should begin when the leaves are 12 to 15 cm. tall and continue (about 3 to 4 weeks) to full and uniform utilization by the normal time of head-in-boot development in late May. If second-crop regrowth is sufficient to justify pasturing, a second grazing can be scheduled after the second crop of shoots has dried up.

The herbage of bluebunch wheatgrass is largely reproductive shoots, because the culmed vegetative shoots generally remain very small. A striking weakness is evident in culm growth. The lowermost elongated internode remains active for several weeks, grows to a length of about 7 cm., and is extremely slender and fragile until about the time of seedhead exertion. Weakness in the lowermost internode makes the plant susceptible to damage by grazing. The great susceptibility of this species to spring grazing has been known for

many years. Also, we have known that heavy grazing in the fall is beneficial to plants and improves range condition (9). Therefore, grazing should begin at about the time of head exertion and may be continued through late summer and late fall.

Appropriate seasons of grazing for big bluegrass, crested wheatgrass, and bluebunch wheatgrass can be integrated in a pasturing sequence as illustrated in fig. 3.

Some grasses are better adapted to a specific season of grazing or to periodic harvest, but some are well adapted to season-long grazing. A good example is blue grama, which has culmless vegetative shoots and a very small percentage of shoots becoming reproductive in natural stands. On the shortgrass plains of Colorado where this grass is dominant, season-long or year-long grazing is a good practice that need not prevent additional fencing and development of livestock water. Since correct stocking rates and the amount of herbage needed to sustain plant growth and nourish livestock have been defined (2), we should not be anxious to recommend complex systems of rotation grazing just because they have been good in other areas.

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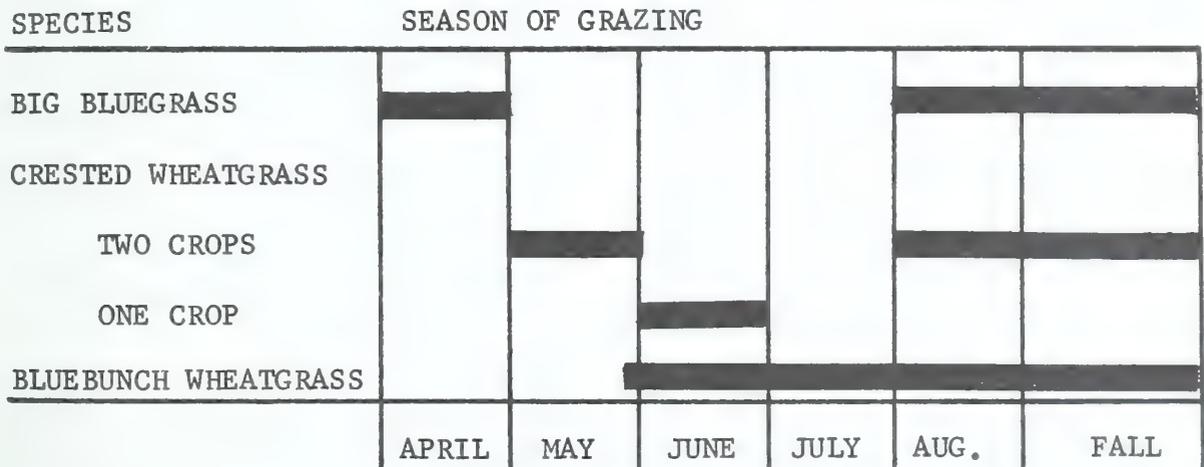


FIGURE 3.—Appropriate seasons of grazing for big bluegrass, crested wheatgrass, and bluebunch wheatgrass.

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MORPHOGENESIS AND MANAGEMENT OF ANNUAL PLANTS IN AUSTRALIA

By R. Milton Moore¹

Abstract

The distribution and characteristics of annuals in pastures and grazing lands of Australia are outlined. The growth and shoot apex development of the most widely occurring sown and naturalized species are described and Australian studies of effects of defoliation are reviewed. Management of annual communities is discussed in relation to the morphology and reaction to grazing of their principal species.

Additional key words: shoot apex, naturalized species, defoliation, grazing.

Annual Species Of Australian Pastures And Grazing Lands

All of the annual species sown in Australia are introduced. Many of the most widely sown are locally occurring biotypes of species accidentally brought into the country and now naturalized in communities grazed by domestic livestock or otherwise subjected to disturbance. Others are not sown but are volunteer in sown pastures and in grazing lands of native species; some of these species are useful, but others are weeds and harmful to animal production.

In some arid and semiarid communities, native annual grasses and forbs germinate rapidly after drought-breaking rains. Although they do not last long, they reduce the grazing pressure on perennials during the early part of a new period of growth.

Figure 1 shows areas where annual pasture

species are of actual or potential significance for animal production in Australia.

There are about 157 million ha. suitable for existing cultivars and varieties of annual pasture species and of these 85 million are in southern or temperate Australia and about 72 million in northern or tropical Australia.

In southern and western Australia, the inland limit of naturalized annual pasture species is approximately the 254 mm. annual isohyet. North of 30°S. latitude in eastern Australia, the proportion of rain falling in the winter months of the year declines and the limits of temperate pasture species are at increasingly higher annual rainfalls until at the northern end of their range the inland boundary is at approximately the 508 mm. annual isohyet (25, 26).

On acid soils in temperate Australia pastures of cool season annual species have evolved under sedentary grazing in a system in which nitrogen, and frequently phosphorus and sulphur as well, are increasing. Nitrogen has been added to the system by introduced legumes and sulphur and phosphorus by applications of superphosphate. (26).

On neutral and alkaline soils *Trifolium* species are replaced in Mediterranean annual pastures by annual species of *Medicago* (26). In sown pastures the common species are barrel medic (*M. truncatula* Gaertn.) and strand medic (*M. littoralis* Rhode), and in volunteer communities the burr medics (*M. minima* (L.) Bartol, *M. polymorpha* L., and *M. laciniata* (L.) Mill.).

Wimmera ryegrass (*Lolium rigidum* Gaud.) is the only grass sown in Mediterranean annual pastures, but barley grass (*Hordeum leporinum* Link.) volunteers and is almost invariably the dominant grass on both neutral and alkaline soils. Barley grass also replaces *L. rigidum* in old pastures on acid soils in eastern Australia.

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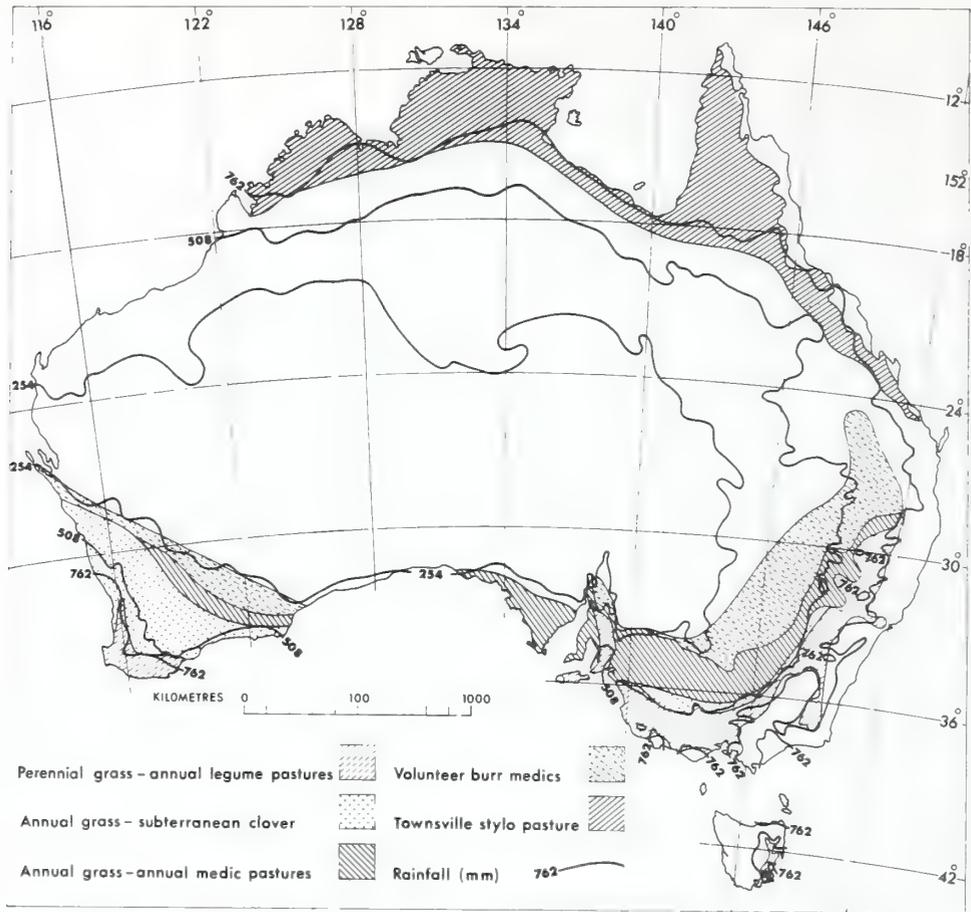


FIGURE 1.—Principal areas in which introduced annuals of value in animal production are sown or naturalized in Australia. (After Moore, 25.)

Other common associates of annual medicagos are silver grasses (*Vulpia bromoides* (L.) S. F. Gray or *V. myuros* L.), saffron thistle (*Carthamus lanatus* L.) or capeweed (*Arctotheca calendula* (L.) Levyns), and the native *Erodium cymorum* Nees. The ecology of Mediterranean annual pastures is discussed by Rossiter (36).

Townsville stylo (*Stylosanthes humilis* H. B. K.) is the only introduced annual of any consequence at present in tropical pastures, although bulrush millet (*Pennisetum typhoides* (Burm.) Staff and C. E. Hubbard) in the Northern Territory, and phasy bean (*Phaseolus lathyroides* L.) and a few other annual legumes are sown to some extent in subtropical pastures. Townsville stylo is adapted to a wide range of soils in areas receiving more than 650 mm. rain annually (see figure 1).

Native annual *Sorghum* spp. are common and frequently dominant in the herbaceous layers of 30 million/ha. of tropical woodlands in the Northern Territory and north of Western Australia. These annuals flower and produce seed early in the season and are of low nutritive value in late summer. However, Robinson and Sageman (33) have drawn attention to the value of *Sorghum australiense* Garber and Snyder in providing feed early in the wet season before perennials have resprouted in northwestern Australia.

In arid shrublands, the common species of ephemeral communities are *Dactyloctenium radulans* (R. Br.) Beauv., *Brachyachne convergens* (F. Muell.) Staff, *Tragus australianus* S. T. Blake, *Aristida contorta* F. Muell., *Enneapogon polyphyllus* (Domin.) N. T. Burbidge, *Chloris truncata* R. Br., *Tripogon loliiformis* (F. Muell.)

C. E. Hubbard, *Helipterum floribundum* DC., and several species of Cruciferae. Species with high frequency in arid tussock-grass grasslands are *Iseilema vaginiflorum* Domin., *Portulaca* spp., *Boerhavia diffusa* L., *Brachyachne convergens*, *Eragrostis tenellula* (Kunth) Steud. and *Sida* spp. Where the rainfall is higher, some of these species may be perennial.

Characteristics Of Annuals

Annuals are adapted to areas with low annual rainfalls and high frequencies of hot dry periods. Because they depend entirely on seeds for survival and regeneration, factors influencing flowering and seed formation are more critical than for perennials. Earliness of flowering is advantageous in dry areas, but there appears to be no close correlation between maturity gradings of subterranean clover strains and lengths of growing season (36); a number of strains varying in maturity gradings may be found at the one site (27).

The composition of communities of annual species may differ from year to year, depending on rainfall-temperature relationships at the start of a new growing season. Composition depends also on chemical and physical properties of the soil, morphological and physiological characteristics and relative numbers of the disseminules present, rates of growth and morphological development of the species that germinate, their reaction to grazing, and production of viable seed.

Spiny, awned and pointed floral structures adhering to caryopses, inflorescences enveloping seeds in a burr and very small seeds or caryopses would seem to aid germination on the surface of uncultivated soils (19, 21, 22, 41, 42). Conversely, seeds and fruits without spiny structures frequently germinate poorly in the absence of cultivation and are more likely to be eaten by animals and harvested by ants (21, 41).

The ecological success of an annual depends in considerable degree also on barriers to germination in periods when chances of seedling survival are low. Annual legumes including subterranean clover, barrel medic and Townsville stylo may have a high proportion of their seeds with hard impermeable coats so that a succession of germinations is possible (10, 27, 36). In these cir-

cumstances death of seedlings from early germinations may not be critical for survival of the species. Most annual grasses germinate over a wide range of temperatures and a majority of seeds produced at the end of one season germinate more or less simultaneously at the beginning of the next growing season.

Some of the best adapted naturalized annuals, barley grass and soft brome (*Bromus mollis* L. (22)), and *Bromus rigidus* Roth. (36) have distinct but short periods of dormancy and appear to depend for success on single peaks of germination, high densities of seedlings, and capacities to produce seeds quickly despite unfavorable conditions for growth. Similarly, freshly harvested seed of *Wimmera* ryegrass is mostly dormant, but dormancy declines during summer and by late autumn a 90-percent germination is possible (G. A. Pearce, 1971 pers. comm.).

Growth And Morphological Development

The developmental morphology of the tiller bud or shoot apex in grasses has been described among others by Sharman (38), and Cooper and Saeed (13). Briefly, the shoot apex is composed of an apical meristem with the youngest cells near the extreme tip. Leaf primordia arise in the shoot apex and eventually ensheath it; the number of leaf primordia formed varies with species, and Sharman (38) has classified shoot apices as long, intermediate, and short according to the number of their leaf primordia.

After a certain number of leaves have been produced—the number varying with species and to a degree with environmental conditions (13)—the shoot apex becomes responsive to temperature and to photoperiod. A tiller that has produced its minimum number of leaves will change from vegetative to reproductive growth when its temperature and photoperiodic requirements are met. At this stage, often referred to as “becoming ripe to flower” (13), formation of leaf primordia is suppressed and spikelet buds are produced. The differentiation of spikelet buds is accompanied or followed shortly by elongation of internodes, elevation of the shoot apex and eventually, emergence of the inflorescence (4).

A quantitative description of the growth of an annual grass is contained in Williams' (47, 48,

49) studies of wheat. Williams showed that, rather than by a single exponential curve, growth could be considered as a sequence of exponential curves; the change from one exponential curve to the next representing successively, initiation of secondary roots, cessation of leaf growth, cessation of stem growth, and the development of floral structures.

In another series of curves Williams (48) showed changes in dry matter production of leaves, stems, and inflorescences (fig. 2).

Figure 2 shows that a decrease in growth of leaves coincides with an increase in growth of stems and a decrease in growth of stems by an increase in growth of inflorescences. In his text, Williams states that root growth stopped at the same time as leaf growth; stem growth declined

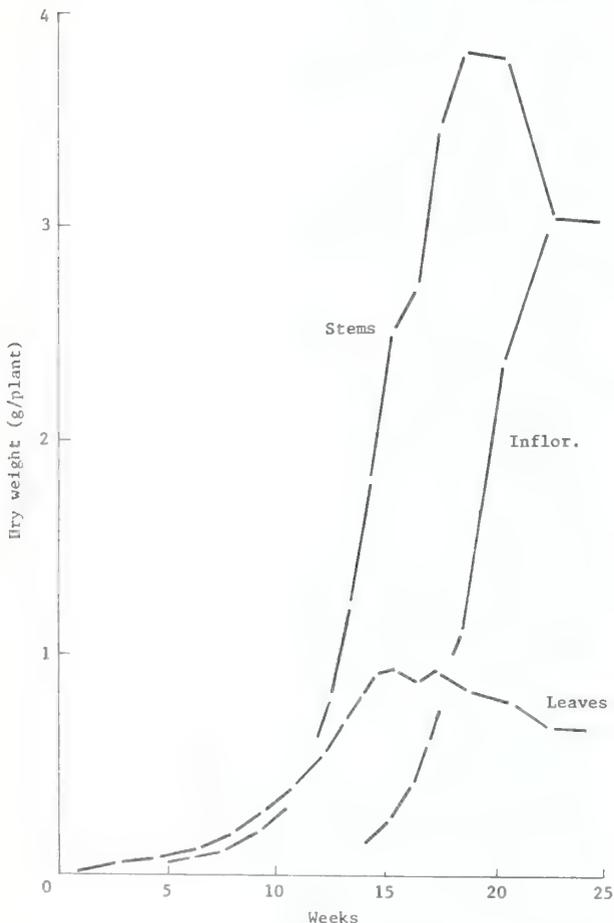


FIGURE 2.—Growth of developing organs of the wheat plant. (After Williams, 48.)

as spikelets developed and, in turn, growth of these declined as the floral parts began to develop rapidly. In effect energy reserves appear to be channelled successively to newly developing organs. This led Williams to suggest that the annual habit may be a result of self-starvation from transference of energy substrates and other nutrients to the developing caryopses, the form of the plant in the dry season.

Defoliation In Relation To Shoot Apex Development

In annuals, growth of tillers is determinate; each tiller produces a single flowerhead and dies after flowering and seed production (13).

At or shortly after floral initiation, elongation of stem internodes raises the shoot apex from near ground level to a height where it eventually becomes accessible to removal by cutting or grazing. Removing the shoot apex of an elongating tiller results in the death of that tiller but may stimulate the growth of lateral buds, and, in most annuals, removal of shoot apices prior to flowering is followed by a resurgence of new tillers.

In some species, continued removal of shoot apices by grazing or cutting may lead to continued production of fertile tillers throughout the season. These tillers become reproductive with fewer leaves than the primary tillers, and they produce flower heads more rapidly. If decapitation takes place after flowering, removal of nutrients in the inflorescence may mean that energy levels could be too low for axillary tiller bud development. As Milthorpe and Davidson (24) showed, axillary tiller growth is slow if the supporting stems carried ripening seeds when they were cut.

Aspinall (6) postulates that development of axillary tillers following decapitation of inflorescences is due to both a growth substance and nutrients and their interaction on apical dominance.

According to McWilliam (23), death of annual pasture grasses is due largely to senescence following water stress at the end of the growing season.

Effects of defoliation at different stages of development are now considered for the following

species, which are significant to livestock production in temperate and tropical Australia and for which data are available.

Hordeum leporinum (barley grass) is a naturalized Mediterranean annual grass. Barley grass, commonly associated with burr medic, invades pastures of Wimmera ryegrass—barrel medic and Wimmera ryegrass—subterranean clover. In recent years, it has also invaded heavily fertilized and heavily grazed perennial grass—subterranean clover pastures. Barley grass provides early winter feed for livestock (41), but its sharp pointed floral structures are a cause of vegetable fault in wool and are injurious to animals, particularly to lambs in the spring (32). Because of these harmful attributes, attempts have been made to eradicate it from sown pastures, and studies have been made of its competitive interrelationships with Wimmera ryegrass, a preferred species.

In a grazing experiment of Robards and Leigh (32) at Deniliquin, New South Wales, Burt (9) determined the height of shoot apices in barley grass at different stages of development. These relationships are shown in figure 3. Using other data from Burt (9) an approximate time scale has been superimposed on the horizontal axis.

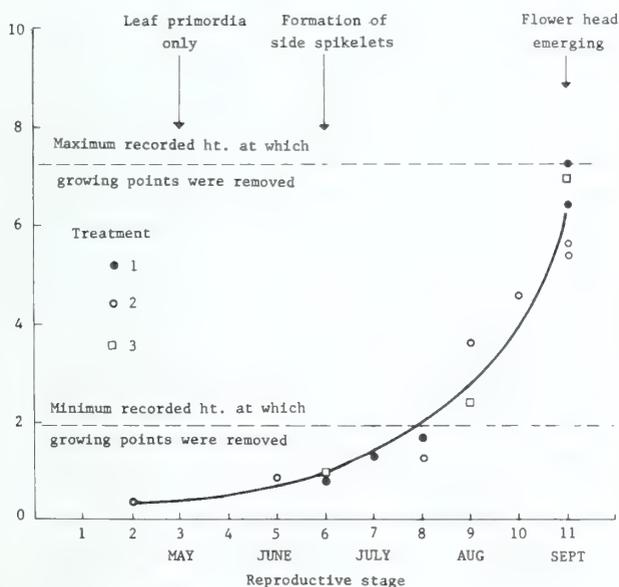


FIGURE 3.—Height of shoot apices in barley grass at different stages of development. (From Burt, 9, with superimposed time scales.)

The relationship between height of shoot apices and various stages of development was not affected by withholding grazing (Treatment 1), grazing in May and June (Treatment 2), and grazing monthly (Treatment 3).

When shoot apices were about 2 cm. above the ground they became accessible to sheep. Ungrazed plants attained this height about the end of July and those grazed monthly, about mid-August. Removal of shoot apices by grazing in August and September stimulated production of axillary tillers from basal buds and increased the number of flower heads in comparison with ungrazed plants. In September, tiller numbers on ungrazed plants were 1.36 per plant compared with 3.74 per plant on monthly grazed plants.

Lolium rigidum (Wimmera ryegrass) is a sown annual grass. Cooper and Saeed (13) made comparative studies of growth and development of Wimmera ryegrass and perennial species of *Lolium*. They found that, under continuous light, the annual species produced 8-12 leaves before floral initiation. Under the same conditions, *Lolium perenne* L. (S24) produced more than 20 leaves before becoming reproductive. When defoliated during stem elongation, Wimmera ryegrass—like barley grass—produced secondary tillers which elongated with fewer leaves and produced flower heads more rapidly than the primary tillers. Because the primary tiller apparently influences the “ripeness to flower” of its axillary buds, Cooper and Saeed argue that individual tillers of the grass plant are not independent.

Sown in Melbourne (lat. 38° S.), Wimmera ryegrass initiated flowers in late June and most shoot apices were 2 cm. above the ground by mid-August (5). This ryegrass is slightly later than barley grass but its seasonal growth pattern is similar.

Silsbury (40) found that tillering in Wimmera ryegrass increased slowly before stem elongation in June and July. It increased rapidly during stem elongation until September when the rate steadied, and then declined to November, the period of flowering and seed formation at lat. 35° S. Cessation of tillering from September onwards appeared to be associated with onset of heading, decrease in soil nitrogen, increase in

photoperiod, and decrease in light intensity at the base of plant.

Wimmera ryegrass, unlike the aggressive barley grass, does not persist in pastures. Because of its desirable properties, such as large yields of easily harvested and easily sown seeds and lack of awns and sharp pointed fruits, reasons have been sought for its poor persistence and for its almost inevitable replacement by barley grass on both acid and alkaline soils.

Smith's comparative studies (41, 43) showed that frost affected barley grass more than Wimmera ryegrass. When frosts were recorded, pure barley grass swards had less herbage after 66 days than after 32, because of leaf loss from frost damage. In the absence of frost, barley grass produced more tillers after defoliation and higher yields than Wimmera ryegrass did in the winter and early spring—periods when feed shortages are likely in southern Australia.

Tiller densities of intact plants of barley grass and Wimmera ryegrass were similar in spring, but in frequently cut plants there were more tillers of barley grass, especially at low-sowing densities. Densities of ryegrass four times greater than those of barley grass were frequently required to give equivalent yields of dry matter.

Both species produced more tillers as a result of nitrogen applied early, but nitrogen applied late during stem elongation had no effect on barley grass tiller production, though it significantly increased tiller number in Wimmera ryegrass. This suggests that the low production of tillers by ryegrass after defoliation, particularly when growing with barley grass, may be due to a deficiency of nitrogen.

As Wimmera ryegrass approached maturity, the growth rate was greater than that of barley grass, and final yields of the two grasses were similar. Smith (43) considers that the heavier seed of barley grass is a factor in its higher productivity during the first 7 to 8 weeks of growth. Initial growth of wheat (Williams 48) and subterranean clover (Black 8) depends on seed reserves.

Pennisetum typhoides (bulrush millet) is a cross-pollinated, summer-growing annual of potential value as first-year companion species for Townsville stylo in cattle pastures in northern Australia. Bulrush millet is more a crop than a

pasture plant but it is the only tropical annual grass for which morphological data have been obtained in Australia.

The main features of its seasonal growth and development and its response to defoliation at different times are shown in figures 4 and 5, taken from Begg (7).

Seedlings emerged 4 days after sowing in mid-January. Tillering began in the second week when the main shoot had 4-5 unfolded leaves and continued rapidly until the fifth week, when tillering ceased at full light interception by the canopy. By this time, the main shoot had 6 to 7 fully expanded leaves. Floral initiation took place in February, and internodes elongated rapidly, with consequent elevation of apical meristems, from then until flowering, 12 to 14 weeks after emergence. As in temperate species, the onset of reproduction, the period of rapid internode elongation, was marked by a high rate of dry matter production.

Recovery from cutting was high in the early and vegetative stages of growth. In contrast, the grass made poor recovery from cutting during internode elongation when growth was rapid and shoot apices were above cutting height.

At this time and particularly in the 7- to 8-week period, little or no new tillers developed from basal buds. Begg reasoned that axillary tillers failed to develop because of a low re-

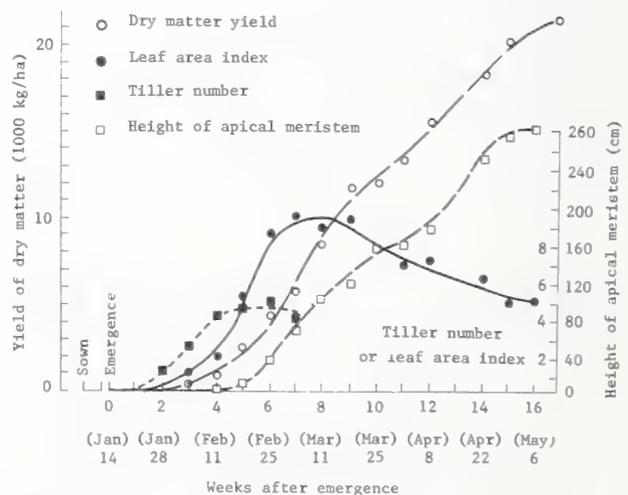


FIGURE 4.—Bulrush millet. Seasonal growth and development and changes in height of shoot apex. (After Begg, 7.)

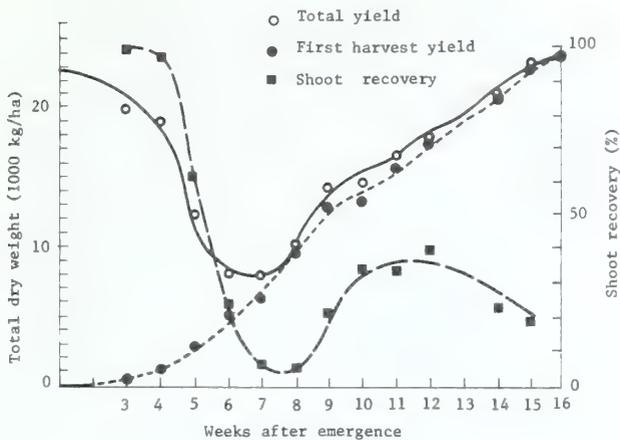


FIGURE 5.—Bulrush millet. Recovery after defoliation at different stages of development. (After Begg, 7.)

sidual level of nutrients following removal of the large main tillers. Later, as growth rates declined, some new tillers developed from basal buds and rapidly became reproductive and produced inflorescences.

Grazing experiments of Norman and Begg (30) showed that the highest cattle gains per hectare and per head were obtained from bulrush millet when cattle were put on early—that is, during the vegetative stage of growth.

Trifolium subterraneum L. (subterranean clover), a cool season Mediterranean annual legume with a prostrate habit, is of potential value as a pasture plant on 3.5 million ha. in southern Australia (27). Aitken (1) described the development of the growing point in subterranean clover. Rate of leaf and node production, about the same for each variety or cultivar of subterranean clover, varies with temperature and is higher in autumn than in winter. Lateral growing points are formed in the axils of the young leaves and may develop into lateral shoots. Those formed at some distance from the apical growing point are vegetative and those in the axils of the youngest leaf may form flower panicles. As in temperate grasses the change from vegetative to flowering state is accompanied by elongation of the lower nodes of the stem. Early flowering varieties initiate floral primordia and develop flowers at low nodes, while late flowering varieties flower at high nodes. Tallarook, a late flowering cultivar sown in early April, initiated flowers in early

September and flowered in October at the 18th node. Dwalganup, an early variety sown at the same time, initiated flowers in early June and flowered in September at the 9th node. Again as in annual grasses, time for floral initiation decreased with lateness of sowing. The node at which the first flowers are formed on lateral stems is lower than that at which flowers develop on main stems (2).

Weight of seed per unit area was 27 percent higher from clover defoliated in July, or in July and September, than from uncut controls. Cutting in July also increased the number of seeds per burr (34). With progressively later defoliations at flowering and seed setting, seed weights fell to the control level and finally to 15 percent below it. A single cut in mid-September—that is, at flowering—reduced seed yields by 33 percent. Early defoliations, after floral induction but before flowering, increased the number of seeds per unit area by 40 percent. The increase was due to the large number of inflorescences on early cut plants. Later defoliations reduced seed numbers to the level of the uncut control. Rossiter (34) concluded that hard grazing of clover swards before flowering would increase seed yields. Mowing for hay after flowering would decrease seed yields but, by reducing competition from grasses, might increase the proportion of clover in mixed swards the following year.

Growth of swards of subterranean clover is described by Davidson and Donald (14).

Medicago spp. (barrel, strand, and burr medic) are sown and naturalized Mediterranean annual legumes. The structure and development of the growing point in annual medics are similar to subterranean clover (3). Commercial barrel medic has a maturity grading like that of the subterranean clover cultivar, Yarloop. Barrel medics, like clover, flower at their lowest nodes when sown in winter and at their highest when sown in summer—that is, when sown early they are vegetative for a longer period, presumably because of high temperatures and diminishing photoperiods. As for clover, the time between sowing and flowering in *Medicago* species was shortest for winter sowings.

Stylosanthes humilis (Townsville stylo) is a sown and naturalized tropical annual legume. Torsell and others (46) established that the

growth curve of dry matter production in Townsville stylo was similar to that of other annual pasture species. Confirmation of this was obtained by Fisher (18) who found that, under favorable conditions, mean growth rates and dry matter production of Townsville stylo were about the same as those of subterranean clover. Townsville stylo, a self-regenerating species, germinates at the end of the dry season. The vertical taproot of the plant penetrates the soil rapidly, but shoot growth initially is slow. Early in the wet season lateral shoots develop, and their growth rate increases. By February in northern Australia, the leaf canopy fully intercepts the light, and, from then on, the growth rate is high until maturation and senescence in the early part of the winter dry season. Cameron described flowering behavior (11, 12).

Loch and Humphreys (20) defoliated Townsville stylo at floral initiation, flower appearance, and advanced flowering. Defoliation at each of the three stages reduced seed production in comparison with no cutting; the reduction being more marked the later the stage of cutting. Unlike the prostrate subterranean clover, which branches and produces more inflorescences when cut or grazed before flowering, Townsville stylo has an erect habit and its buds are more vulnerable to cutting or grazing. Defoliation of Townsville stylo also reduced the number of florets that set seed. This was due perhaps in part to later flowering as a result of cutting, and consequently to maturation of seed during falling temperatures and intensities of radiation (20).

Defoliation did not affect the growth rate significantly, stem and inflorescence growth were reduced, but leaf growth rate was increased.

Management Of Annual Communities

Smith's (41) defoliation experiments indicated that decapitation during the period of elongation promoted tillering and seed setting in barley grass. These results were confirmed by the grazing experiments of Robards and Leigh (32) and Burt (9). In another experiment, Smith (43, 44) had a series of plots grazed until mid-August, the onset of stem elongation, and then imposed, among others, the following differential treatments in both 1962 and 1963:

1. No grazing after mid-August (late winter).
2. Grazed for an additional month that is until mid-September (early spring).
3. Cut as for silage—October 4, 1962, and October 22, 1963.
4. Cut as for hay—October 16, 1962, and October 30, 1963.

Seed yields from plots grazed in September, that is, during a period of rapid stem elongation, were higher than from plots cut for silage or for hay in October. Yields from grazed plots were no lower and in two instances were higher than from plots not grazed after the onset of the reproductive stage. The highest yields of viable seed were recorded also from plots grazed during stem elongation.

Cutting for hay at seed formation in October reduced yields of seed to a greater extent than cutting at flowering for silage. Results for all treatments were similar in 1962 and 1963.

In 1963 some plots were oversown with subterranean clover and, in the presence of clover, less seed was produced by barley grass on all treatments.

In the year following the last application of treatments, oversown plots cut previously for silage or hay, and particularly those cut late for hay, had less barley grass and more clover than grazed plots. Seed yields of clover were highest on plots cut for grass hay or silage in the previous 2 years, that is, on those plots yielding the least barley grass. On grazed plots, inflorescences of barley grass were closer to the ground than on other treatments, presumably because of the shorter vegetative stage and earlier floral initiation in axillary tillers. Seed heads close to the ground are less likely to be injurious to grazing animals than the erect inflorescences normal in lightly grazed barley grass.

Late mowing offers some scope for reducing the proportion of other annual grasses, except perhaps the early maturing *Vulpia* spp. but allows ingress of other annuals, such as capeweed and erodium.

In a drier environment in southwestern New South Wales, Robards and Leigh (32) found that the critical months for grazing barley grass were August and September—as in Smith's experiment, the period of stem elongation. The highest yields of dry matter were from plots grazed every

month from May to November, but all plots grazed in August and September yielded more than those not grazed in either of these 2 months.

McGowan (21) conducted studies on methods of keeping ryegrass in new pastures and of restoring it to old pastures in which it had been replaced by barley grass and silver grass. The studies showed that grazing at low and seemingly impracticable stocking rates was the only way of maintaining ryegrass in a new pasture. Inflorescences and seeds of ryegrass and soft brome are eaten by livestock, whereas those of barley grass and silver grass are not. Harvester ants collect ryegrass seeds but not barley seeds and are more active in heavily than in lightly grazed pastures. The larger quantity of seed available for regeneration in autumn and the deeper cover of plant litter on lightly grazed plots are considered to be responsible, at least in part, for better regeneration of ryegrass at low stocking rates.

Annual grass pastures that are late cut for hay in early November are generally silver grass dominant in the following year unless resown with ryegrass (21). Seeds of silver grass mature earlier than those of ryegrass or barley grass and may have fallen by time of hay cutting in November. The awned seeds of silver grass establish well on ground bared by hay cutting. Plots that were cut in mid-October for silage when silver grass was heading had twice as many ryegrass seedlings and only 5 percent as many silver grass seedlings in the following year as those cut for hay. Silver grass, unlike the later maturing barley grass, did not produce further tillers after cutting in October.

McGowan concluded that the only way of restoring Wimmera ryegrass to old pastures other than by ploughing, sowing to crops and later re-sowing, was to sod-seed with ryegrass seed in autumn after cutting for hay the previous year. Shier (39) claims that autumn cultivation every 3 years will sustain ryegrass in pastures in the Southwest.

Smith (41, 42) studied the balance between grass and clover in annual pastures and proved, experimentally, the commonly held view that an early break in the season—that is, autumn rain—results in clover dominance, whereas a late break favors grass dominance. He found that the most

pronounced dominance of clover followed an early break in absence of moisture stress, and that the greatest grass dominance resulted from a late break and subsequent moisture stress especially in the presence of high nitrogen. A factor in grass dominance following a late break is the relatively slow growth rate of clover at low temperatures.

The negative relationship between barley grass and clover yields is a possible explanation of the seemingly anomalous results of Myers and Squires (29) who found that deferment of grazing for 20 days, and to a lesser extent for 40 days, followed by continuous heavy grazing for the rest of the season virtually eliminated barley grass from a barley grass-clover pasture. The early break of growing season, induced experimentally in mid-February by irrigation, favored clover; and from the spring yields of dry matter, 2106, 3508, and 2700 kg./ha. for the 10-, 20-, and 40-day deferment, respectively, it would appear that some protection from grazing was also advantageous to clover. Shading of barley grass stem bases by the early growing clover presumably inhibited basal bud formation and, consequently, the replacement of primary tillers removed by grazing. For example, Puckeridge (31) suggested that tiller production ceases at high plant densities because of low light intensities below the herbaceous canopy. At low densities, however, tillering is limited apparently by nitrogen rather than by tiller bud numbers. Aspinall (6) showed that tillers do not elongate at low light intensities and postulated that tiller buds and developing seeds compete for nutrients. At low light intensities, carbohydrate levels would be low and in such circumstances it may be inferred from Williams (48) that amounts channelled to tiller buds would be small.

Shoot apices are elevated earlier and floral initiation is more rapid at high densities. It has already been suggested that late defoliations may not stimulate tillering because by then most of the nutrients would have been channelled to inflorescences subsequently removed by cutting. This is a possible explanation of the different effects of defoliation on seed production observed by Rossiter (34) on subterranean clover and those by Loch and Humphreys (20) on Townsville stylo. Earlier defoliation of the more erect tropical

legume to allow access of light and induction of branching and flowering at lower nodes may possibly prevent losses in seed production from grazing prior to flowering, but experiments are needed to verify this.

The failure of bulrush millet to develop axillary tillers, following removal of shoot apices by cutting or grazing, may be due also to low light intensities at stem bases and to competing demands of large and rapidly growing stems for nutrients. Here, again, the possibility of altering the morphology of the plant by grazing appears worthy of study.

From the few data available at present, it appears that the stages of morphological development in which annuals can be utilized most effectively may differ for tropical and temperate species. Grazing after floral initiation and during stem elongation stimulated seed production in temperate but not in tropical species. Grazing at this stage also increased dry matter production in barley grass but, again, not in the tropical bulrush millet.

According to Smith (41, 42) the most important single factor in winter productivity of annual pastures is plant density, thus emphasizing the importance of seed setting, seed survival and germination on composition and productivity. Donald (15, 16, 17) showed that yields of dry matter per unit area of both clover and ryegrass increased steeply to a maximum and remained constant, despite further increases in plant density. However, the number of seeds per unit area reached a maximum and then declined with further increases in density. The highest numbers of seeds per plant were attained at the lowest density, but the individual seed weights and numbers of seeds per inflorescence were greatest at higher densities. Donald (17) explains these results on the basis of intraplant competition—at the lowest density there would be no competition during the early stages of growth, and flower primordia would develop in large numbers. Consequently, at flowering and seed setting, inflorescences would be numerous, and competition among them would reduce seed production per inflorescence and size of seeds. At higher densities, interplant competition would be operative at floral initiation and would reduce the number

of inflorescences and, thus, subsequent competition among them.

The developmental morphology of the temperate annual pasture species for which data are available appears to be similar, and the principal problem in the management of annual pastures appears to be control of species composition.

Grazing from the beginning of the growing season, with high stocking rates during the period of stem elongation to promote seed production, would seem to be the most appropriate management system for self-regenerating temperate grasses and legumes. Adverse effects of high stocking rates are discussed by Sharkey and others (37) and by Rossiter (36). Beneficial effects are discussed by Davidson and Donald (14) and by Smith (41, 44).

Deferment of grazing in the early part of the season, mowing when grasses are in head, or both, appears to promote legume dominance. In the early part of the season, grasses are favored by grazing and by high levels of nitrogen and phosphorus (28, 35, 45, 50). It seems that where animal production depends on annuals, an effective system of husbandry would be to have grass and legume dominant pastures and to manage them to achieve changes in dominance every few years.

There seems little scope for management in arid areas, other than for the preservation of the perennials of the community and the maintenance of soil conditions suitable for the reestablishment of annuals.

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MORPHOGENESIS AND MANAGEMENT OF ANNUAL RANGE PLANTS IN THE UNITED STATES

By Cyrus M. McKell¹

The annual range plant community is a dynamic aggregation of plant species which fluctuates yearly and seasonally in response to changing weather conditions. Application of various management practices such as grazing management, fertilization, burning, seeding, and chemical sprays can enhance productivity, improve species composition, and change quality tremendously in annual rangelands. The annual range is surprisingly more responsive than any other rangeland type.

The stage of plant development is equally as important as the management practices employed. By careful attention to stages of morphogenesis, including germination, vegetative growth, stem elongation, flowering, and seed production, the application of management practices can enhance the value of annual rangelands in the United States.

Location Of Annual Rangelands

Annual range plant communities predominate in two major types of climates in the United States. In California, the Mediterranean-type climate consists of moist cool winters and dry hot summers (28). The most favorable periods for plant growth, therefore, occur in the fall, after the onset of precipitation but before low temperatures limit plant growth and near the end of the moist season in spring, as temperatures rise after the cool winter period. Plant species that can complete their growth cycle, produce seed, and then escape the long summer drought, appear to be well adapted to the Mediterranean-type climate. Considerably fewer perennial plant species can withstand extreme drought for up to 5 or 6 months. With range deterioration, the peren-

nial species give way to the invasion of introduced grasses and forbs from the Mediterranean region.

Annual plant species also are important in the middle-latitude desert, classified as BSK by Koppen (28). The northern Great Basin and Columbia Basin plains have cold winters with precipitation often occurring as snow. Spring growing conditions become favorable as temperatures increase and precipitation remains adequate for a short period. Precipitation continues at a low level through much of the summer but is often undependable, and long periods of drought prevail. Deterioration of the original vegetative cover of this region allowed the invasion of annual species which were able to germinate, grow, and mature in a short period of time or to endure the periods of summer drought.

The southern extension of middle-latitude deserts in the United States, covering large expanses of the Southwest, also have an important component of the vegetation comprised of annual species. However, in these desert areas the annual vegetation occurs as a minor understory to the dominant shrubby vegetation and, therefore, is not considered of high importance from a management or forage production standpoint. However, in an occasionally favorable year, the profuse growth of desert annual species is an interesting phenomenon and cannot be dismissed lightly (55). Such desert annual communities serve an important function in the ecosystem by recycling nutrients, by furnishing food and habitat to small animals, and by forming a protective plant and litter cover over the soil surface under shrubs.

The annual range plant community in California is a very dynamic aggregation of plant species that fluctuates, not only yearly but seasonally, in response to the factors and interrelation-

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ships of the ecosystem (48). Such predictions as "This is going to be a good clover," "filaree," or "grass year" are commonly made in recognition of the dynamic nature of the annual range plant community which may have a significantly different species composition each year. Talbot and others (50) reported such variations (table 1).

The date of opening rains is an important factor in determining the species composition. *Bromus mollis* L. and *Erodium botrys* (Cav.) Bertol. are likely to be abundant with early effective rains, while the initiation of rains later in the season appears to favor a greater range of species, including the annual legumes. A drought period often follows the first rain. Under such conditions, species which are more drought resistant in the seedling stage are likely to be the most abundant. Subsequent studies by many workers (11, 12, 21) on the California annual range type confirm that yearly variations in species composition are caused by weather patterns that follow the early period of germination.

Species composition changes are also subject to annual fluctuations in the upper Great Basin and Columbia Basin regions. In these regions, composition does not change as much as the density of the stand does in response to favorable or unfavorable weather conditions. Klemmedson and Smith (26) reported that, at Arrow Rock, Idaho, one year's cheatgrass production was 361 pounds per acre, and in the following year, it was 3,461 pounds per acre—a tenfold increase, primarily in response to favorable precipitation.

TABLE 1.—Year to year fluctuations between plant groups. (From data published by Talbot and Biswell (50))

Plant group	Percentage by years				
	1935	1936	1937	1938	1939
Annual broadleaved plants	74.8	53.2	43.5	61.7	52.6
Annual grasses	20.6	45.4	55.5	34.1	47.1
Annual grasslike plants	2.9	.5	.5	3.6	¹ T
Total	98.3	99.2	99.5	99.4	99.7

¹ T=trace.

Is the annual range of sufficient importance to maintain it as a type without considering conversion to perennial grass? Many of the early studies dealt with intensity of grazing, to determine the effect on stand density and whether management could favor the return of perennial grasses. Talbot and Biswell (50) stated that, at the San Joaquin Experimental Range in the central valley of California, the sparse perennial grasses showed no increase in response to management during a 5-year study period. Even in completely protected places the stand of annual grasses and forbs continued to predominate. A report of later work (3) indicated an average of 4,400 pounds per acre harvested forage in swales as compared with 1,850 pounds of air dry forage on open rolling slopes in good years. During a 12-year study period, the estimated average production of air dry herbage per acre was 1,660 pounds, with the extremes fluctuating from 1,200 pounds to almost 2,400 pounds per acre. During this time the average precipitation was about 20 inches.

Bentley and Talbot (3) concluded that restoring the original cover did not appear possible, nor was it necessarily a logical objective. Instead, they recommended range management that would produce a forage cover composed of the better species of introduced and native annuals and perennials. Also range management should be aimed at effective use of the annual plant forage in its most productive condition with adjustments to increase the valuable perennial plants where they are important in the stands. They hoped that it was possible to produce a forage crop superior to the original cover. These statements have proved to be true, especially in view of more recent work in which improved management practices, particularly fertilization, have produced forage yields as high as 4,400 pounds with the addition of super-phosphate and introduced annual legumes (62) in the foothills of the Sacramento Valley. Nitrogen fertilizers at rates of N up to 80 pounds have increased total yield more than threefold (15, 21). A combination of 100 pounds of nitrogen and 88 pounds of phosphorus in the Sacramento Valley have produced yields of over 4,000 pounds per acre (39).

Annual cheatgrass range in the northern Great Basin and parts of the Columbia Basin are extremely important to the livestock industries in

those areas. Hall and Pechanek (17) stated that cheatgrass was probably the most important forage in southern Idaho. A U.S. Forest Service report (51) stated that cheatgrass provided the bulk of early spring grazing for all classes of stock on millions of acres in the Intermountain West. Not only is the forage abundant in good years but it also has a high nutritive value. In Montana, Hurtt (18) found that the condition of horses grazed on cheatgrass pasture compared very favorably with horses grazed on adjacent perennial grass pasture. In southern Idaho, the average grazing capacity of 5 to 8 acres per animal unit month (AUM) is realistic for most of the cheatgrass (26). However, the contrast in yields between poor and good forage years is extreme. In southern Idaho under a mean annual precipitation of 18 inches, the yield of cheatgrass in 1943 was 361 pounds per acre, while in the following year it was 3,461 pounds per acre—a tenfold increase. These data illustrate Piemeisel's observation (46) that forage production of cheatgrass fluctuates greatly from year to year in response to weather and is greater than that of perennial grasses.

The question may be asked, "How did the annual range plant community come into being where originally the plant cover was a mixture of perennial grasses and some annual species?" Most range ecologists will concede that in every location where cheatgrass thrives its successful establishment can be associated in some way or other with a disturbance or a deterioration of the range ecosystem. Various factors are responsible for this, including fire and abandonment of cropland. Daubenmire (5) considered that, inasmuch as cheatgrass does as well as the indigenous species of similar life form, it is a thoroughly naturalized alien in the *Agropyronetum*.

In the California annual type, Biswell (4) concluded that the kind of plant cover existing over the region before white man came can never be determined precisely, since there is no early literature that adequately describes it, and virtually no samples remain of it. However, many ecologists postulate that the original vegetation in the present California annual range type was a bunchgrass, primarily composed of *Stipa* species, plus numerous indigenous annual forbs and grasses of limited plant vigor.

Management Practices Which May Condition Or Alter Plant Development

In contrast with the opportunities available to the farmer, the range manager has fewer tools at his disposal to manipulate and manage rangeland vegetation. However, because of the more responsive nature and dynamic characteristic of annual plants, management may improve the productivity and quality of annual rangelands more than those of perennial rangelands. Results of management practices are often obtained the same year in which they are applied. Some of the more common management practices that are useful on annual ranges include grazing management, fertilization, seeding, burning, and application of herbicides. In some situations a single management practice may suffice; whereas, in others a combination of two or more may be necessary to accomplish the desired ends. In practically every case where a management practice is applied, it produces an impact on a particular stage of plant development that alters the course of subsequent growth, and often the impact radiates to the rest of the plant community.

Grazing management practices involve removal of plant tissue. Too early grazing of plant tissue reduces the photosynthetic area of the plant, and cuts down the production of photosynthate to feed the growing plant and to support reproduction. Growing points may be removed; this will thwart further development of certain parts of the plant.

Range improvement by seeding involves many stages of development, but the most important ones are germination and establishment. Stands will not become established where the existing plant community is not sufficiently open to allow introduction of seeded species. Seeding operations must also give some competitive advantage, by seed placement in a favorable position in the soil or by earlier placement, to provide a time advantage against early germinating seeds.

Range fertilization is most efficient if applied when environmental conditions are most favorable for plant development. In the fall, when seedlings are just developing, root growth and top growth must proceed at a rapid rate in order to develop an adequate root system and sufficient top growth to withstand the cool winter ahead. In the spring, when precipitation and moisture

are again favorable and plants are in the rosette stage, favorable nutrition will aid rapid development towards maturity.

Fire may be used as a management tool during seed development and at the mature plant stage. The mature plant stage is not really a stage of growth but of existence in which the fire reduces dry litter and concentrates the surviving seed at the soil surface. The desired result is not to stimulate plant growth but to reduce undesirable species growth. Herbicides may be applied to reduce or eliminate seed formation of undesirable species, to retain plants in a given stage of development or to restrict other species from competing in the early seedling establishment phase.

In the following sections these management practices are described as they work specifically on developmental stages of annual range species.

Comparative Phenology

In dense populations of annual forb and grass seedlings, rapid growth results in a high demand for light, moisture, nutrients and other environmental factors (9). Plant survival under such circumstances will be attained only by seedlings of high vigor, or by those with different rates of morphogenesis which allows them to avoid the stress period by earlier or later development. In reporting the characteristic growth curve for the annual type, Ratliff and Heady (47) reported that the period of most rapid growth extended from March 28 to April 24. In 1960, growth of *Erodium botrys* and *Medicago hispida* Gaertn. was earliest, followed by *Avena barbata* Brot., *Bromus rigidus* Roth, and *Bromus mollis*, with *Lolium multiflorum* Lam. being latest. The progression of plants towards maturity reached a static period of maximum herbage weight at the time of seed development. *Medicago hispida* was an exception, in that the maximum period extended from the onset of flowering to the time of leaf shatter. After the peak of maturity, plants began to lose weight as seeds were cast, but ryegrass lost its weight only half as fast as the other species.

Species with delayed maturity often present opportunities for applying management practices. Tarweed (*Hemizonia* spp.), a summer-maturing, noxious plant, can be controlled simply by range fertilization which stimulates the growth of

earlier maturing species and thus depletes the supply of soil moisture available for tarweed summer growth (65). *Lotus purshianus* (Benth.) Clements & Clements and *Taeniatherum asperum* (Sim.) Nevski also have late growth habit and depend on the soil moisture remaining after other range species have matured (39, 40).

Bromus tectorum L. is normally a winter annual, germinating in the fall when rain is sufficient and growing rapidly until cold temperatures set in, but it may act as a spring annual if there is too little fall moisture available for germination. Hulbert (16) noted striking variation in the phenology of plants grown at Lewiston, Idaho, from seeds obtained from several geographic locations. There was a range of about 25 days in the time of emergence of the inflorescences, and about 20 days in the time when plants turn completely brown. These ranges in dates of maturity are in striking contrast with the phenological development of the perennial grasses with which cheatgrass is a competitor in the northern Great Basin.

The implications of differences in phenological development for grazing management systems are not exactly clear. Much more knowledge is needed about the physiological status of plants in relation to morphogenesis before improved techniques, such as hormone sprays and herbicides, can be used to condition plant development.

Germination

The seemingly simple process of seed germination initiates a long series of morphogenetic changes that ultimately lead to a mature plant and reproduction of the species once again. The annual habit allows a rapid turnover of the gene pool and the annual exposure of all possible genetic combinations to environmental stresses, thus eliminating the unfit individuals from the population. Perhaps this is why annual species are so highly adaptable and vigorous; it is simply a matter of selection for such habitats.

Favorable temperature and moisture are essential for successful development of the seedling during the first critical stages of growth. Numerous management practices can be used to stimulate, retard, or eliminate plant growth during germination and seedling establishment.

A high degree of priority exists for seedlings

with a rapid growth rate during the early stages. Variability in speed of germination exists among widely differing geographic collections of *Taeniatherum asperum* seeds in the United States (41). Collections from areas with a higher degree of uncertainty in the first rainfall appeared to germinate at a more rapid pace than did seeds from more mesic sites in the coastal region of Oregon.

Whalley and others (58) showed that increasing soil fertility increased seed size and rate of germination. Soil moisture stress during seed production reduced the number of seeds, but seed quality apparently was not materially affected. Inasmuch as seed size apparently is a critical factor in promoting greater seedling vigor (57), any management practice which would result in improving seed size should have a correspondingly beneficial affect on seedling vigor and establishment.

Rapid mobilization of food reserves in the seed to soluble forms has been postulated as a possible index to seedling vigor (56). Species known for low seedling vigor apparently were slower in the

mobilization of food reserves than was a species known for its higher degree of seedling vigor (fig. 1). Seed size in itself does not appear to be a sole criterion of seedling vigor but is meaningful only within a species or closely related group. Rapidity of carbohydrate mobilization varies among species. However, one of the most rapid mobilizations reported in the literature is that of *Schismus arabicus* (Nees.) (57). In this extremely small-seeded annual grass, mobilization of stored carbohydrate was almost complete within a 48-hour period.

Seedcoat hardness or impermeability often retards germination. This problem, however, is less common among grasses than among dicotyledonous species, particularly the annual legumes. The hard seedcoat may have an ecological advantage. Williams (61) demonstrated that hard seeds of *Trifolium hirtum* All. provided sufficient seed for survival of the species, when the seedlings which germinated first were eliminated by drought, following the originally favorable conditions for germination. The remaining hard

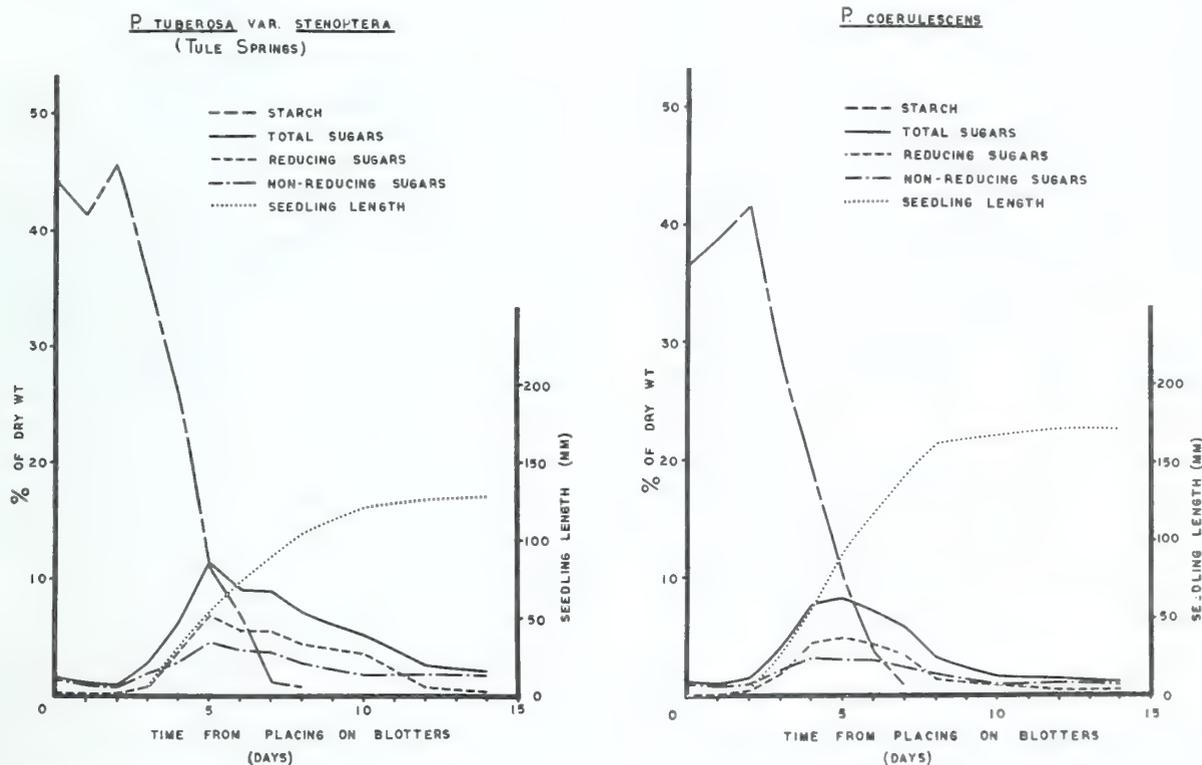


FIGURE 1.—Mobilization of carbohydrate reserves in early seed germination. (Whalley and McKell, (58).)

seeds in the litter provided a sufficient reserve for a second wave of germination. Seed dormancies of from 50 to 80 percent were regarded as a valuable mechanism for survival of the species.

In general, germination is reduced with increasing age of seeds. Older seeds often produce malformed seedlings, some without the appearance of a root or radical. Removal of a portion of the seed awn of *T. asperum* (45) appeared to increase germination of older seeds, however.

Williams (59) evaluated the emergence force exerted by small legumes. On the basis of differences in the force exerted, he concluded that the seedling size was not always a reliable index as to the force that the seedling was capable of exerting. In heavy soils, choosing the species with the ability to emerge under difficult conditions would be a wise management decision for seeding depleted annual rangelands. Grass species differ significantly in their ability to emerge from different planting depths. The data in table 2 show that *T. asperum* has a limited ability to emerge from soil depths greater than 2 inches.

Emergence of seedlings is often taken as an indication that establishment has fully occurred. This may be a reasonable criteria for the germination laboratory or in a humid environment, but under annual range conditions, establishment is not secure at this point. The number of plants early in the growing season has been reported (11) to vary from 20 to nearly 100 per square inch. Considerable reduction in this number takes place as the season progresses. In a review of seedling vigor, McKell (36) stated that establishment may not be fully assured until a grand rate of plant growth has been demonstrated (fig. 2).

Fertilizer may be applied in the area imme-

TABLE 2.—Seedling emergence from 1-, 2-, 3-, and 4-inch planting depths. Each figure is an average of 15 observations

Species	Number of seedlings emerging from depth of			
	1 in.	2 in.	3 in.	4 in.
<i>Trifolium hirtum</i> -----	160	91	22	1
<i>Bromus mollis</i> -----	259	42	1	0
<i>Taeniatherum asperum</i> ..	287	32	0	0

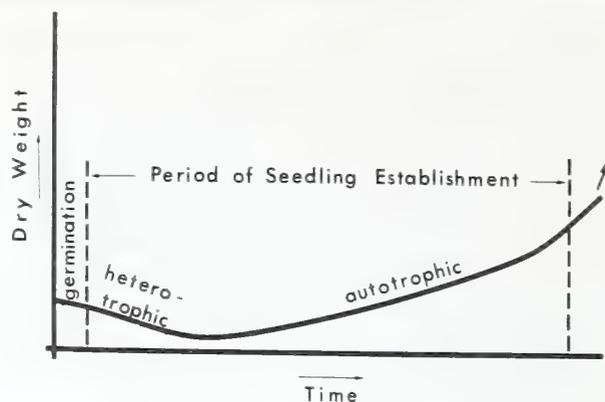


FIGURE 2.—Period of seedling establishment in relation to succeeding stages of plant growth. (After McKell, 37.)

diately adjacent to grass seedlings (53). However, *Lolium multiflorum* seedlings supplied with extra nitrogen (1) failed to grow roots and tops as fast as seedlings receiving no additional nitrogen. The ability to utilize nitrogen efficiently must develop later, because older *Lolium* seedlings are known to be highly efficient users of fertilizer nitrogen.

Artificial Seeding

The management of annual rangelands often requires that improved species be introduced to the plant community. The choice of adapted annual grasses and legumes is extremely important and has received considerable study over the past several years. Good management usually includes drill seeding, fertilization, reduction of competition by grazing management, proper depth of planting, and follow-up grazing management to assure favorable conditions for seedling establishment.

In *Bromus tectorum* areas, concern has been expressed that sites formerly dominated by perennial range grasses are almost impossible to reclaim to perennial grasses because of the intense competition offered by *B. tectorum*. Otherwise, grazing management of the existing stand of annual grasses appears to be the only solution available at the present time. Recent work by USDA's Agricultural Research Service rangeland scientists in Nevada and Washington appear to provide some answers for establishing perennial grasses in the areas dominated by *Bromus*

tectorum (7). These studies show that the competition for soil moisture by cheatgrass growing with *Agropyron* spp. is intense.

Herbicides have been used to manipulate plant competition during the seedling stage. Kay and McKell (24) used preemergence herbicides to control competing annual range species, and favor the establishment of *Trifolium hirtum* and *Phalaris tuberosa* L. var. *stenoptera* (Hack.) Hitch. Before weather conditions became favorable for seeding, an experimental area was burned to remove old litter and concentrate seeds at the soil surface. Subsequently, preemergence herbicides were applied to the surface. Two months later, after favorable moisture conditions occurred, the experimental plots were seeded with the introduced species. Competition from annual weeds was sufficiently controlled to allow successful stand establishment of the introduced species. Chemical treatments which were most effective included atrazine, simazine, and EPTC at rates from 2 to 4 pounds per acre. Subsequent refinements of the original techniques have resulted in considerable success. Kay² applies a 12-inch band of paraquat, then seeds introduced species below it. The seeds are protected by the soil from the effect of the chemical, which destroys the young annual grasses and forbs on the surface.

Root Growth

Rapid root growth is fundamental to establishment and development in annual rangeland communities, particularly when moisture stress is a constant threat during the period of plant establishment. Species may acquire a competitive advantage under stress conditions by (a) a faster rate of root growth, or (b) the ability to remain active in both root and top growth for a longer period. This extra growth is most important at a time when competing plants are inactive, or at the end of the growing period. Harris and Wilson (10) reported that rapidly elongating *B. tectorum* and *T. asperum* roots penetrated the soil ahead of *Agropyron spicatum* (Pursh) Scribn. & Smith, because they were able to continue root growth at low temperatures. Field studies indicated that *B. tectorum* roots grew well at temper-

atures as low as 3° C, while *A. spicatum* roots grew very slowly at temperatures below 8° to 10°. Therefore, *B. tectorum* seedlings are able to gain a competitive advantage over seedlings of *A. spicatum* by rapidly elongating their roots during winter months and using moisture through a large portion of the soil profile.

Any management practices which influence root growth are extremely important as tools in manipulating the annual plant forage resource. Fertilization has been shown to increase the overall abundance of roots in the areas normally occupied by roots of annual range species, although rooting depth was not changed much (39).

Grazing management also has a significant effect on root growth. Numerous studies (19, 20) have shown that intense grazing decreases root growth. In general, plants which are grazed excessively will have a much shallower root system than will plants which are grazed conservatively or not at all (31). This favors greater root development and greater seed production of less palatable species, and of late-growing weedy species, such as tarweed and other noxious annual forbs.

Grazing management may also be used as a means of balancing competition during the establishment phase of annual and perennial seeded species. Love (32) recommends a moderate amount of grazing during the early spring period, when plant competition is extreme. If competition is not reduced, growth of seeded species is retarded.

Top Growth

In the developing annual seedling, expansion of leaf blades proceeds at a rapid pace. With the development of tillers upon tillers, the increase in diameter of the grass plant can be rapid; this increase may begin in the late fall and proceed into the early spring period of growth. Under extremely crowded conditions, tillers do not form, and only single stemmed grass plants result. Competition with other species is critical to the development and survival of annual range species at this point. With sufficient space, most species begin to expand the diameter of the plant. Under very dense crowding, little if any expansion takes place, and grasses continue to grow with a single upright rolled leaf sheath

² Personal communication, 1971.

and blade. Broadleaved species, such as *Erodium* and the annual legumes, also show the effects of crowding in the early seedling stage. Knight and Hollowell (27) pointed out that stand density has a marked effect on the number of vegetative stems, and later on the number of seed heads, produced by *Trifolium incarnatum* L. *Erodium* plants tend to spread out and form a mat when surface area is available. This morphological characteristic may or may not be an advantage in competition with the annual grasses.

With the onset of cool weather and lower light intensities during the winter months, many of the annual range species will maintain themselves in a rosette stage, to continue through the less favorable growing conditions. Because of a temporary plateau of the growth curve at this point, it might be appropriate to refer to the typical annual range species as a winter biennial. However, because annuals do not continue their growth through the dry summer period they actually do complete their growth in the single season typical of annual plants.

Low temperatures often stimulate the axillary buds on stems to produce additional new tillers. Davis and Laude (6) found that the main culm produced more shoots and more heads than did later developing tillers. Reduced light intensity at the basal tissues of closely spaced shoots, and shading by screens, reduced tillering in the annual grass, *Bromus mollis*. This would correspond to the plant response seen in the field, under less favorable environmental conditions of winter. Competition for light among species of annual clovers was also found to be a critical matter in the morphology of the seedlings. Williams (60) found that leaf area and leaf position in the foliage canopy of *Trifolium hirtum*, *T. incarnatum*, and *T. subterraneum* Linn. was related to the size of the cotyledonary leaves. This advantage was later extended to larger unifoliate leaves and in the higher elevation of unifoliate and first trifoliate leaves.

Some species seem to influence or interfere with the growth of other species. *Lolium multiflorum* (37) in a mixture of species always had a detrimental effect on the growth of these species, particularly during the seedling stage. The implications of these findings are clear for the

range manager who uses a seeding mixture containing the highly competitive *L. multiflorum*.

McCowan and Williams (35) found that *Erodium botrys*, grown with *Bromus mollis*, acquired a disproportionate share of available sulfur, because of its more rapid root extension. However, at high sulfur levels *Bromus* became increasingly competitive and, as its population density was increased, *Erodium* was virtually eliminated. Many studies (2, 13, 22, 23, 63, 64) have shown that fertilizer stimulates plant growth, even during periods of cool temperatures. Fertilized plants appear to have an increase in cold tolerance. The amount of litter left remaining on the ground from the previous season may be useful as an insulating layer (11).

Species of annual legumes appear to have differing abilities to take up phosphorus from the soil. Apparently, introduced legumes have a higher potential for phosphorus uptake than some of the native species (42). Additionally, there appears to be an advantage in phosphorus uptake to offset the effects of low temperature. Other workers (8, 43, 54) have shown that application of fertilizers during the seedling stage will accelerate growth and provide for earlier range readiness than plants which have not been fertilized.

Rapid Vegetative Development

Upon emerging from the cool winter periods, plant morphogenesis begins dramatic changes. The significant morphogenetic changes are leaf sheath and blade elongation in grasses and stem and leaf growth in forbs. Root and top growth of plants begin a rapid rate of increase, and competition for nutrients, light, water, and space again becomes extremely critical. Only those species which have been able to develop an adequate leaf area and root system will be capable of survival and development in this more active period of growth (3).

Under some conditions, an earlier rate of readiness can be obtained through fertilization (34). Fertilization, through its effect on differential species response, also has a significant impact on species composition. Evans (18) reported differences in nitrogen uptake among three species of the annual grassland type. Combinations of grazing with fertilization have a significant im-

pact upon species composition. Jones and Evans (21) reported that the percentage of *Bromus mollis* in a resident annual range was increased by nitrogen fertilization for 2 or 3 years, but increased only in the first year on ungrazed plots. Walker and William (54) reported a nitrogen buildup in the soil by annual legumes which had been fertilized with sulfur. The nitrogen buildup increased grass production. Most of these species composition changes occurred as a result of interspecific competition, during seedling establishment stage and the initial stages of rapid growth at the end of winter.

Removal of plant tissue at the beginning or soon after the initiation of rapid plant development, by either clipping or grazing, reduces plant vigor and encourages less palatable and competitive species to predominate. However, if grazing is not excessive in the early stages, annual vegetation has a remarkable ability to sustain a high intensity of grazing and yet to continue its growth and proceed towards maturity. It is during this period of active growth that the annual range begins its period of highest productivity.

Stem Elongation

Under continued favorable environment, the meristematic regions at the base of each internode in the compact grass stem take on new activity. Formation of new cells and cell elongation are responsible for the relatively rapid growth of the culm in the grass plant.

Competition for space is extremely intensive at this stage. Some plants, by their greater vigor or by a leaf display pattern, may have the edge in competition with other species. Again, grazing and fertilization are most important during the stem elongation stage. Grazing may remove the immature inflorescences, which grow in the protection of the rolled sheath or in the boot. Some workers (30, 49) pointed out that not all species react the same to herbage removal. *B. mollis* was found to continue tillering and heading much longer than *Festuca megalura* Nutt., when clipped in a like manner. If grazing were continued to the growth terminal stage of *F. megalura*, it would depress this species, yet would still permit tillering and abundant heading in *B. mollis*.

High levels of fertilization on annual range species stimulate active growth but also accelerate the use of soil moisture. In years of inadequate rainfall, fertilization may cause the utilization of available soil moisture before the plants mature a full crop of seeds (38). However, under other conditions, the more efficient utilization of soil moisture will leave none for summer growing weeds (65). Studies in the Sacramento Valley on fertilized range indicate a 300 percent increase in efficient use of soil moisture where plots were fertilized with 100 lb./acre of nitrogen and 88 lb./acre of phosphorus (39).

Clipping, as opposed to grazing for clearing an area, may alter species composition. Murphy, Jones, and Love (44) reported that clipping encourages the summer growing forbs. Clipping appears to increase the level of soil moisture remaining for species which develop late in the summer.

To preserve the high content of protein, phosphorus, and carbohydrate, Kay and Torell (25) suggest using a chemical preservative, such as paraquat (1,1'-dimethyl-4,4'-bipyridinium dichloride), to stop plant development and "cure" the standing forage for use by grazing animals. With greater emphasis on forage quality in the future, and where there is no need for the replenishment of seeds for stand reestablishment, the practice of chemical curing may offer advantages to land managers.

Boot Stage To Flowering

At this stage of morphogenesis, the inflorescence is ready to emerge from the rolled leaf sheath, and to continue development towards anthesis and seed maturity. In annual grasses this is a vulnerable stage, because plants are still palatable and the immature seed heads may be subjected to grazing. In annual forbs the problem is not so critical, because many of them do not have a determinant type of flowering, but produce flowers on lateral branches, sometimes throughout the spring period. *Erodium* and *Medicago hispida* are particularly well adapted in this regard; flowers appear very early and continue until very late. Some of the annual legumes, such as *T. incarnatum* and *T. hirtum*, have a determinant flowering pattern, and are more vulnerable to grazing during these late

stages. Only through the formation of lateral flower stems is this vulnerability rendered less critical. The high density of plants growing on annual range virtually assures adequate seed production in most years, if intense grazing does not destroy the developing inflorescences. However, the number of plants which survive to the flowering stage is drastically reduced from the number of plants which germinated at the beginning of the season.

In earlier growth stages, fertilization was valuable in encouraging plant growth, but at flowering there is little benefit from fertilization. In fact, it may be detrimental if it has hastened maturity by depleting the soil moisture supply.

Palatability often changes as flowering approaches. *T. asperum* becomes much less palatable at the boot stage (33). Many forbs, particularly the annual legumes, take on a degree of unpalatability at this stage. Silica and fiber contents increase, and many plants become much rougher and stiffer in character.

Seed Maturity

As seeds begin to develop, carbohydrates are translocated to the seed heads of grasses and forbs. Concurrently, maturation of other plant parts proceeds rapidly. Photosynthesis is exceeded by respiration in older plant parts, and lower leaves begin to die. In the annual range, soil moisture stress is a common and prevalent environmental condition and becomes an overriding effect in hastening plant maturity and seed ripening. Management of annual rangelands at this stage may concentrate on several practices designed to manipulate the plant cover or to make continued use of the forage resource.

Range fertilization increases plant palatability, which provides excellent opportunities for continued grazing of the dry herbage. Less palatable species, when fertilized, have been observed to be consumed readily by livestock (43). The forage produced by fertilization is high in protein and other nutrients for the grazing animal (52).

Seed maturity of undesirable species can be prevented with herbicides during the period of seed maturation (9). Aminotriazol has effectively prevented the development of seeds of *T. asperum*, a late-maturing species. Late-maturing,

weedy species have been controlled by fire, which destroys their immature seeds after the desirable forage species have matured (14). During a critical period of 1 or 2 weeks, the early-maturing, annual forage species are dry enough to furnish fuel to support a fire which will destroy the maturing crop of medusahead seeds (41). Burning after the maturity of medusahead seeds is considerably less effective, because the hard seeds have been cast from the heads and lost into the litter, where they are protected by the volume of plant material and are unaffected by the passing of a fire over the area. In addition, mature seeds are less susceptible to the effects of high temperature (29).

Seed Dissemination

Dissemination of seeds from annual range species occurs at various times following maturity, depending on weather conditions and the structure of particular species. Seeds may be cast individually, as in *Bromus tectorum*, *Bromus mollis*, *Taeniatherum asperum*, *Avena barbata*, and *Trifolium subterraneum*; or by dehiscence of entire seed heads of *Aegilops triuncialis* L.

Seeds of annual species often have undesirable characteristics, such as spines, stout barbed awns, or coiled seed stalks, which catch in the fleece of sheep and reduce its value. These structures for attachment may provide an effective means of dissemination and even a means of transport and invasion to new range areas.

Management practices that may affect seed dissemination include removal of grazing animals (*Erodium* areas) before seed dissemination, restriction of livestock to weed-free areas, and burning. Some are ineffective; burning may actually scarify seeds, reduce litter cover and improve conditions for seedling establishment. Removal of livestock may not be realistic unless alternate feed sources are available.

Summary

Management of annual rangelands has gradually developed on a foundation of established biological principles. For example, we utilize information on nutritional requirements and phenology of plants as a basis for management decisions.

Much remains to be done to utilize existing knowledge in improving management practices. Because of their diversity, biological plasticity, and aggressive growth habits, annual species offer interesting opportunities for forage production. More information is needed on responses to manipulation by grazing and fertilization and on ways to manipulate competition during seedling establishment.

Annual forage plants have not always received the credit due them because of preconceived ideas embodied in range management practices that are based on climax concepts. Annuals are generally regarded as invaders (indeed most are) and they are listed as prime indicators of depleted or poor range conditions (which very well can be true in many cases). However, in some areas, annuals represent a tremendous grazing resource where they are relatively stable from year to year. Annuals often keep the community closed and make the most of the potential of favorable weather conditions.

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STRATEGIES AVAILABLE FOR MANAGING MULTISPECIFIC COMMUNITIES IN AUSTRALIA

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Abstract

Possible strategies for managing multispecific plant communities are discussed in the context of the geographic, climatic, social, political, economic, and biological environments of Australian rangelands.

Additional key words: Rangeland types, range management, range ecology.

Introduction

In the long term, the prime purpose of range management is the maintenance of the biological and physical environments—the renewable natural resources—on which the future viability of the ecosystem depend. It follows that the long term needs of the land and vegetation are of paramount importance, and should overshadow any conflicting shorter term needs of animals. Grazing industries must be financially viable, but maintenance of the resource must be the first consideration. Lands on which the resource cannot be maintained economically, under long term grazing, should not be used for this purpose.

The object of managing multispecific communities is to increase desirable species and decrease undesirable species by using strategies which manipulate the population dynamics of the species in the particular communities. These strategies exploit the inherent strengths and weaknesses in the life histories of the component species, and should be derived from a knowledge of the phenologies of those species.

The definition and application of management strategies for maintaining a desirable spe-

cies mix is difficult enough for any one multispecific community managed as a separate entity. The problems are much greater when several multispecific communities occur in a single grazing area. In most such situations, the preference of animals for a particular community and the conflicting management needs of the various communities make it difficult, or even impossible, to define or apply suitable management strategies for the whole complex. This, in itself, raises an important management principle; as far as possible, rangelands should be subdivided into reasonably homogeneous grazing units so that appropriate management strategies can be applied to each plant community separately. This ideal situation is commonly unattainable in practice and the real-world manager is concerned mostly with mixtures or mosaics of communities. He is faced constantly with the alternatives of managing for conservation of the most susceptible communities or of sacrificing their condition in the interests of greater production from the complex.

At a broad general level, the principles of range management are world wide. However, the strategies available for, appropriate to, or which can be devised for, the management of particular communities in a particular country depend on a host of local and national factors. The most obvious are biological; the species in the community, their characteristics and reaction to management practices, and possibly the availability of complementary communities to either absorb stock, or from which stock can be drawn, to implement the particular practice. Less obvious are the geographic, climatic, economic, social, and political environments within which the grazing enterprise operates and which all impose constraints on possible management practices (27).

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General Environment

Geography

Australia's rangelands consist of a single vast area (5,700,000 square kilometers) extending more than 3,200 kilometers from east to west and more than 2,000 kilometers from north to south (figure 1). Its relatively low latitudes (16°S. to 35°S.) are more akin to those of Mexico than U.S.A. The highest point is 1,500 meters above sea level, but all the country used for grazing lies between sea level and 700 meters. No large, permanently flowing rivers, capable of supporting irrigation agriculture, cross the area. About half the area is drained by ephemeral streams which flow toward internal drainage basins; the remainder has no organized drainage system (8). The low relief is in marked contrast to much of the U.S. rangelands; for example, there are no mountain rangelands in Australia suitable for summer use only. This partly explains the lack of development of, or interest in, seasonal grazing systems in Australia, although such systems are widely used on similar terrain in southern Africa.

The human population is very low (about 300,000) and this, combined with the fact that the area is broken by large areas of unoccupied spinifex sand plains and dune fields, explains the poor communications and transport systems. No railways or sealed (hard-surfaced) roads cross the area in any direction; those which do exist mainly link scattered mining towns with coastal cities. As most of the materials required by the grazing industries have to be brought from coastal cities and most of the produce despatched to them, the poor transport system and the long distances involved mean that the industries have to bear high freight costs. The freight problem is further aggravated because little of the produce is used domestically, most of it being exported from Australia and sold on international markets. Compared with the United States, the net result is relatively high costs and lower return.

Another aspect of the low population of rangeland Australia is that there are no large cities, no universities and only a few scattered small research centers—a very different situation from the United States.

Climate

The whole of rangeland Australia is arid or semiarid. In the north, rain falls only in the summer, but in the remainder there is no well defined rainy season, and rain may fall in either summer or winter, or both, or neither (25). Everywhere rainfall is erratic and, as the winters are not cold enough to inhibit plant growth, each fall of rain tends to produce a short, discrete plant growth period; winter rainfall is not accumulated in the soil to produce a reliable spring growth period, as is common in the U.S.A.

Because of the short, erratic plant growing periods, there is little in the way of regular rhythms in the vegetation, which is probably another reason for the lack of serious consideration of seasonal grazing systems in the past. It also means that any seasonal grazing strategies developed in the future will need to be flexible, and their application related more to actual periods of rain than to a calendar or seasonal basis. An example of one such strategy is given in Burrows' paper where, for control of *Eremophila gilesii*, he recommends heavy stocking following any winter fall of rain greater than 40 mm.

Another aspect of the erratic rainfall is that long periods (greater than a year) without any significant growing periods are common (9). Any management strategies must take cognizance of this; any system designed to take advantage of seasonal characteristics or responses of vegetation can only be superimposed on general drought management strategies.

Social And Political Aspects

Most of Australia's rangelands are leased to individuals or companies, from State governments or, in the Northern Territory, from the Commonwealth. The leases are large and the leases long term—30 to 50 years, in some States perpetual—(11). No counterpart exists in the United States for this system of land tenure, but in practice the long term leasehold system approaches that of private ownership in the United States. In fact, the leaseholders are commonly referred to as owners. In Australia's rangelands, there is no equivalent of the U.S. Federal or

State forest lands, or of the lands administered by the Bureau of Land Management. This is possibly a reason for the lack, in Australia, of any strong Federal or State agencies for rangeland research and management. It also means that management of the rangelands is largely the prerogative of the individual leaseholders, for whom no training facilities are available in Australia. Everywhere management strategies designed from research results will have to be extended to individuals; nowhere are they applied directly by government agencies.

The rangelands are administered by the Lands Department of each State and the Northern Territory. Legislative provisions against overstocking and degeneration of leases exist in each State, the penalty for nonobservance generally being forfeiture of the lease. However, the means for applying the legislation, that is, range monitoring services and range condition and trend standards, are nonexistent. Under the Australian land tenure system, individual flocks and herds graze year-long within the confines of individual stations; there are no summer or winter leases. Similarly, nomadism is precluded by the lack of common land, although stock routes are used to a certain extent for a similar purpose.

Economics

The main features relevant to the application of management strategies is the very extensive nature of the grazing enterprises. Large stations with large flocks and herds are operated with low capital and low labor inputs. Returns per unit area are extremely low, returns per animal are low, but, until recently, returns to capital and labor have both been high in both the sheep and cattle industries. In recent years, depressed prices for wool and rising costs have reduced the profitability of the sheep industry, and many stations, particularly smaller ones, are facing financial problems. Some amalgamation of properties, itself a management strategy, is inevitable.

The important point is that profitability has in the past depended on low capital and low labor. Any management strategies which increase capital or labor inputs, without more-than-com-

mensurate increases in productivity, are impracticable.

Animals

Broadly speaking, sheep are grazed in the south and cattle in the north, although in recent years there has been a tendency for sheep properties to also carry some cattle or, in some cases, to convert entirely to cattle. Under the extensive system described earlier, the cattle and sheep are able to range widely in large paddocks. If these paddocks contain several plant communities, the stock are free to select the areas they graze at any time, thus complicating management strategies.

Domestic stock are not the only herbivores supported on the rangelands. Introduced rabbits occur in the south, and reach plague proportions at times. Kangaroos and other marsupials are widespread. In many areas, termites possibly account for as much as half of the animal biomass and grass consumption. Other invertebrates, such as grasshoppers and caterpillars, can be important at times. All these animals must be considered in devising and applying management strategies. For example, resting areas from domestic stock may have little effect if rabbits are not controlled. In another example (from southern Queensland), the increased grass production following destruction of mulga trees caused a buildup of grass-eating termites, the end result being a bare area almost completely covered with termite nests (34). The inference from this example is that the mulga-grass-termite-sheep system was stable but the grass-termite-sheep system was self-destructive, at least in this particular area.

Management Tools

The management tools available in the United States are also available in Australia, but there will be differences between the two countries as to the practicability of applying them and the results obtained. The methods include burning, chemical sprays, mechanical treatments, and grazing management.

Essentially rangeland grazing enterprises are climate/land/plant/animal systems, and it is desirable that their future stability and produc-

tivity be ensured by manipulating intensity of use, season of use, and distribution of stock and kind and class of animals, according to ecologic principles. Burning, chemical spraying, and mechanical clearing are violent tools which bring about drastic changes in the ecosystem. More often than not, the need to resort to them is brought about by poor grazing management.

Fire seldom is used or recommended as a management tool for Australian ranges because, under an erratic rainfall regime, a burnt area may remain bare, unproductive, and susceptible to erosion for long periods. Burning is used on spinifex communities, particularly in areas of reasonably reliable rainfall. Here the main fuel is coarse, unpalatable spinifex, and the areas are revegetated within a reasonable period (24).

Selective herbicides have not been used to control undesirable species on Australian rangelands, probably because of the high costs and the large areas involved. For the same reasons, the use of mechanical methods for clearing timber on the rangelands has been limited except near the higher rainfall margins where the response in terms of increased forage is greater. Little use has been made of pitting, furrowing, water spreading, and range reseeding, although there is considerable interest in them. Very variable responses have been obtained where they have been tried, partly because of the vagaries of climate, but partly because insufficient attention has been paid to selecting the right techniques for particular situations and the best sites on which to start.

Ecological management of the composition of range plant communities by manipulating various aspects of grazing use (intensity of grazing, season of use, and so forth) is generally the cheapest form of management to apply. However, because of the wide range in kind and degree of possible practices, and the slow nature of the response, it is often difficult to give precise prescriptions. The effectiveness of grazing management, in manipulating the kind and amount of vegetation, depends on the degree of animal control available to the operator. For maximum efficiency, the operator needs to be able to graze plant communities individually, and to get the desired grazing pressure evenly distributed over the area. Thus, management through control of

intensity of use and season of use is likely to be more effective on the more intensively developed United States rangelands than on the very extensively managed Australian rangelands. In many Australian situations, additional fencing and water supplies, and possibly extra labor, would be needed, and these may be economically impracticable. However, strategies involving grazing management should not be dismissed in Australia because they could be effective in many situations, even with the existing degree of stock control.

Management Strategies For Australian Rangelands

With such a large and diverse area, it is only possible to consider management strategies in a very general way, but it is possible to select some as being appropriate and to reject others. Two extreme strategies sometimes advocated—removal of stock from the entire area and intensive use followed by abandonment—will not be considered.

The overriding factor affecting management is climatic. The highly erratic rainfall, coupled with the lack of winters cold enough to inhibit growth, causes forage production to be highly variable both in amount and season. Some form of nomadism, moving stock to wherever forage is available, would seem best suited to the situation (21, 30). The land tenure system precludes true nomadism, but systems incorporating some of its features are used and could be used more widely. The important feature is flexible stock numbers. One way of achieving this is for operators to own several stations in different districts, and move stock from one to the other, depending on the forage situation. Stock can also be sent to other areas on agistment. Another practice is to reserve part of the property (generally a part with perennial grass or browse species) for use only during long dry periods. Another possibility would be to establish State-owned grazing reserves, which could be kept for use only during droughts. Such reserves could be established fairly easily in some of the sheep grazing areas by the purchase of uneconomic leases and might play a somewhat similar role to Federal lands in the United States. However, the success of the reserves would depend on the

establishment of strong and competent administrative agencies to define proper management practices. In the absence of professionally-qualified agencies, such reserves would be open to misuse, and the lands would probably be better managed by experienced graziers under the present system.

Another way of achieving flexibility of stock numbers is through selecting an appropriate grazing enterprise. For example, in the cattle industry, stock numbers are fairly inflexible in an enterprise aimed at producing 3- or 4-year old steers, where annual turnoff is 15 percent or less of the herd. More flexibility is possible in enterprises producing young animals; in poor years, calves can be turned off at weaning but in good years kept for sale as yearlings. In the sheep industry, wethers can be kept in good years but disposed of in poor years. These systems enable rapid reduction of flocks and herds to a breeding nucleus but result in rather large fluctuations in income from year to year. Their use could be encouraged by developing methods of averaging income over periods of longer than a year. Some progress in this direction has been made in Australia, for example, the drought bonds scheme, and the provision for graziers to average income over several years for taxation purposes.

As far as grazing systems are concerned, only one—yearlong set stocking—is in general use. Stock are spread over the whole property for the whole year, some regard being given to differential stock carrying capacities of different parts but none to differential season-of-use requirements for maintaining a desirable composition in particular communities. Under such a system, it is not surprising that range degeneration is commonly equated to overstocking, whereas in many circumstances it is probably due to mismanagement or undermanagement.

It is clear from the widespread deterioration in some range types that they have been stocked too intensively, at least under the yearlong system and possibly under any system. It is likely that lower intensities would not only improve range condition, but would be financially rewarding, because better nutrition would increase productivity and reproduction per animal. Administrative bodies and graziers are slowly be-

coming aware of the need to adjust stocking intensity to the long term needs of the land. A system, based on the nature and condition of the land types, for estimating safe carrying capacities of properties in normal and drought periods has been developed (7). The system stipulates the degree of reduction of stocking intensity needed as droughts proceed. Like all such systems, there is a danger that the landholder will take the calculated stocking rates, intended as guides, as fixed and legal minimum levels.

Few trials of rotational grazing systems have been carried out on Australian rangelands. Roe and Allen (31), working on a Mitchell grass pasture in southwest Queensland, found no difference in wool production between continuous and rotational grazing under stocking intensities of 1 sheep per 1 to 3 ha., but a tendency for liveweights to be lower under rotational systems. Mitchell grass was reduced under heavy grazing with all systems, and under medium and light stocking intensities on the summer stocked treatments. Plant production was higher under continuous grazing—in fact it was higher for continuous grazing at the medium stocking rate than for rotational grazing at the low rate. Tupper (unpublished data), working on a *Danthonia* grassland in a winter rainfall area, has shown that a system in which forage on part of the areas is saved for late summer/early autumn grazing has no advantage, in terms of animal production, over continuous grazing.

There is undoubtedly scope for testing and applying seasonal grazing systems, in which intensity of stocking on particular communities is varied in different seasons, according to the effect on the species in that community. The need for such systems and the detailed specifications vary tremendously. The main difficulty in devising seasonal grazing systems is the lack of precise knowledge of the phenology of the plant species and of their reaction to grazing at different stages. The main problem in their application is adequate control of stock.

Some rangelands, particularly in southern Australia, are in such poor condition that grazing management alone (even no grazing for very long periods) may not be sufficient to effect recovery. Regeneration will need to be assisted by mechanical treatments such as pitting, furrow-

ing, and reseeded. Such treatments have generally been dismissed as uneconomic in Australia, at least in the short term. Most trials have yielded unspectacular results, but no serious attempts have been made to design, from first principles, specific methods for particular landscapes and problems. When only spare time labor is used, costs can be as low as 12 to 15 cents per hectare.

Rangeland Types And Their Management

Australia's rangelands contain a multitude of climate/soil/vegetation types arranged in many spatial combinations. Common features are infertile soils and a low forage production of low nutritive value. In recent years, several descriptions using a similar broad general classification

have been published (18, 22, 25). The classification grossly oversimplifies the situation but provides a comprehensible framework within which to discuss general management requirements and strategies. The main types are Mitchell grass grasslands, chenopod shrublands, low woodland, spinifex, and floodplains.

Mitchell Grass Grasslands

These mainly occur in a broad arc across the north and north-eastern part of the area (3, 24, 28) (figure 1), and have a higher primary productivity and higher stock carrying capacity than other types. Rainfall is comparatively high (mostly 200-500 mm.) and reliable, almost entirely restricted to summer in the north but with

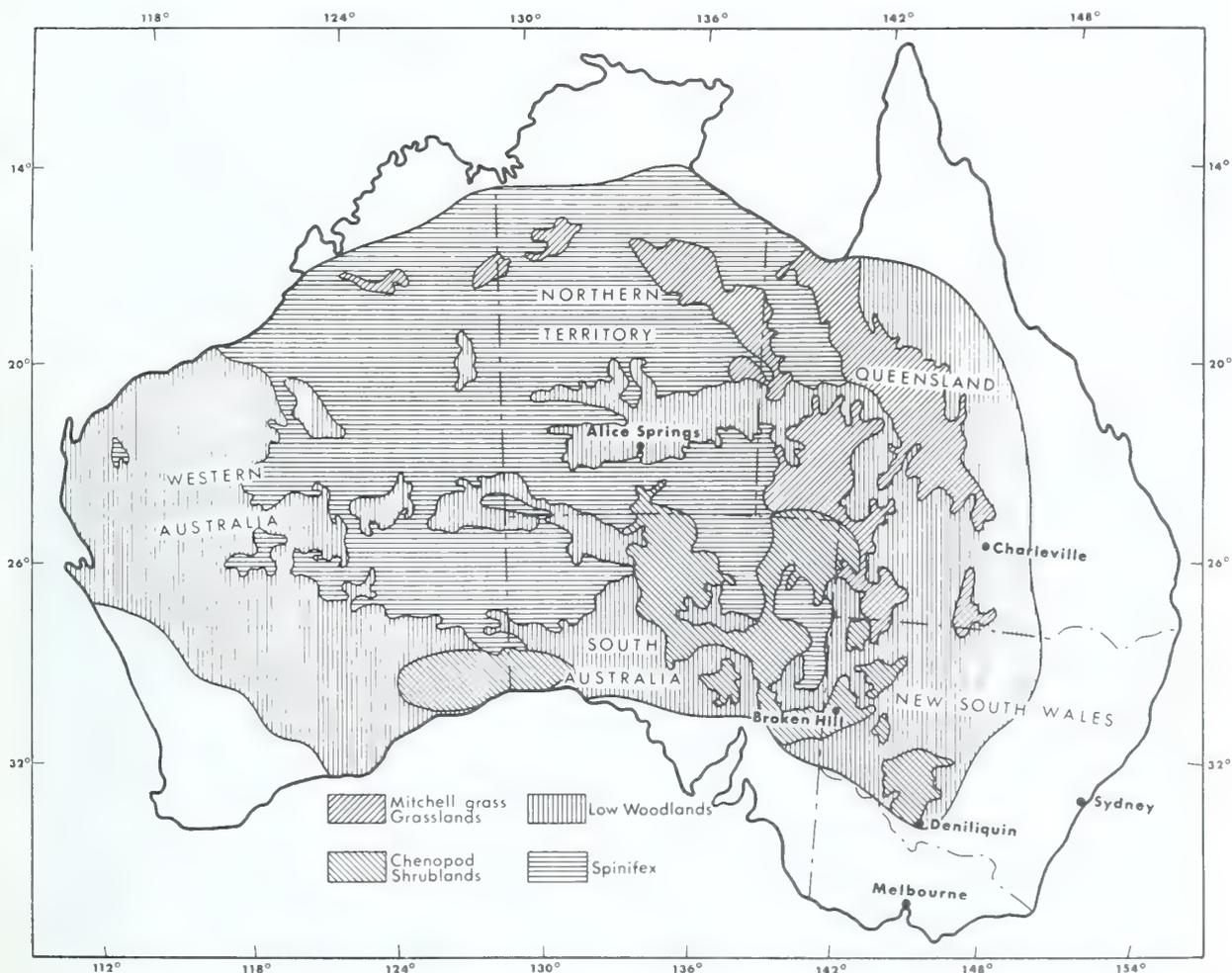


FIGURE 1.—Map of Australia, showing rangelands.

a significant winter component in southern and central Queensland. The soils are everywhere fine-textured cracking clays, and relief ranges from flat to very gently undulating. The landscapes are essentially stable, with little risk of either water or wind erosion. The vegetation is dominated by one or several of the Mitchell grasses (*Astrebla* spp.), which are all rather coarse bunch grasses (figure 2). Following rains, a cover of mainly palatable annual grasses and forbs is produced in the interspaces between the bunch grasses. Livestock concentrate on these palatable annuals. Normally, by late winter the annuals have been consumed, and the stock then graze the less palatable and less nutritious bunch grasses, which nevertheless provide a reserve of low quality standing hay to maintain stock until the next summer. In the event of failure of summer rains, there is little forage to carry stock through another winter.

Mitchell grasses respond to small falls of rain by sprouting from axillary buds on the lower 12 to 20 cm. of the dry culms. Larger falls of rain also produce new tillers from basal buds and rhizomes (14).

In these communities, where the desirable perennial Mitchell grasses are naturally deferred by stock, yearlong grazing appears to be a satisfactory system, provided that intensity of stock-

ing is so adjusted that the Mitchell grasses are not grazed shorter than 15-20 cm., so that they retain their capacity to respond to small falls of rain. If summer rains fail, the only forage available to stock is Mitchell grass stubble remaining from the previous year. In this event, stock should be removed, not only to retain the capacity of Mitchell grass to respond to small rains, but because there is evidence of heavy mortalities in plants grazed below 3 to 5 cm.

A century of grazing by livestock has caused very little erosion in Mitchell grass country and little apparent change in the vegetation of most areas. However, there are some exceptions to this general picture. On large areas of the Barkly Tableland in the Northern Territory, Mitchell grass has decreased dramatically over the last 2 decades; in fact, in some areas it has been virtually eliminated, and the community transformed to an annual grassland. With the low erosion hazard, the landscape remains stable, but the late winter/early summer forage reserve no longer exists, and thus the community has lost its stable yearlong stock carrying capacity. The cause of the degeneration is almost certainly heavy grazing of the Mitchell grass plants, probably during attempts to carry stock on the stubble remaining during a year following failure of summer rainfall. Rest periods following summer



FIGURE 2.—Mitchell grass grassland near Charleville in central Queensland.

rains are probably required to allow new stands of Mitchell grass to develop, although it is not known whether Mitchell grass will reestablish in competition with the vigorous annual community which replaces it. Another possible exception to the general picture of stability in Mitchell grass communities is the increase in less desirable bunch grasses, particularly *Aristida latifolia*, in some areas in Queensland (29).

Chenopod Shrublands

The chenopod shrublands (figure 3) are restricted to southern Australia where, on the average, summer rains account for 50 to 70 percent of the annual total, but winter rains are more reliable and effective. The shrublands are dominated by various species of *Atriplex* and *Kochia* (2, 12, 13, 32), and are structurally somewhat similar to sagebrush communities in U.S.A. As with Mitchell grass communities, stock graze the annuals produced between the shrubs following rains; but during long dry periods, the less palatable shrubs provide a reserve of forage (15, 16).

The chenopod shrublands of the Riverine Plain (figure 1) in southern New South Wales are quite different from those of other areas. Here they occur under a mean annual rainfall between 250 and 400 mm., on flat plains of fine-textured clay soils similar to those of the Mitchell grass rangelands, and with a similar low erosion hazard. Rainfall is relatively high and

reliable, as is the stocking rate (1 sheep to between 1 and 2 hectares). Because of this, the Riverine Plain carries about half the total stock carried on all shrublands, although its area is small compared with the total. On the higher rainfall part of the Plain, grazing in the past has converted the shrublands into a disclimax perennial grassland (dominated by *Danthonia caespitosa* and *Stipa variabilis*), which is as productive as the original community (36, 37). On these parts, and on other areas of the Plain where it can be demonstrated that a grassland will be produced, the shrubs can be considered as undesirable and management can be aimed at reducing or eliminating them. This is simple, as it has been shown that a single complete defoliation is sufficient to kill *Atriplex vesicaria* (17), which dominates most of the nongrass part of the Plain.

Most of the chenopod shrublands are different from those of the Riverine Plain. They occur under a mean annual rainfall less than 250 mm., on undulating terrain with mostly texture-contrast or coarse to medium textured calcareous soils. Stocking rates do not exceed 1 sheep to 4 hectares and are as low as 1 sheep to 15 hectares. If the shrub cover is destroyed, a bare landscape with an ephemeral cover following rains is left. Erosion hazard is high, and it is essential to maintain a stand of vigorous shrubs adequate to protect the landscapes and to provide reserve forage during long droughts. In saltbush communities, the aforementioned ease of killing



FIGURE 3.—Shrubland of *Kochia pyramidata*.

Atriplex vesicaria makes it difficult to maintain stands. On the other hand, it has been shown that moderately heavy grazing improves the vigor and health of *Atriplex vesicaria* stands (23). As seedlings of saltbush establish following autumn rains (4), it is likely that rest periods at such times will result in better stands. However in Western Australia, Wilcox (private communication) has observed that winter use and summer rest has resulted in better stands of *Atriplex paludosa*, *A. rhagodioides*, and *Kochia pyramidata* than yearlong grazing at similar intensities. He has no observations on summer use and winter rest, which may be even better.

With some of the other shrub species, the original shrub cover was so dense that herbaceous production between the shrubs was inhibited. In such cases, some reduction in shrub density is warranted (12). Thus the various shrubland communities provide good examples of managing for a balance between species; the aim being to maintain stands of vigorous shrubs, open enough to get as much herbaceous production as possible. A means of assessing this balance, in terms of the physical protection afforded by the shrubs, has been proposed by Marshall (19).

The management problem is to maintain a balance between enough low trees and bushes to provide landscape protection and reserve forage for long dry periods, and an open enough stand to allow a good ground cover to develop after rains. Because of the many different species involved, the wide range of climate and land environments, and the large variation in present condition, the actual management strategies required differ greatly from place to place. This can be illustrated by reference to mulga (*Acacia aneura*), which is the most widespread and best known of the dominant low trees. In the south, most areas of mulga country are in poor or very poor condition; the tree cover has greatly decreased to a few scattered old trees or none at all, ground cover has also decreased, and some areas have been reduced to bare scalds or surface sand drifts. The reduction in trees is generally attributed to lack of recruitment of young trees into the population (6), probably because young seedlings are consumed by sheep or rabbits. From our knowledge of the biology

of mulga (*Acacia aneura*), it appears that establishment requires a long sequence of events to ensure flowering, seed set, breaking of dormancy, and germination (10). In the south, the conditions apparently occur infrequently. Rest following such occurrences may allow regeneration, although rabbits probably would need to be controlled also. These southern areas of mulga country clearly require management practices for stabilizing the soil surface, increasing the tree cover to an adequate level, and increasing the ground cover; in many cases mechanical treatments will be required to aid regeneration.

Large areas of the chenopod shrublands have been reduced to poor or very poor condition, and some areas are severely eroded. Because of this, the main direction of management should be towards regeneration, and in many cases this will not be achieved by grazing management alone; mechanical treatments, with or without reseeding, will be required.

Low Woodlands

Low woodlands (figure 4) are widespread throughout all the rangelands, except the far north, and cover nearly a third of the total area (2, 3, 12, 13, 24, 32). Mean annual rainfall ranges from 125 to 500 mm. Relief varies from flat to undulating, and soils from coarse to medium textures. Sensitivity to erosion varies from high on undulating country to very slight on flat areas on old Tertiary land surfaces. Many different communities, dominated by various species of *Acacia* and other trees of similar stature (for example, *Heterodendrum oleifolium* and *Casuarina cristata*), are included. The trees range from about 2 to 10 meters in height. There is commonly a scattering of shrubs and a ground cover of mostly annual grasses and forbs, with a perennial grass component in some areas. It is possible that perennial grasses were originally more widespread and that the low tree/annual communities are a degenerate stage. Structurally, many of the communities superficially resemble mesquite rangelands in the United States.

Following rains, stock graze the ground cover but, in long dry periods, are maintained by browsing the bushes and low trees, which may



FIGURE 4.—Low woodland of mulga (*Acacia aneura*).

have to be cut with chain saws or pushed over with bulldozers.

In central Australia and some parts of Western Australia, mulga stands have a cover of 500 or so trees per hectare, and a reduction in density is desirable (26, 35). It has been shown in trials in Western Australia that clearing thick mulga promotes *Danthonia* and *Neurachne* (both perennial grasses) and forbs. Production is increased by 50 percent, and carrying capacity, lamb marking percentages, and wool production per head are all raised (35).

In central and southern Queensland, mulga has increased under grazing and impenetrable stands, with as many as 8,000 trees per hectare and virtually no ground cover, have been produced (5). In this area, mulga is clearly a weed and management for reducing it is required. Beale (personal communication) has found in a trial of various tree densities that ground yield was similar for 160 and 40 trees per hectare. The higher density has the advantage of additional drought forage reserves. He also found that mulga germination was highest at 160 trees per hectare, but probably

could be controlled by heavy stocking at the time seedlings are present.

In some areas of mulga, unpalatable shrubs, especially *Eremophila* spp., have increased. In the Goldfields District of Western Australia, unpalatable forms of mulga itself have replaced original stands cut for timber and firewood for mining operations.

In the higher rainfall parts of the rangelands in northern New South Wales, the original open, low woodland on an undulating topography has been converted to dense unproductive scrub through the increase in unpalatable shrubs and low trees (1, 20). It has been suggested that burning or heavy stocking by goats might be solutions to the woody weed infestation, but it is likely that mechanical or chemical treatment will be necessary. It is doubtful if this can be done economically at present, although much of the area is suited to water spreading, the use of which would raise productivity.

Spinifex

The vast areas of spinifex sand plains (fig. 5) and dunefields are mostly unoccupied because they

will not support livestock, so the question of management does not arise. However, in the north some areas of spinifex (mainly *Triodia pungens* and *Plectrachne* spp.) are grazed (24). In the Pilbara area of Western Australia, the original communities were dominated by unpalatable spinifex but contained a small proportion of better perennial grasses. Under grazing, the softer grass component was eliminated and replaced by spinifex, making the country useless for grazing. On the deeper soils, it has been found (33) that palatable grasses can be maintained by a combination of burning in the summer to kill the spinifex and deferment to allow the softer grasses to develop.

Flood Plains

Flood plains (fig. 6) or frontage country occur along the larger watercourses, but there are also a very large number of small flood plains associated with minor channels and scattered throughout other rangeland types. Many of the natural waterholes are in the flood plains and so they were the first areas stocked. Stock tend to con-

centrate on them and so they have been heavily grazed since settlement. As a result, most are in poor condition and many areas are severely eroded. However, even in their poor condition they produce short, attractive forage following rain or floods, and are preferentially grazed by stock. Where large enough, they should be fenced and managed separately. Where too small to manage separately, the management of the complex in which they occur should be based on their needs and condition, because of their importance in stock carrying capacity and performance.

In most cases, mechanical treatment will be necessary to restore their productivity, or even to prevent further degeneration. Where large amounts of flood water are involved, the treatments will need to be carefully engineered.

Conclusion

Australia generally lags behind the United States in the application of scientific principles



FIGURE 5.—Spinifex sand plain dominated by *Triodia basedowii*.



FIGURE 6.—Flood plain in poor condition, showing bare scalded areas.

to the management of rangelands. We have little knowledge of the phenology of even the major range species, and what we have has not been tested in field trials.

For the development and application of better management strategies for Australian rangelands, the fundamental requirement is the acceptance of the fact that the long term success of grazing enterprises depends on the maintenance of good range condition. From this would follow a recognition of the importance of maintaining range condition rather than stock condition. In turn, range condition and trend standards would be developed and applied, and plants recognized as increasers and decreaseers. This would create a demand for strategies for managing the increase or decrease of particular species. Such strategies would need to be based on a knowledge of the life histories of the species concerned.

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A REVIEW OF RESEARCH RELATED TO DEVELOPMENT OF GRAZING SYSTEMS ON NATIVE RANGES OF THE WESTERN UNITED STATES¹

By Carlton H. Herbel²

Abstract

Research studies on grazing systems on native range in the 17 contiguous Western States are reviewed. Yearlong-continuous grazing was superior to seasonal grazing on the California annual rangelands. There was only limited success with any grazing scheme other than continuous on rangelands grazed only for a part of the year (seasonal ranges). The deferred-rotation system at Sonora, Tex., has resulted in sufficient range improvement to permit a 33-percent increase in stocking as compared to continuous grazing.

Grazing research should include studies on the entire ecosystem, not on just a few of the major species. Livestock performance per unit area may be more important in evaluating grazing studies than individual animal performance. Grazing studies should be flexible to permit consideration of fluctuation in plant attributes due to variations in weather conditions. Much additional study is needed to develop the most productive grazing scheme for each range operation.

Additional key words: Grazing management, grazing systems, continuous grazing, deferred-rotation grazing, rest-rotation grazing.

Introduction

This review is concerned primarily with research on grazing systems on native range in the

17 Western States. Only studies including some scheme of livestock manipulation other than continuous grazing are considered. Basic information on climate and vegetation are presented, so that results may be interpolated as widely as possible.

Grazing terminology follows that of the American Society of Range Management (29). Deferred-rotation grazing is to leave a range unit, or units, ungrazed for part of a year and to rotate the deferment among range units, in succeeding years. Rest-rotation grazing is to leave a range unit, or units, ungrazed for at least one year and to rotate the deferment from grazing among range units in succeeding years.

California Annual Rangeland

In the California valleys and foothills, annual grasses dominate the vegetation. Before the white man settled here, the area was probably dominated by perennial grasses, such as *Stipa cernua* Stebbins and Love, *S. pulchra* Hitchc., *Poa scabrella* (Thurb.) Benth. ex Vasey, *Melica imperfecta* Trin., *Sitanion hystrix* (Nutt.) J. G. Smith, and *Elymus triticoides* Buckl. (37). Because of fire and heavy grazing, the area is now dominated by annuals, *Avena fatua* L., *Bromus hordaceus* L., *B. mollis* L., *B. rubens* L., *B. rigidus* Roth., *B. tectorum* L., *Hordeum murinum* Huds., *H. pusillum* Nutt., *Festuca myuros* L., and *F. megalura* Nutt. While forbs are not abundant on this type, they are important to the grazing animal. The most important are *Medicago hispida* Gaertn., *Erodium cicutarium* (L.) L' Her., and *E. botrys* (Cav.) Bertol. On foothill ranges, an open savanna of *Pinus* L. sp., *Quercus* L. sp., and *Ceanothus* L. sp. forms an overstory over the annual grass type (36).

At Hopland, Calif., about 160 km. north of San Francisco and 91 cm. average annual pre-

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precipitation, the annual plants germinate in the fall, grow slowly until early spring, grow rapidly for about 6 weeks, and are usually mature and dry by June 1 (10). The size of the forage crop is related to weather conditions and may differ over 100 percent between years. The species composition also varies widely from year to year. The various species mature at different times during the spring. In planning a grazing strategy, several points are important; the short and variable time when species mature, variable maturation dates of desirable and undesirable plants, a wide difference in forage quality as related to available moisture and stage of maturity, and fluctuations in stage of maturity due to site (10).

Light utilization by livestock results in an increase of the tall annual grasses and a decrease of the desirable forbs. Heavy grazing use in the fall reduces plant growth in the winter (2). Heady (9) showed that mulch in excess of about 784 kg./ha. favored the tallest grasses. With no mulch, the vegetation was composed of undesirable forbs and grasses, and the herbage yields were reduced to about half of the mulch plots. From these studies, Heady (10) concluded that degree of utilization is important in determining the characteristics of the next crop.

Hervey (14) changed the species composition with burning treatments and Heady (10) with seeding and mulch manipulation. There seems little doubt that composition of the annual type can be changed, but the results are temporary and last only as long as the treatment is maintained.

Studies at the San Joaquin Experimental Range in central California (average annual precipitation of 46 cm.) showed a consistent advantage of yearlong-continuous grazing over seasonal grazing in breeding cow performance and calf weaning weights. The best balance of seasonally preferred plant species occurred on ranges grazed continuously yearlong (5). Similar results were obtained with sheep at Hopland. One range unit was divided into three divisions. One division was grazed in the early part of the growing season, one in the middle, and the third near the end of the growing season. The stocking period was rotated on an annual basis so that each division was grazed at each time only once in 3 years. The sheep were allowed to graze all three

divisions during the dry season. The average weaning weight of lambs has been consistently higher in the range unit with yearlong-continuous grazing. The grazing treatments did not affect species composition, density, or herbage production.

The Pacific Bunchgrass Region

A study conducted at the Burgess Spring Experimental Range in northeastern California during 1936-51 (16) led to the design of a rest-rotation grazing system. Numerous lava flows and a few high peaks top an extensive plateau with an elevation that ranges from 1,068 to 2,440 m. Interspersed among the mountains are many plains and valleys. Some of the valleys are closed or poorly drained. Annual precipitation during 1935-54 averaged 46 cm. at Blacks Mountain Experimental Forest, 19 km. from Burgess Spring. On the average, 74 percent of the total occurred October 1-April 1, primarily as snow; 21 percent occurred April 1-July 1; and 5 percent during July 1-October 1. The snowpack averaged 46 cm. Average daily temperatures ranged from -5° C. in January to 14° C. in July.

Grassland, sagebrush, juniper, and pine types occupied 63 percent of the total area at Burgess Spring and furnished most of the forage used by livestock. The remaining area, of little use to livestock, was dominated by trees and shrubs. On 97 percent of the grazeable range, the primary species were bunchgrasses and other perennial plants that reproduce from seed. The grassland type was made up of wet meadow, closed basin, drained basin, and terrace sites. The major plants were *Festuca idahoensis* Elmer., *Poa nevadensis* Vasey ex. Scribn., *P. secunda* Presl., *Deschampsia caespitosa* (L.) Beauv., *Sitanion hystrix*, several *Carex* L. sp., and various forbs, shrubs, and trees.

The average seasonal development of herbaceous vegetation in the pine type was illustrated with *Festuca idahoensis*. Growth began about April 1 after the snowpack melted, and ended with seed ripening in early August. Half the seasonal yield of herbage was produced by the end of May and 90 percent by the end of June. Some plant species developed earlier and some later than *Festuca*; development also varied as much as 33 days from year to year. Herbage

production varied from 51 percent below average to 43 percent above average during the study periods (16). Clipping *Festuca* plants 3.8 cm. above ground surface at any time of the season reduced herbage production, basal cover, flower stalks, and height. The effects were more detrimental during periods of rapid growth. Basal area of *Festuca* plants was reduced about 50 percent the year following clipping, even when clipped 50 days following seed ripening. Four years of rest following 4 years of clipping at the milk stage resulted in little or no recovery of basal area. No flower stalks were produced in the first year of rest, but good production was obtained in subsequent years (16).

Cattle grazed season-long (late May-late October) in three fenced units; one was representative of cutover pine type, and two were representative of grassland types. In both the grassland and pine types, cattle grazed certain plants and certain areas more consistently than others. This resulted in a very uneven utilization of the range. The pattern of use was similar from year to year. Nearly all of the plant species in the pine type were grazed. However, 12 species supplied 95 percent of the forage consumed by cattle. The degree of use of a species was affected by its abundance, distribution, and the seasonal preference of the cattle. Use of *Festuca* averaged only 32 percent during 1936-46 in the pine type. It was 65 percent in 1945 and 80 percent in 1946. By 1946, grazed areas had fewer, smaller, and less productive *Festuca* plants than comparable ungrazed plots.

Gains of yearling heifers continued until early October, with the highest weight gains during the period of rapid *Festuca* growth (prebloom to maturity).

Hormay and Talbot (16) concluded that under continuous seasonal grazing, the desirable plants are destroyed by selective grazing. Selective grazing cannot be prevented by adjusting the stocking rate, but its harmful effects can be reduced by not grazing the range at appropriate intervals. The improvement of bunchgrass range depends on restoring the vigor of desirable plants so that there can be an abundant reproduction of these plants. To obtain reproduction, it is necessary to rest the range from grazing for three specific reasons: (1) To restore plant vigor, (2)

to insure seed development, and (3) to insure seedling establishment. Based on the information developed at Burgess Spring, Hormay and Talbot proposed a rest-rotation grazing system with the following steps: (1) Graze all season for maximum livestock production, which may result in a reduction of plant vigor; (2) rest one or two seasons, until plant vigor is restored and there is some accumulation of litter; (3) rest until seed is ripe, then graze remainder of season to trample seed into soil and for maximum livestock production; and (4) rest one or two seasons, to permit establishment of new plants. The time required for each step depends on the growth requirements of the key species of the range.

The vegetation in the rested units constitutes a forage reserve that can be used in drought years. Range improvements, such as seeding and control of noxious plants, may be scheduled during rest periods. Stocking is based on the utilization of all forage species. Fairly heavy stocking forces greater use of the less palatable forage species and the less accessible grazing areas (16).

A trial of rest-rotation grazing was initiated on the Harvey Valley allotment of the Lassen National Forest in 1954 (15). That area has similar soils, vegetation, and climate to Burgess Spring. Good stands of *Bromus inermis* Leyss, *Agropyron desertorum* (Fisch.) Schult., and *A. intermedium* (Host) Beauv. were established by seeding and the native grass stands were improved on some areas by controlling the shrubby *Artemisia* L. sp.

There was a drought in Harvey Valley in 1959-61. The precipitation from July 1, 1960, to June 30, 1961, was 27 cm. or 59 percent of average. Ratliff and Rader (31) concluded that forage production was adequate for normal grazing and that the cattle made good gains. However, the stocking in 1961 was 81 percent of the rated capacity.

Ratliff (30) reported that preferential grazing occurred under rest-rotation grazing at Harvey Valley. He used a combination of fencing, salting, water development, and riding to obtain more even distribution of grazing.

Ratliff and Reppert (32), summarizing results of the grazing study at Harvey Valley after 13 years, concluded that the performance of individual animals was about the same with rest-rotation grazing as with season-long grazing. They

indicated that they still have a long way to go to double the capacity of the Harvey Valley allotment. In 1967, the livestock permittee was granted a length of grazing season increase with no change in permitted numbers. When the trial at Harvey Valley was established, it was expected that the grazing capacity would be doubled in 20 years (15).

Conifer Forest Ranges

Pinus ponderosa Dougl. ex Lawson forests are the most important forest grazing area in the Western United States. In Washington and Oregon, approximately 10 million ha. of forest grazing land furnishes summer forage for 250,000 cattle and nearly as many sheep (34). Effects of cattle grazing on herbage production were investigated 1954-66 on the Starkey Experimental Forest and Range near La Grande, Oreg. Elevations vary between 1,000 and 1,500 m. Annual precipitation averages 54 cm. Summer is the driest season. Open stands of *Pinus* and *Pseudotsuga menziesii* (Mirb.) Franco have an understory of *Carex geyeri* Boott., *Calamagrostis rubescens* Buckl., and a variety of forbs. Principal species in intermingled grassland openings are *Agropyron spicatum* (Pursh) Scribn. & Smith, *Poa secunda*, and *Danthonia spicata* (L.) Beauv. ex. Roem. & Schult.

Deferred-rotation and season-long grazing at three intensities were compared (34). The grazing period was about June 15 to October 15. Under deferred-rotation, the cattle were placed in half of the range for 2 months and then moved to the other half. The following year, the early and late pattern was reversed. Systems of grazing did not cause significant difference in production of any major plant group or species in the grassland type. In the forest type, heavy stocking reduced production of *Carex* from 455 kg./ha. to 227 kg./ha. *Carex* was very susceptible to grazing. It retained its production during the 12-year period only with light stocking in the deferred-rotation system. There was essentially no difference in reduction of *Carex* production under deferred-rotation and season-long grazing with moderate and heavy stocking. Skovlin and Harris (34) suggested that herbaceous forest vegetation may have been adversely affected by general reduction in May-July precipitation from

15 cm. in 1957 to less than 10 cm. in 1966. Initial intensive management practices such as fencing, water development, and salting were effective in increasing cattle use in the forest type (8).

Smith et al. (35) compared moderate rotation, heavy rotation, and moderate season-long grazing in the Big Horn Mountains near Burgess Junction, Wyoming. The elevation is 2,440 m. The major forage species is *Festuca idahoensis*, but there is a variety of herbaceous and browse species. The average annual precipitation is 79 cm.; about 40 percent occurs April-June. Frost and snow may occur at any time. The grazing season is June 20-September 20. In the rotation units, steers were moved among the three divisions at about monthly intervals. The rotation was such that the same division was not grazed at the same time in consecutive years. The study covered the 1959-64 period. There was no significant difference in daily gain between moderately stocked units (about 0.95 kg.). The daily gain on the heavy rotation unit averaged 0.82 kg. On soils of granitic origin, production of *Festuca* was maintained equally well on the three treatments. On soils derived from sedimentary deposits, the abundance of *Festuca* declined within the heavy rotation unit. Cover and production of *Festuca* was best maintained with season-long grazing. However, it generally was not utilized until mid-August on the season-long unit; whereas, it was moderately utilized as early as late July in the rotation units. In that area, *Festuca* makes little regrowth in the year it is grazed regardless of the time or amount of herbage removal (35). During 1961-63, use of *Festuca* averaged from 20 to 43 percent for the three grazing treatments. However, production declined during the study even though precipitation during the latter part of the study was above average. From the evidence presented, it appears that *Festuca* is not well adapted to grazing at the rate termed moderate at Burgess Junction.

Intermountain Shrub Region

Season-long grazing was compared with deferred-rotation grazing at the Squaw-Butte Experiment Station in southeastern Oregon during 1938-48 (19). The elevation is 1,375 m. and the average annual precipitation is 30 cm. Two-thirds of the precipitation occurs as snow in the

winter and the remainder as rain during the spring. The major plant species are *Artemisia tridentata* Nutt., *Agropyron spicatum*, *Festuca idahoensis*, and *Poa secunda*. Three range units were grazed with cows under a 6-year rotation system that included two consecutive years of late spring use (May 1–June 20), followed by 1 year of early summer grazing (June 20–August 10), 2 years of late summer grazing (August 10–October 1), and 1 year of early summer grazing. The growing season usually begins April 1 and ends June 30. A fourth range unit was grazed with cows season-long, approximately May 1 to October 1. The stocking rate was approximately the same under both systems and each year. The cows on the season-long range had an average annual advantage in weight gain of 4.1 kg. over those on the deferred-rotation range (19).

Grazing was more evenly distributed under deferred-rotation than under season-long grazing. Even though the season-long range unit was utilized more heavily than the units under deferred-rotation, vegetation density increased 22 percent under season-long grazing and 20 percent on the deferred-rotation units. The desirable grasses increased more than twice as much under season-long grazing as under deferred-rotation grazing. However, most of this increase was in the lightly grazed area in the season-long unit. Hyder and Sawyer (19) concluded that concentrating the cattle on a single unit of the three-unit, deferred-rotation system during the growing season for 2 consecutive years seriously reduced plant vigor. Hyder (18) recognized that the heavy grazing pressure during the growing season placed this deferred-rotation system at a disadvantage.

Northern Great Plains

Deferred-rotation and season-long grazing were compared at the Northern Great Plains Field Station during the period 1918–45 (33). The average annual precipitation during this period was 39 cm.—about half occurred from May–July and three-fourths from April–September. The dominant plant species are *Bouteloua gracilis* (H.B.K.) Lag. ex. Steud., *Agropyron smithii* Rydb., *Carex filifolia* Nutt., and *Stipa comata* Trin. & Rupr. The experimental range units were stocked with steers from May 16 to

October 13. Each of the three divisions in the deferred-rotation system was grazed approximately one-third of the season. The 6-year rotation grazing included 2 consecutive years of spring use, 1 year of summer use, 2 consecutive years of late summer and early fall use, and 1 year of summer use.

Rogler (33) reported that moderate stocking was about the correct rate on a season-long basis. At that rate, vegetation changes were influenced primarily by differences in precipitation. The vegetation in the heavily stocked unit was definitely overgrazed for the 1918–34 period. During the wetter 1938–45 period, the heavily stocked unit was not considered overgrazed in any year. The vegetation in the rotation units did not show the adverse effects of grazing during 1918–34 as did the unit grazed season-long at the same rate. There was no evidence that the rotation units benefitted from any natural seeding that theoretically should have occurred in the fall grazed units.

The average increase in seasonal gain of steers on rotation over season-long at the same intensity was 16 kg. per head for 1918–34. The steers grazed season-long at the moderate rate gained 20 kg. per head more than those on rotation. During the period of 1938–45 when there was no shortage of forage in any of the range units, the steers in the moderate season-long unit gained 13 kg. per head per season more than those in the rotation units. The steers in the heavily stocked season-long unit gained 9 kg. per head more than those in the rotation units (33).

Rogler (33) concluded that steer gains could not be increased by using a rotation system when there was sufficient forage for season-long grazing. There would seem to be some merit in a rotation system for improving range that has been damaged by overgrazing. Rogler suggested, however, that complete deferment until the range condition recovers would be a more rapid method of improvement. A rotation system might be used when it is necessary to stock at a high rate during occasional years and with older cattle. One of the advantages of continuous grazing is that cattle have access to all the plants in the range unit when highest in nutritive value. Young cattle are less likely to gain under a rotation system because they do not utilize the mature for-

age in the summer and fall units as well as older cattle.

Lewis and others (21) compared season-long grazing with ewes at three intensities with rest-rotation grazing at a moderate intensity at Antelope Range near Buffalo, S. Dak., for the period of 1964-69. The average annual precipitation is 34 cm., but it was above average during this study period. Season of use was rotated on the four rest-rotation units, and one unit was rested each year. Time of ewe movement was based on utilization (about 50 percent). Year differences due to blizzards, spring storms, precipitation, and disease have contributed to a greater variation in the results than the grazing treatments. Contrary to results obtained during a dry phase (7), ewe performance in this wet phase under heavy grazing has been about equal to that of ewes on lightly and moderately grazed units. Rest-rotation grazing resulted in good range improvement. However, ewe and lamb production was lower with rotation grazing than with any of the season-long treatments. Heavy utilization in spots is a problem in all units. Combination stocking with sheep and cattle may alleviate this problem.

Southern Great Plains

Several grazing systems were compared at the Southern Great Plains Field Station near Woodward, Okla. (24). The average annual precipitation is 58 cm., 70 percent of which occurs April-September. The major plants are *Artemisia filifolia* Torr., *Bouteloua gracilis*, *Sporobolus cryptandrus* (Torr.) A. Gray, *Eragrostis trichodes* (Nutt.) Wood, *Andropogon scoparius* Michx., *A. hallii* Hack., *Panicum virgatum* L., *Paspalum stramineum* Nash, and *Leptoloma cognatum* (Schult.) Chase.

Continuous summer grazing (April-October) was compared with three-division rotation grazing at both heavy and moderate stocking rates (23.) The steers were rotated among divisions at 2-month intervals in 1942 and at 1-month or shorter intervals for 1943-51. Rotation grazing in 1942 reduced steer gains 29 kg. per head at the heavy rate and 17 kg. at the moderate rate. There was no real difference between gains in the other years when the rotation was shortened. The more desirable tall grasses, and also some of the forbs,

increased most under rotation grazing at both rates. The less desirable *Paspalum stramineum*, *Leptoloma cognatum*, and *Bouteloua hirsuta* Lag. increased most under continuous grazing. However, McIlvain and Savage (23) concluded that this type of rotation could not be recommended over continuous grazing as an improved management practice.

McIlvain and Shoop (24) concluded that the following grazing systems have not proved superior to continuous yearlong grazing at the same stocking rates at Woodward: (1) summer and winter grazing, (2) alternate-year grazing, (3) three-unit rotations with rotations at 2-month, 1-month, 15-day, and 10-day intervals, (4) two-unit, 6-week, one-herd rotation when grass is growing, and (5) six-unit, 6-day, one-herd rotation. They cited some major reasons for the success of continuous yearlong grazing in the Southern Great Plains as (1) forage production is primarily dependent upon summer rainfall—and monthly forage production during the summer can vary from 22 to 672 kg./ha., (2) most species are grazed by cattle at one time or another; (3) many of the "increaser" species are excellent grazing plants and they may be very productive under certain conditions; (4) cattle compete with natural losses of forages and with other consumers; (5) young and regrowth forage is more palatable and more nutritious than more mature forage; (6) grazed plants save soil moisture for later green growth; and (7) favorable growing seasons combined with proper management allow ranges to recover a desirable species composition. Some additional reasons for the success of yearlong-continuous grazing may be (1) utilization during the growing season is light, and (2) lighter stocking per unit area means less soil compaction by livestock during wet periods.

Edwards Plateau

Merrill (25) compared continuous yearlong grazing at three intensities with deferred-rotation grazing at a moderate rate near Sonora, Tex. The major forage species is *Hilaria belangeri* (Steud.) Nash with minor amounts of *Tridens pilosus* (Buckl.) Hitchc. *Aristida* L. sp., *Bouteloua curtipendula* (Michx.) Torr., *B. hirsuta*, *Bothriochloa saccharoides* Rydb., *Andropogon*

seoparius, *Leptoloma cognatum*, and *Stipa leucotricha* Trin. & Rupr. There is an overstory of *Juniperus* L. sp. and *Quercus* L. sp. There is also a variety of forbs under certain weather conditions. The average annual precipitation is 61 cm. The average monthly precipitation is highest in spring and fall. Midsummer can be droughty. In the four-unit rotation system, each unit is grazed 12 months, then rested 4 months. Thus, during a 4-year cycle, each unit is deferred once during each of the 4-month periods. Stocking was with a combination of cattle, sheep, and goats. The study was initiated in 1949. After 11 years, the stocking rate of the units in the deferred-rotation system has increased 33 percent from 12.4 animal units/km.² to 16.6 animal units/km.² (26). These units carried the increased grazing pressure and at the same time made greater range improvement than any of the units grazed continuously. Average annual net returns for 1959-65 were \$1.78, \$2.91, and \$1.63 per ha. with continuous stocking at the rate of 6-, 12-, and 19-animal units/km.². The average net return for the same period on the rotation units was \$4.15/ha. (26).

A two-unit rotation, a four-unit rotation, and yearlong-continuous grazing were compared near Barnhart, Tex. (17). The most abundant grasses are *Buchloe dactyloides* (Nutt.) Engelm., *Hilaria belangeri*, and *H. mutica* (Buckl.) Benth. There are also other perennial and annual grasses and forbes, and an overstory of *Prosopis juliflora* (Sw.) DC. The mean annual precipitation is about 46 cm. with about the same average seasonal distribution as Sonora. The four-unit rotation is the same as the one described by Merrill (25). In the two-unit rotation, the units are alternately grazed and deferred for 3- and 6-month periods (for example, one unit is deferred March 1-June 1, grazed June 1-December 1, and deferred December 1-March 1). During a 2-year period each unit was deferred 12 months with deferment during each season. All treatments were stocked with cattle and sheep at 10-animal units/km.² During 1959-65, the average annual net-returns per animal unit were \$30.63, \$39.03, and \$41.71 for continuous, four-unit rotation, and two-unit rotation grazing, respectively (17). Huss and Allen (17) found that combination use of cattle and sheep was more profitable than

grazing either class alone. Merrill (26) also found that combination grazing with cattle, sheep, and goats was more profitable at Sonora than using sheep alone or cattle alone.

Southern Rolling Plains

Fisher and Marion (6) compared rotation and continuous grazing at a moderate rate at Spur, Tex. The major forage species are *Buchloe dactyloides*, *Hilaria mutica*, and *Panicum obtusum* (H. B. K.). The average annual precipitation is 54 cm. The average monthly precipitation is well distributed from April-October. The remainder of the year is drier. The grazing season was about May 1-October 1. The rotation system consisted of grazing each of three units for one month and deferring it for two months for the 1942-49 period. Fisher and Marion (6) concluded that (1) rotation grazing did not improve the vegetational composition from 1942 to 1947; (2) rotation grazing increased differential use of *Buchloe* and *Hilaria* as the season progressed or in drought, and in some instances resulted in less moisture penetration on sites occupied by the more desirable species; and (3) gains of yearling steers grazing on the rotation units were slightly lower than those grazing on the continuous units.

Various grazing systems were compared at the Texas Experimental Ranch near Throckmorton during 1960-68 (20). The major plant species are *Stipa leucotricha*, *Buchloe dactyloides*, *Bouteloua curtipendula*, *Prosopis juliflora*, and *Condalia obtusifolia* (Hook.) Weberb. There is a wide variety of other plants in the flora. The average annual precipitation is 63 cm. There is a tendency for the precipitation to be distributed in the spring and fall with a slight depression in midsummer and in the winter. A moderate stocking rate with cows and supplemental feeding level of 0.7 kg./day of cottonseed cake during winter were used in comparing grazing systems. The three systems were yearling-continuous, two-unit rotation similar to that studied at Barnhart, Tex., by Huss and Allen (17), and a four-unit rotation similar to that studied at Barnhart by Huss and Allen and at Sonora by Merrill (25). Calf production per animal unit averaged 200, 208, and 221 kg. for the moderate continuous, two-unit rotation, and four-unit rotation, respectively, for the 8

years. Precipitation was near average or above average during the study.

Semidesert Grassland

A number of studies on the Jornada Experimental Range, 40 km. north of Las Cruces, N. Mex., have contributed to developing a grazing system (13). The major forage species on the light- to medium-textured soils are *Bouteloua eriopoda* (Torr.) Torr. and *Sporobolus flexuosus* (Thurb.) Rydb. *Hilaria mutica* and *Scleropogon brevifolius* Phil. grow on the heavier soils. Under certain weather conditions, there may be an abundance of a variety of forbs and annual grasses. The average annual precipitation is 22.5 cm. The average precipitation during the summer growing season is 12.5 cm. The average annual evaporation from a Weather Bureau pan is 225 cm. or ten times the precipitation. However, Herbel and Nelson (13) showed that precipitation averages had little meaning. During 53 years of record, 45 percent of the years had seasonal precipitation of less than 85 percent of average, and 34 percent of the years had seasonal precipitation greater than 115 percent of average. Furthermore, summer rainfall occurs as localized, convective thunderstorms.

Forty years ago, there were two major vegetation types on the Jornada; one dominated by *Bouteloua eriopoda*, and the other dominated by *Hilaria mutica* and *Scleropogon brevifolius*. Because *Hilaria* and *Scleropogon* are more palatable and can withstand moderate grazing during the summer growing season, the grazing system consisted of grazing the *Hilaria-Scleropogon* type in summer and early fall, and then grazing the *Bouteloua* type from late fall until the next summer (28). However, considerable *Bouteloua* was lost during the severe drought of 1951-56 and due to a rapid increase of *Prosopis juliflora* on sandy soils (3). Now there are other vegetation types made up of a multiplicity of forbs and a few grasses. They can provide a considerable part of the forage crop in some years. Their production is not as reliable as the long-lived perennial grasses, but they have a high nutritive value (27). Herbel and Nelson (12) found that cattle grazed, to some extent, all species available to them, including a variety of forbs and shrub-like species. They also found that there

were definite seasonal preferences for some species.

Using weather and plant information, and considering livestock needs, Herbel and Nelson (13) developed the Best Pasture Grazing System. The system consists of establishing an objective for each range unit and stocking accordingly. The system is opportunistic in that the use of forbes and short-lived grasses is maximized. They are of little value to the permanent range resource but contribute much to livestock nutrition. No set stocking plan is established for a specific time period because of considerable variations in weather conditions that affect plant growth. The system involves a rotation scheme where the livestock are moved when the vegetation on a deferred unit can be grazed to the advantage of both plants and animals as compared with the unit being grazed. In the large range units occurring in parts of the West, periodic opening and closing of watering places can be used to rotate grazing pressure to different areas within a range unit (22).

Conclusions

Studies on California Annual Rangelands have indicated that yearlong-continuous grazing is superior to seasonal grazing. However, species composition can be manipulated by grazing intensity, burning, and seeding. This may indicate that a highly flexible grazing system, involving some form of manipulation on part of a ranch operation, may provide a higher quality, quantity, or both of forage for part of the year.

There was only limited success with any grazing scheme other than continuous on rangelands grazed only for a part of the year. There has only been a modest increase of the grazing period at Harvey Valley following 13 years of rest-rotation grazing, and this may be due to range improvements such as seeding, brush control, fencing, and water development. At the Starkey Experimental Forest, the production of *Carex geyeri* was maintained only with light stocking in a deferred-rotation system. However, there was a spring drought during the study and *Carex* is very susceptible to grazing. At Mandan, the vegetation in the rotation units did not show the adverse effects of grazing during a period of below-average precipitation as did the unit grazed

season-long at the same rate. However, improvement in range condition would be more rapid under complete deferment for 1 or 2 years. At Antelope Range, rest-rotation grazing resulted in good improvement in range condition, but sheep production was lower than with season-long grazing. At Manhattan, Kans., an earlier study showed an advantage in vegetation response to deferred-rotation grazing, but a later study showed no advantage in vegetation by deferred-rotation grazing and a disadvantage in livestock performance (1, 11).

In the northern part of the West, early plant growth is generally dependent upon winter-spring precipitation and periods of warm weather. Many workers recognize that grazing or clipping during the early part of seasonal growth is detrimental to subsequent plant vigor (for example, 4, 16). On ranges grazed seasonally, several studies have shown an advantage to spring deferment, but this must be balanced against the detrimental effects of concentrating livestock during this critical period of plant growth. At Squaw-Butte, nonuse during the growing season for 4 years did not overcome the detrimental effects of 2 consecutive years of concentrating the stock during the growing season. In the areas with short growing seasons, an important question, often not considered, is: how many of the desirable plants are actually grazed during the critical period of growth under a moderate stocking rate in a continuous system? At Burgess Junction, Wyo., *Festuca idahoensis* was not utilized until mid-August on the season-long unit, whereas it was moderately utilized as early as late July in the rotation units. It appears that any deferment period on ranges grazed only for part of a year should be brief, and that it should coincide with a critical period of growth. It should be recognized that the dates of this critical period vary from year to year depending on phenological development.

Another important consideration on ranges grazed seasonally is: Are range managers trying to maintain the right species? Undoubtedly, we must have species that will maintain the soil resource. However, from the evidence presented in this paper, *Festuca idahoensis*, *Carex geyeri*, *Agropyron spicatum*, and possibly others, are poorly adapted to grazing by livestock in some

areas. Species that are not well adapted climatically also should not be considered important in many instances. For example, although *Bouteloua gracilis* is quite resistant to grazing, its production is low in some high altitudes in the Southwest.

At Woodward, a number of studies have shown no advantage to rotation grazing over continuous grazing in livestock performance. An early study showed an improvement in floristic composition due to grazing. The Woodward station is located in a broad regional ecotone with considerable fluctuations in floristic composition due to weather conditions. There is a reduction in percentage of tall grasses in the floristic composition in a series of dry years regardless of grazing treatment. Similarly, during a series of wet years, the tall grasses increase rapidly under any grazing treatment other than heavy stocking. This wide fluctuation in floristic composition due to weather conditions is common to some other parts of the West. With this situation, a classification of range condition at any point in time must allow for previous weather conditions.

Of the studies reviewed, the deferred-rotation system at Sonora, Tex., has shown the most striking results. At that location, a range unit is grazed with a combination of livestock for 12 months and deferred for 4 months. This infrequency of livestock movement means that the livestock must adjust to new forage conditions only once a year. Livestock are in a given unit for a complete cycle of plant growth. The major species, *Hilaria belangeri*, is quite resistant to heavy grazing. Another point is that there may be some growth of at least some of the plant species at anytime of the year when there is sufficient moisture. Therefore, a 4-month deferment during each third of the year every 4 years has resulted in a substantial improvement in carrying capacity.

Most studies have shown that livestock production per animal is the same or lower for a rotation system compared to continuous grazing. Generally, there must be an improvement in range condition, and subsequently in carrying capacity, to justify a rotation scheme using livestock performance as a criterion. Animal performance per unit area is more important than performance of individual animals. In some instances, it may take

several years to have enough range improvement to justify an increase in stocking.

When a rotation scheme is initiated, range improvements such as seeding, brush control, fencing, and water developments are often not properly credited for observed differences when compared to unimproved ranges. Rather, there is a tendency to credit the rotation scheme for observed improvements in range condition or animal performance. Any improvement that aids livestock distribution will result in greater productivity. The entire management plan, including both range improvements and grazing scheme, is the important consideration. All of the beneficial, economical practices should be integrated into the overall management plan.

Most grazing studies have been established at a fixed stocking rate. Downward adjustments in livestock numbers were made only in severe droughts. A fluctuating forage crop was given little thought in establishing grazing studies. This is probably another reason why many of the grazing studies have failed to show much improvement in range condition. When ranch operators adopt a grazing system other than continuous grazing, they often allow for a flexibility in time of grazing and deferral, and the number of livestock grazed. This flexibility may be the difference between success or failure of the grazing scheme.

A grazing system must be highly flexible. Plant and animal requirements must be considered. For example, some of the range units in a ranch operation may be manipulated to furnish highly nutritious forage during the time of the year when livestock need a higher plane of nutrition. This may be done at a sacrifice of some of the highly desirable range species on those units. Furthermore, it should be recognized that the critical growth stage of plants varies from year to year because of weather conditions. Due to grazing history and weather conditions, it may be more important to defer grazing in some years than in others.

Grazing systems should also be tailored to fit a variety of vegetation types, soil types, and herd management plans. This means that there may be considerable variation in specific details from one ranch operation to the next. In some areas, continuous grazing may be the most profitable sys-

tem. It may be desirable to use a certain grazing system to attain a certain measure of improvement and then change to a different system.

Much has been learned about grazing management. However, much needs to be done to develop and adapt the most productive grazing scheme to each range operation. In many grazing studies, the major emphasis has been centered on a few species. The value of all plants growing on an area must be considered. Even minor amounts of a few species may contribute much to animal performance for a brief, but critical, part of the year. Few studies have given attention to forbs and shrubs. Grazing research should include studies on the effects on the entire ecosystem, not just the effects on the livestock and a few of the major plant species.

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A STUDY OF THE PHENOLOGY AND GERMINATION OF *EREMOPHILA GILESII* IN SEMIARID QUEENSLAND¹

By W. H. Burrows²

Abstract

The status of *Eremophila gilesii* as a weed in semiarid Queensland was examined. The studies show that *E. gilesii* is restricted in distribution to those areas receiving both summer and winter rainfall. The species is increasing in density, apparently due to light stocking. Frequent flowering in summer is not necessarily followed by abundant fruit production. Fruiting may only be significant following rains of more than 40 mm. in the cooler months of the year. High germination percentages only occur following protracted fruit weathering in the field. Germination may be severely inhibited by soil temperatures in excess of 40° C. On the basis of the preceding information, a management system to control *E. gilesii* is proposed. It is suggested that from March to September inclusive land on which *E. gilesii* is a weed should be heavily stocked following rainfalls greater than 40 mm. The need to consider the ecological system as a whole when formulating control measures is discussed.

Additional key words: Green turkey bush, shrub control

Introduction

Woody plants are troublesome weeds in much of the world's rangelands (14, 15, 22, 24, 33). There appears to be general agreement about the processes leading to increases in shrub density. Usually these increases are attributable to overgrazing (9) and the process is described succinctly by Weaver and Clements (40). The ab-

sence of fire (42) is also considered a major cause of brush encroachment, although in some circumstances repeated burning may lead to increase in woody plants (15.)

Regeneration of unpalatable trees and shrubs is presently widespread in summer rainfall zones of semiarid Australia (25). The increase is not so much an invasion of new territory as an increase in density of the stand in the vicinity of parent plants.

High costs limit the use of chemical and mechanical weed control measures on semiarid rangelands. Naveh (28) considered that ecological and biological methods, such as grazing and burning, will be for a long time to come the chief tools for the economic management and improvement of East African rangelands. This approach was supported by Whyte (44), who advocated the use of cheap methods for broad scale improvements and the concentration of limited resources on particularly favorable areas.

In South Africa, Scott (33) urged greater emphasis on autecological studies to determine new lines of ecological control of unwanted species. Few detailed studies of the germination and dormancy characteristics of seeds of pasture weeds have been made in Australia despite their relevance to weed control methods (21).

Observations on morphogenesis and phenology of woody plants in semiarid Australia are limited. Davies (7) and Slayter (34) studied growth of mulga (*Acacia aneura* F. Muell.), an important fodder tree. Published work on morphogenesis and phenology of woody weeds appears restricted to *A. harpophylla* F. Muell. (16, 43), which is a problem in more mesic parts of the summer rainfall semiarid zone.

An important woody weed of semiarid Queensland is green turkey bush (*Eremophila gilesii* F. Muell.). This is a small shrub which grows up

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to 1 m. in height and attains densities in excess of 12,000 bushes per hectare on an estimated 2-3 million hectares of rangeland. The leaves are unpalatable to domestic stock except in the more xeric habitats where it may be eaten during protracted droughts. By contrast, the plant flowers profusely after rain and if stocking rate is high the flowers are readily eaten by sheep. This observation suggests that stock numbers may be manipulated to control the species by preventing regeneration from seed.

A detailed study of the ecology of *Eremophila gilesii* is currently being undertaken by staff of the Charleville Pastoral Laboratory and preliminary results are presented here.

Of the weed control measures listed by Klingman (17), only grazing management, biological control, and fire appear to have application in semiarid Queensland. Lands with woody weed problems in this area are currently valued at less than \$A4 per hectare (\$A=Australian dollar=approximately \$1.25 U.S.). Development of management techniques and biological control measures necessarily call for long term research programs. Use of fire as a controlling agent is dependent on the production of enough herbage within the stand to fuel a burn of sufficient intensity to kill the weed. In southwest Queensland, standing crops of grasses in areas where woody plant infestation is high seldom reach 100g./m.² and are commonly much lower (8). Moreover the buildup of fuel over several years, as advocated by West (42) on South African veld, is prevented in Queensland by the depredations of grass harvesting termites (38). Thus, ecological control measures (including grazing management) seem at present the only practical means of reducing shrub densities in southwest Queensland. There is general agreement among Australian workers on the need to look at the ecological system as a whole rather than at individual species (10, 21, 22). However, studies in which this principle is adopted are rare. Moore (23) pointed out that, in semiarid shrub woodlands, removing one woody species may increase the density of others.

Distribution

A distribution map for *Eremophila gilesii* was constructed from information supplied by her-

baria of mainland Australia (excluding Victoria). This map (fig. 1) indicates the climatic adaptability and range of the plant. The distribution closely follows that of *Acacia aneura* (12). This is not surprising in view of the highly significant associations found between *A. aneura* and *Eremophila* spp. by Burrows and Beale (3). Nevertheless the plant is a problem only in southwest Queensland, the most mesic part of its geographical range.

An examination of the climatic data presented by Perry (31) showed that the species is largely confined to areas receiving between 60 and 70 percent of the annual rainfall during the summer months (October-March). All areas where it occurs receive significant cool season rains. Temperatures experienced throughout the range are very similar. For Charleville, mean monthly maximum and minimum temperatures for the hottest month are 36° and 22° C., respectively. Corresponding temperatures for the coldest month are 20° and 4°.

Experiments

Methods

Temporal changes in species density were recorded in small enclosures (40 m. by 10 m.) placed on two spatially distant stands of *Eremophila gilesii* during 1966. The Maxvale enclosure is situated 15 km. and the Lanherne enclosure 150 km. west of Charleville. Plant density and position were recorded within an 80-cm. wide transect through the center of each enclosure. For purposes of analysis each transect was divided into 80 cm.-by-80 cm. quadrats. The enclosures have been read irregularly since 1966.

Changes in plant density under grazing were determined by re-recording, in 1969, a 15-km. length of a 2-m. wide belt transect laid down at Humeburn (150 km. southwest of Charleville) in 1965. The vegetation on this transect and the method of recording it are given by Burrows and Beale (3). For purposes of the present analysis, the transect was divided into 200-m.² quadrats. Those portions of the transect traversing alkaline soils, on which *E. gilesii* rarely occurs, were omitted. Stocking rate for the period 1965-69 was light and never exceeded one sheep to 5 hectares.

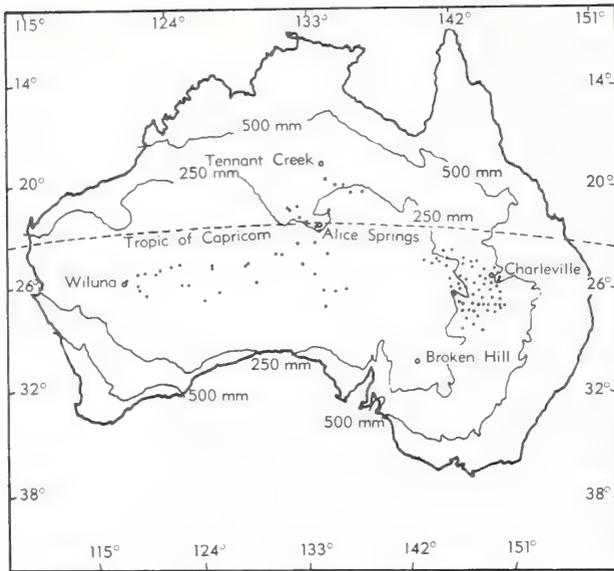


FIGURE 1.—Australian distribution of *Eremophila gilesii* F. Muell. Data provided by Herbaria of mainland Australia (excluding Victoria). Dots represent location of specimens and have no relation to plant density. Rainfall isohyets for 250 and 500 mm. are indicated.

Observations of the phenology and leaf growth of *E. gilesii* were made on the Charleville Experimental Reserve. The study area (30 m. by 30 m.) was fenced to provide it with a 5-m. internal and 10-m. external buffer zone. Plant density within the plot was determined from randomly placed quadrats. Phenology observations were obtained for 3 bushes in each of 4 height classes (0 to 7.5, 7.5 to 22.5, 22.5 to 45, and >45 cm.) at weekly intervals during active growth and bi-weekly when there was little apparent growth. Single twigs were tagged with plastic labels near the apex of each plant (active shoots) and in the lower third of its height (senescent shoots). At each reading, total number of leaves, buds, flowers, and fruits above every permanent tag were recorded. Adequate sampling of reproductive phases was ensured by also tagging a large branch on each bush on which bud, flower, and fruit number alone were counted. Readings were made over a 12-month period from November 1969.

Soil moisture was determined gravimetrically each fortnight in the internal buffer area of the

plot, the number of samples varying from 4 to 10, depending on time since last fall of rain. Rainfall was recorded in a gauge placed in the center of the plot, while temperature records were obtained from a Commonwealth Meteorological Station situated 500 m. distant.

Germination studies were made in both the field and the laboratory. Fruit density on the ground was determined on the phenology plot, and the number of fruits germinating in March and September 1970 was recorded along transects placed across the plot. Within these transects, 50 seedlings were marked with colored pins after each germination event and their subsequent survival followed.

In November 1969 about 40,000 fruit were collected from bushes in the study areas. These were presumably produced following 70-mm. rain in March 1969. After collection, the fruits were mixed and divided into two equal portions. One-half was stored at room temperature in a dry cabinet in the laboratory. The remaining fruit were placed in fiberglass mesh bags (0.25m.²) in the phenology plot to be weathered under natural conditions. The fruits in each bag were restricted to a single layer and each was in close contact with the soil surface. After 6 months and at approximately 4-month intervals thereafter, germination and oven-dry weight of weathered and laboratory stored fruit were recorded.

Field observations suggested that maximum and not minimum temperatures could be limiting germination. To confirm this and to estimate a suitable temperature at which to test the weathered fruits, germination studies were made in a controlled environment cabinet with fruit obtained from the soil surface in an *E. gilesii* stand. The age of these fruits was not known but was believed to be more than 3 years. Germination is negligible from unweathered fruit and it is impossible to remove the soft seeds enclosed in the hard woody pericarp without damaging the embryos.

Eight replicates of 100 fruits were placed in petri dishes on two layers of filter paper kept moist with distilled water. The fruits were exposed to constant temperatures in darkness at 10°, 15°, 25°, 35°, and 40° C. Germination was recorded at daily intervals for 14 days.

Results And Discussion

E. gilesii is increasing in density under both light grazing pressure and where stock are excluded (table 1). An exception is the fall in density recorded at Maxvale between 1967 and 1970. This change is known to have been caused in 1969 by a wingless grasshopper (*Monistria postulifera* Walk.) which sometimes attacks isolated stands of *E. gilesii*.

It was further observed that sustained heavy stocking actually resulted in a decrease in *E. gilesii* density. This is shown in figure 2.

Evidence suggests that *E. gilesii* increases in density under light rather than heavy stocking. This conclusion is seemingly in contrast to the often stated view that overstocking leads to brush encroachment (9, 14, 21, 22). A decline in grass cover in semiarid eastern Australia since settlement was recorded by Beadle (1). For many years there has been a trend to lighter stocking in such areas, including those carrying *E. gilesii*. But while fewer stock have been carried on an area basis the actual grazing pressure on surviving fodder plants is high. This has permitted unpalatable species, such as *E. gilesii*, to further increase at the expense of more useful species.

The large variation in plant density found in *E. gilesii* communities is shown in table 1. Appreciable changes in plant density occur within *E. gilesii* communities over short periods of time.

This is probably near the maximum shrub density attainable.

Trends in leaf, bud, flower, and fruit production for the >45 cm. height class, along with rainfall records, are presented in figure 3. Minimum bush height at which flowering occurs is about 25 cm. Trends in total bud, flower, and fruit production in relation to rainfall are shown for the taller bush classes (>22.5 cm. high) in figure 4.

Changes in soil moisture for each depth of sampling are shown in figure 5. Also, shown in this figure are the 15 atmosphere and 0.1 atmosphere percentage moisture for each depth interval.

The data in figures 3 and 4 require confirmation, particularly for absolute rates of production of buds, flowers, and fruits, but trends are of interest. Irrespective of time of year, rainfall greater than 15 mm. appears to promote a rapid increase in leaf numbers on *E. gilesii* at the study site. This is not surprising as the distribution of this evergreen plant broadly coincides with those areas experiencing both summer and winter rainfall.

Oppenheimer (29) observed that reduction in number and size of leaves is an adaptation to drought. Other studies support this view (4, 6, 30). A similar drought evading mechanism appears to function in *E. gilesii* (fig. 3). As soil moisture is depleted, the more mature and larger

TABLE 1.—Density of *Eremophila gilesii* at widely separated sites in southwest Queensland

Site	Plants per hectare					Mean annual rainfall, mm.
	1965	1966	1967	1969	1970	
Hume transect	447±86	n.a. ¹	n.a.	1001 ±194	n.a.	340
Maxvale enclosure	n.a.	20780 ±2810	37190 ±6875	n.a.	11875 ±3125	470
Lanherne enclosure	n.a.	44375 ±7500	48900 ±5625	n.a.	54060 ±7660	365
Charleville experimental reserve	n.a.	n.a.	n.a.	69200 ±5900	n.a.	483

¹ n.a.—not available.



FIGURE 2.—Fence line contrast between two properties. Note dense *Eremophila gilesii* at right of fence (stocking rate approximately 1 sheep per 5 ha. since 1965). Little *E. gilesii* can be seen on left side of fence (stocking rate approximately 1 sheep per 3 ha. since 1956). Tree in background is *Acacia aneura*. Broad-leaved trees on right are *Eucalyptus populnea* Hook. Note lack of grass on either property.

leaves are shed while smaller but still functional leaves remain on the branch apices. Cunningham and Strain (6) found that seasonal variability in leaf numbers enhances the capacity of desert shrubs to maintain a favorable water balance under stress conditions and thus remain photosynthetically active further into dry periods. It seems that it may be physiologically advantageous for plants in arid and semiarid regions to have smaller leaves because of their lower leaf temperatures (11).

Data from figures 3 and 4 suggest that all phases of reproduction can occur at any time of the year. The number of buds retained in a dormant state during drought is proportionately few but permits the plant to rapidly produce some flowers in response to rainfall which otherwise may be insufficient for flowering. However, favorable conditions for vegetative, bud, and flower development do not necessarily result in production of fruits. This is particularly noticeable dur-

ing the summer months. Reasons for this could be excessive heat leading to desiccation of floral parts, inactivation of insect pollinators, or both. Alternatively, the soil profile could be insufficiently moist (fig. 5) to permit complete maturation of fruits.

Fruit production occurs only following rainfall in excess of 60 mm. This is not to imply that 60 mm. is a minimum for fruit production as other factors including antecedent moisture levels are involved. Zahner (48) concluded from horticultural studies that final size and quality of individual fruits are regulated by the amount of water available during enlargement. The implication of this finding for the present study is that where fruit have developed at low soil moisture levels their viability is probably impaired. It was observed that fruit produced in the summer months were noticeably smaller than those produced following autumn and early spring rains.

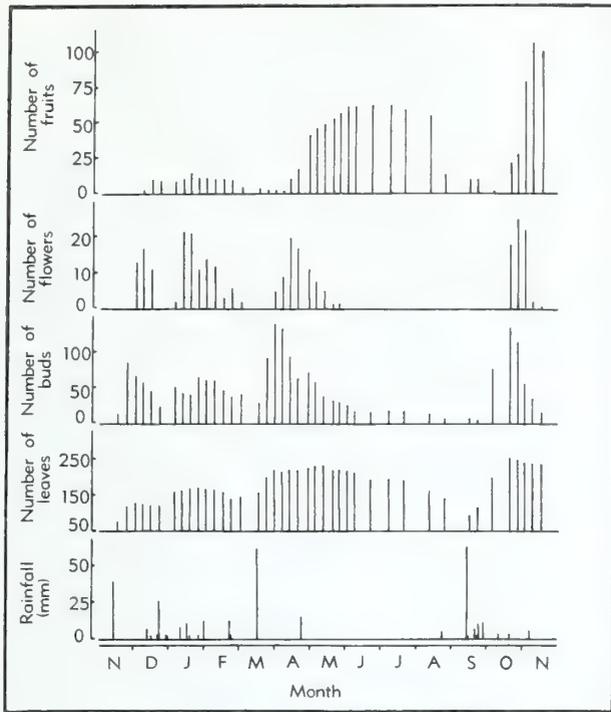


FIGURE 3.—Trends in numbers of leaves, flower buds, flowers, and fruits on marked branches of *Eremophila gilesii* during 1969-70. (>45 cm. height class).

Walter (39) has stated that the water balance of isolated plants in the desert is not as unfavorable as is usually believed. In effect, he suggests that the density of vegetational cover is generally proportional to precipitation so that, per unit of transpiring surface, plants in arid areas receive the same quantity of water as those in humid climates. The soil moisture data presented in figure 5 for the *E. gilesii* community suggests that Walter's conclusion may not be valid for *E. gilesii*. For many months of the year, soil moisture to 1 m. depth is below the 15 atmosphere percentage. Similar results have been noted in other arid communities (13, 32, 36). Nevertheless, Slatyer (35) cautioned against a too literal interpretation of available soil water data. He points out that increased rooting depth in the profile as a whole can compensate for a narrow available water range in each horizon. Also, in many soils, the range of water available for transpiration and survival is substantially greater than that available for growth alone.

The environmental data being collected in this

study may eventually facilitate predictions of flowering and fruit set. This is a fundamental requirement in formulating ecological control measures. Blaisdell (2) has shown how growth and yield of sagebrush vegetation can be related to precipitation and temperature. In the present study, the effects of temperature (if any) were masked by the response to precipitation (figure 4). Wetherell (34) suggested that increases in leaf growth of brigalow (*Acacia harpophylla*) in spring require higher air temperatures than in the autumn because of the influence of soil temperatures. The slower response of *E. gilesii* to September rainfall may be due partly to lower soil temperatures prevailing at that time in comparison with those following equivalent rains in March.

Fruit density on the ground and field germination are shown in table 2. The results suggest that the number of fruits germinating is only a small proportion of the total. Only two germination events (March and September) occurred from November 1969 to November 1970, and seedling survival from both was negligible. Fruits

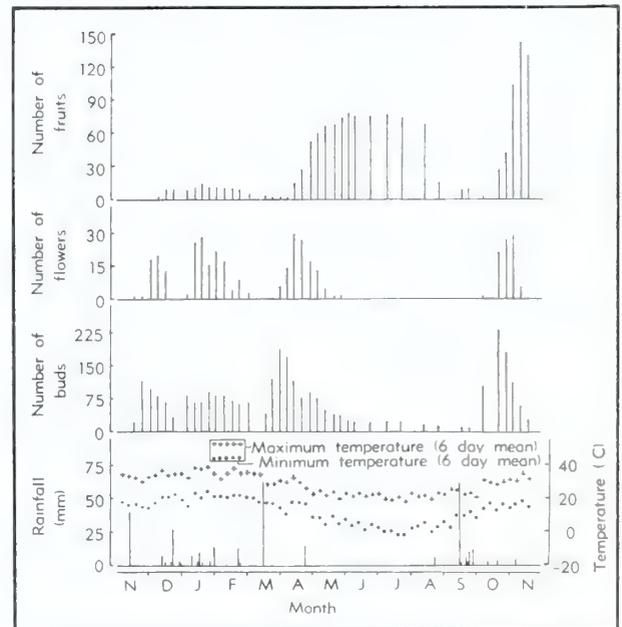


FIGURE 4.—Trends in numbers of buds, flowers, and fruits on marked branches of *Eremophila gilesii* during 1969-70. Data obtained by combining that from height classes of 22.5 to 45 cm. and >45 cm. Rainfall and temperature means for the period of observation are indicated.

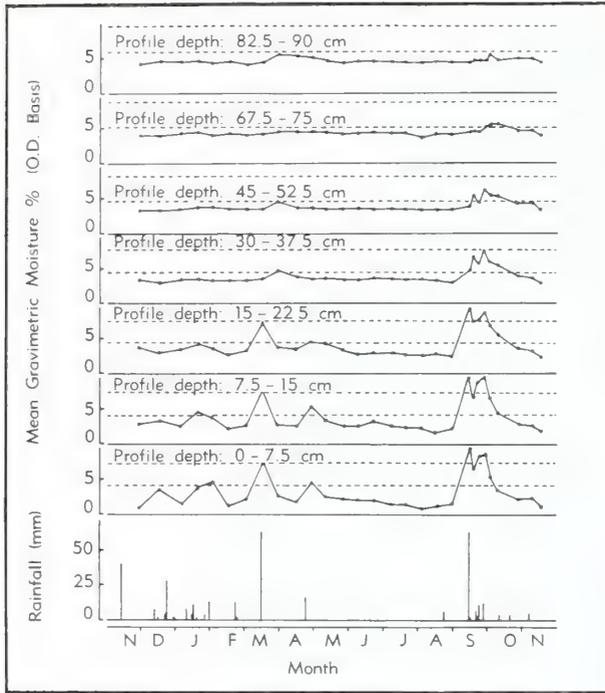


FIGURE 5.—Variations in soil moisture in phenology plot during 1969-70. Upper dashed line in each graph represents 0.1 atmosphere percentage, lower dashed line 15 atmosphere percentage.

are seldom completely buried and germination usually occurs on the soil surface. Seeds will not germinate under conditions of high moisture stress. This could be an adaptive characteristic of species subjected to severe drought conditions (5, 26, 47).

The effect of fruit weathering on germination was followed for only 14 months but indications are that germination improves exponentially (fig. 6). A tentative prediction is that a germination of 40 to 50 percent could be attained about 3 years after fruit matures. Low initial germination is attributed to an impervious, woody pericarp. There is no evidence of toxic inhibitors controlling seed germination of this arid shrub (18, 41).

Maximum germination at constant temperatures occurs between 15° and 25°C. Koller (19) suggested that temperature controls germination when rainfall is nonseasonal. Further, optimal conditions are more likely to be those inducing the most rapid rather than the highest percentage germination. Rate of germination is defined as

TABLE 2.—Field germination (thousands/ha.) of *Eremophila gilesii* fruits over 14 days following 60 mm rain in March and September 1970

Period	Ground fruit	Number germinated	Percent germination
March	4285±475	74±13	1.7
September	4285±475	278±22	6.5

the reciprocal of the number of days to reach 50 percent of final germination (27). For *E. gilesii*, the maximum rate (derived from fig. 7) occurs between 25° and 35° C.

While the lower range of temperatures tested may be suboptimal for germination it can be inferred from figure 7 that temperatures higher than 40° C. could be lethal. Turner (37) showed a relationship between maximum screen and soil surface temperatures in Central Australia. The community and soil of his study were similar to those in which *E. gilesii* occurs. At screen maximum temperatures of 30° and 40° soil temperatures were approximately 50° and 70°, respectively. A similar relationship can be expected in the present study area.

Although Turner's relationship applies only to cloudless periods at least one week after last rain, the effect is of such magnitude that temperatures inhibitory to germination can be anticipated

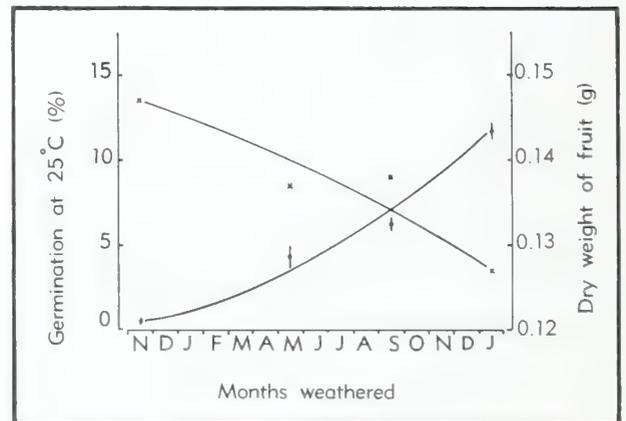


FIGURE 6.—Effect of weathering on fruit weight (x) and germination (.) in *Eremophila gilesii*. Germination data presented ± standard error. Fruit weight is mean of 1,000 fruits. Both curves fitted by eye.

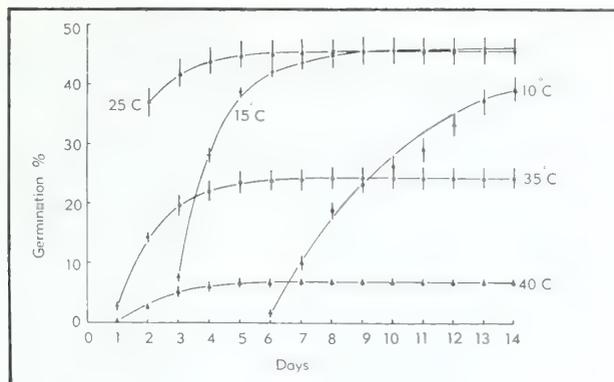


FIGURE 7.—Germination of *Eremophila gilesii* fruits at fixed temperature in the dark. Data presented \pm standard error. Fruits had been field weathered, and were estimated to be 3 years old.

within 1 or 2 days of most summer rains. The expected failure of *E. gilesii* to germinate during summer was borne out by field observations in this study. However, temperature relationships alone are not sufficient to explain behavior in the field because dormancy and moisture are also involved (21).

Conclusions

These studies have shown the following:

E. gilesii is restricted in distribution to those areas receiving both summer and winter rainfall (fig. 1).

Light stocking rates are resulting in further increase in *E. gilesii* (table 1).

Fruit production may only be significant following suitable rains (>40 mm.) in the cooler months of the year (fig. 4).

Frequent flowering in summer is not necessarily followed by abundant fruit production (figs. 3, 4).

High germination percentages occur following protracted fruit weathering in the field (fig. 6).

Germination may be severely inhibited by soil temperatures in excess of 40° C. (fig. 7).

With the use of this information, a hypothetical management system for *E. gilesii* may be formulated. It is proposed that from March to September inclusive land on which *E. gilesii* is a weed should be heavily stocked following falls of rain greater than 40 mm. A stocking rate of at least 2 sheep per hectare is envisaged for a pe-

riod of 4 weeks commencing about 2 weeks after the rain falls. It is anticipated that this would have the effect of removing both flowers and many of the young seedlings. This practice, repeated over a number of years, could severely curtail reestablishment and lead eventually to a decline of the stand. Damage to grass would be minimal as growth and seed germination in these communities occurs in response to summer rather than winter rains (45). Light stocking during the summer months would encourage grasses to fill niches created as *E. gilesii* gradually declines in density. Everist (personal communication) considers individual *E. gilesii* plants have life spans of little more than 10 years.

The problems of brush control in semiarid grazing lands is complex. Wilson (46) has pointed out the lengthy time scale involved in converting areas occupied by shrubs and trees to stable grassland. Unpalatable woody species may serve a useful purpose in providing ground cover and erosion protection (20) in areas otherwise denuded of grass and herbage. Removing the shrubs without consideration of what species, if any, will take their place could lead to further deterioration in the grazing value and stability of the ecosystem. Unless this is fully appreciated, the usefulness of any control measure could be negated.

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STRATEGIES USED IN MANAGING BLUE-GRAMA RANGE ON THE CENTRAL GREAT PLAINS¹

By R. E. Bement²

Abstract

To manage his range efficiently, a rancher must be equally concerned about forage harvest and forage production. Maximum cattle return (\$/ha.) from blue-grama ranges was reached when pastures were stocked at rates which left 336 kg./ha. of ungrazed herbage standing on the pasture at the end of a 6-month summer grazing season. When a growth opportunity occurred, 336 kg./ha. of ungrazed herbage provided sufficient leaf material to insure fast herbage growth and optimum livestock production.

Additional key words: Stocking rates, beef production, forage production

Introduction

The rancher who stocks his range pasture during the period when he expects it to make its growth must be concerned as much about forage production as he is about forage harvest. His objective must be to simultaneously obtain optimum forage and livestock production.

A strategy is a plan for attaining a specific objective. There are limited strategies a rancher can employ to reach his objective of optimum forage and livestock production. He has flexibility for strategy selection in only a few areas such as stocking rate, season of grazing, and distribution of grazing. By maneuvering in these three areas he can influence the quantity and quality of his herbage crop. The strategies he

uses to reach his objective must fit both his range and his livestock.

While strategy is defined as a plan, tactics is defined as the arranging and maneuvering of forces in action. The rancher, as a strategist, must realize what factors he can manipulate and what results he can expect from the manipulation. As a tactician, he must know when, where, and how to maneuver his forces. To maneuver efficiently, he must be able to answer four basic questions about each of his pastures. These are:

1. How many animals shall I put on the pasture?
2. When should they go on?
3. When should they come off?
4. Where should I go with them?

The rancher needs basic information to answer these questions on a day to day basis. The amount of ungrazed herbage standing on a pasture is a quantitative factor that he can readily recognize and relate to animal and plant performance.

At Central Plains Experimental Range, principles have been developed for the management of shortgrass range dominated by blue grama (*Bouteloua gracilis* (H.B.K.) Lag. ex Steud.). The Experimental Range is located in the 25- to 38-cm. precipitation zone on sandy loam soils 61 km. northeast of Fort Collins, Colo., U.S.A.

Optimum Livestock Production

Let us consider first the management principles concerned with optimum livestock production or forage harvest. The quantity and quality of forage available to livestock, and the use they make of it determine grazing efficiency. Grazing efficiency is readily altered by changes in stocking rate. At Central Plains Experimental Range,

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light stocking rates result in high animal gains and low animal gain per hectare, while moderate-to heavy-stocking rates result in low animal daily gains and high animal gain per hectare. A stocking-rate guide (table 1) for blue-grama range grazed from May 1 to October 31 was developed from 19 years of grazing-intensity studies at the Experimental Range.³

Maximum beef gain per hectare was made when 280 kg. of ungrazed herbage per hectare was left at the end of a 6-month summer grazing season, and maximum daily gains per animal were made when at least 392 kg. of herbage per hectare remained ungrazed.

³ BEMENT, R. E. A STOCKING-RATE GUIDE FOR BEEF PRODUCTION ON BLUE-GRAMA RANGE. *J. Range Mangt.* 22: 83-86. 1969.

Cattle sale data for the years 1964, 1965, and 1966 were used to evaluate the effects of stocking rate on cattle return per hectare (table 2).³ Maximum dollar return per hectare was made when 336 kg. of ungrazed herbage was left at the end of the grazing season. When 280 kg./ha. of ungrazed herbage was left, average cattle return per hectare was reduced 39 cents. Leaving as much as 392 kg./ha. of ungrazed herbage lowered average cattle return per hectare 27 cents. Efficient forage utilization was made over a very narrow range in the amount of standing vegetation left ungrazed.

From the optimum livestock production standpoint, the rancher operating on ranges similar to those at Central Plains Experimental Range now has information to help him answer the four

TABLE 1.—*Stocking rates for beef production on upland blue-grama pastures grazed May 1 through October 31*

Hectares/heifer month	Ungrazed herbage left (kg./ha.)	Gain/head/day (kg.)	Gain/hectare (kg.)
0.65	168	0.32	14.67
.75	224	.41	16.34
.89	280	.50	16.89
1.06	336	.59	16.61
1.26	392	.64	15.28
1.40	448	.66	14.15
1.50	504	.66	13.16
1.54	560	.66	12.85

TABLE 2.—*Cattle returns (\$) per hectare from May 1 to October 31, grazing at different stocking levels, using price data from 1964, 1965, and 1966*

Hectares/heifer month	Ungrazed herbage left (kg./ha.)	Cattle return per hectare (\$)			
		1964	1965	1966	Average
0.65	168	2.22	4.84	2.62	3.22
.75	224	2.55	5.93	4.10	4.19
.89	280	3.39	6.50	4.23	4.71
1.06	336	3.85	6.67	4.79	5.10
1.26	392	3.73	6.15	4.62	4.83
1.40	448	3.51	5.73	4.35	4.53
1.50	504	3.29	5.36	4.05	4.23
1.54	560	3.16	5.19	3.93	4.09

basic questions about a given pasture.

If he plans to graze the pasture for the usual 6-month summer season, the stocking-rate guide gives him the approximate number of animals to use. The guide indicates he should stock the pasture when he has more than 336 kg./ha. of standing herbage. He should get off the pasture when it is down to 336 kg./ha. of standing herbage. He can move his livestock to a pasture that still has more than 336 kg./ha. of standing vegetation, take them to a corral where they can be fed, or sell them.

If the rancher is to maneuver wisely, he must know how his range looks with 336 kg./ha. of standing herbage. Figures 1, 2, and 3 show upland blue-grama ranges in October with ungrazed herbage in the amounts of 448, 336, and 224 kg./ha., respectively. It is relatively easy to see this

difference. One can readily learn to recognize 336 kg./ha. of standing vegetation.

Optimum Forage Production

Thus far we have considered the management principles concerned with optimum livestock production or forage harvest. Now let us consider the management principles concerned with optimum forage production and look at the vegetation as leaf tissue rather than forage.

Blue-grama ranges usually make their herbage growth in brief spurts when moisture becomes available. The amount of leaf tissue active during these spurts of growth affects the quantity of herbage produced. For optimum forage production, blue-grama ranges should be managed to provide sufficient leaf tissue to insure fast herbage growth when a growth opportunity occurs. The



FIGURE 1.—Blue grama range with 448 kg. ha. of ungrazed herbage remaining at the end of a May 1 to October 31 grazing season.



FIGURE 2.—Blue grama range with 336 kg./ha. of ungrazed herbage remaining at the end of a May 1 to October 31 grazing season

amount of standing vegetation gives a good estimate of the amount of leaf tissue present during a given growth period.

At Central Plains Experimental Range, the amount of standing vegetation on a 130 hectare pasture was determined by taking herbage-weight measurements at approximately 2-week intervals. For each period, the amount of forage eaten by the cattle grazing on the pasture was determined by the water intake method.^{4,5} The difference in the amount of standing vegetation at the begin-

ning and the end of a given period plus the amount of herbage grazed by the cattle was considered as the amount of forage produced during the period. Herbage growth rate in kg./ha./day was then calculated by dividing total herbage produced during the period by the number of days in the period. Herbage losses due to translocation, weathering, trampling, diseases, insects, rodents, and other wild animals were not measured.

Tables 3, 4, and 5 show herbage growth rate for the 1965, 1966, and 1967 growing seasons, respectively.⁶ Growing season precipitation for 1965 was above average following the most severe drought year on record at the Experimental

⁴HYDER, D. N., R. E. BEMENT, and J. J. NORRIS. SAMPLING REQUIREMENTS OF THE WATER-INTAKE METHOD OF ESTIMATING FORAGE INTAKE BY GRAZING CATTLE. *J. Range Mangt.* 21: 392-397. 1968.

⁵HYDER, D. N., R. E. BEMENT, J. J. NORRIS, and M. J. MORRIS. EVALUATING HERBAGE SPECIES BY GRAZING CATTLE. PART I, FOOD INTAKE. *Internatl. Grassland Cong., Proc.*, 10: 970-974. 1966.

⁶BEMENT, R. E. HERBAGE GROWTH RATE AND FORAGE QUALITY ON SHORTGRASS RANGE. Ph.D. Thesis. Colorado State Univ., 53 pp. 1968.



FIGURE 3.—Blue grama range with 224 kg./ha. of ungrazed herbage remaining at the end of a May 1 to October 31 grazing season.

TABLE 3.—*Standing vegetation, forage grazed, herbage growth, and precipitation on pasture 7W in 1965*

Period		Days	Precipitation	Standing vegetation ¹		Forage grazed	Herbage growth	
From	To			At end of period	Difference of beginning and end of period		Period	Per day
		Number	Cm.	Kg./ha.	Kg./ha.	Kg./ha.	Kg./ha.	Kg./ha.
---	5/17	--	1.42	139				
5/18	5/27	10	2.13	177	38	3	41	4.1
5/28	6/9	13	2.44	159	-18	11	-7	-0.5
6/10	6/24	15	10.16	187	28	15	43	2.9
6/25	7/8	14	0	330	143	15	158	11.3
7/9	7/21	13	4.67	299	-31	11	-20	-1.5
7/22	8/5	15	3.68	443	144	10	154	10.3
8/6	8/18	13	0.51	465	22	11	33	2.5
8/19	9/3	16	0	402	-63	11	-52	-3.2

¹ Grasses and sedges, ovendry.

Range. Growing season precipitation was near average in 1966 and was the highest recorded at the site in 1967. Standing vegetation varied from a low of 139 kg./ha. in 1965 to a high of 1,060 in 1967.

Herbage growth occurred in 14 of the 21 periods observed. During eight of these periods, a growth rate exceeding 9 kg./ha./day was attained. Table 6 shows the standing vegetation available at the beginning of each of these periods and the rate of herbage growth during the

period. Growth rates of over 9 kg./ha./day occurred when amounts of standing vegetation varied from 187 to 939 kg./ha.

Herbage growth rate varies with the amount of water available, temperature conditions, and the amount of leaf material present. When moisture and temperature conditions present an opportunity for herbage growth, reasonable forage production can be expected through a relatively wide range in the amount of standing vegetation present.

TABLE 4.—*Standing vegetation, forage grazed, herbage growth, and precipitation on pasture 7W in 1966*

Period		Days	Precipitation	Standing vegetation ¹		Forage grazed	Herbage growth	
From	To			At end of period	Difference beginning and end of period		Period	Per day
		<i>Number</i>	<i>Cm.</i>	<i>Kg./ha.</i>	<i>Kg./ha.</i>	<i>Kg./ha.</i>	<i>Kg./ha.</i>	<i>Kg./ha.</i>
----	6/22	--	----	425				
6/23	6/28	6	5.66	510	85	7	92	15.3
6/29	7/12	14	0.08	465	-45	10	-35	-2.5
7/13	7/26	14	0.97	363	-102	10	-92	-6.6
7/27	8/9	14	1.04	436	73	10	83	5.9
8/10	8/16	7	7.90	609	173	6	179	25.6
8/17	9/9	24	0.48	684	75	16	91	3.8

¹ Grasses and sedges, ovendry.

TABLE 5.—*Standing vegetation, forage grazed, herbage growth, precipitation on pasture 7W in 1967*

Period		Days	Precipitation	Standing vegetation ¹		Forage grazed	Herbage growth	
From	To			At end of period	Difference beginning and end of period		Period	Per day
		<i>Number</i>	<i>Cm.</i>	<i>Kg./ha.</i>	<i>Kg./ha.</i>	<i>Kg./ha.</i>	<i>Kg./ha.</i>	<i>Kg./ha.</i>
----	5/28	--	----	390				
5/29	6/11	14	11.56	525	135	0	135	9.6
6/12	6/25	14	9.73	566	41	16	57	4.1
6/26	7/10	15	8.08	819	253	11	264	17.6
7/11	7/24	14	4.11	939	120	11	131	9.4
7/25	8/7	14	0.15	1059	120	29	149	10.6
8/8	8/21	14	0	1060	1	25	26	1.9
8/22	9/4	14	2.92	969	-91	25	-66	-4.7

¹ Grasses and sedges, ovendry.

TABLE 6.—*Standing vegetation (kg./ha.) available at the beginning of the period, and herbage growth rate (kg./ha./day) for eight periods of herbage growth*

Standing vegetation (kg./ha) at beginning of period	Herbage growth rate (kg./ha./day)
187	11.3
299	10.3
390	9.6
425	15.3
436	25.6
566	17.6
819	9.4
939	10.6

Leaf Weight Management

Optimum livestock production was made when 336 kg./ha. of herbage was left ungrazed. Stocking rates which altered the amount of ungrazed herbage only slightly from 336 kg./ha. reduced livestock production efficiency. Fast herbage growth was made through a relatively wide range in the amount of standing vegetation present. The 336 kg./ha. of ungrazed herbage which produced optimum livestock production is well within the limits that produced fast herbage growth. Therefore, the key to stocking rates and grazing systems on this kind of range is 336 kg./ha. of ungrazed herbage. The objective should be leaf-weight management to maintain 336 kg./ha. of herbage throughout the grazing season. Strategies used in managing blue-grama range should be geared to this principle.

EFFECTS OF STOCK ON MICROENVIRONMENTS IN AUSTRALIAN RANGELANDS

By J. K. Marshall¹

Abstract

The paucity of investigations inquiring specifically into the question of the effects of stock on microenvironments is noted. There is, however, a fair coverage of related investigations. From these and the inclusion of new information the interactions of stock grazing, trampling and excretion are considered in relation to four micro-environmental components: water balance, nutrient balance, soil stability, and radiation microclimate.

Of the possible total of 12 stock-microenvironment interactions (3 x 4), eight are identified and discussed, four associated with grazing, three with trampling, and one with excretion. In addition, two interactions between microenvironmental components, namely, between water balance and soil stability and between soil stability and nutrient balance are discussed.

The relative simplicity of these interactions is contrasted with the complexity of interrelationships between them in a discussion of scald formation and of microenvironmental diversity. Finally, the capacity of microenvironments to recover and the importance of prediction of susceptible (or relatively unstable) and nonsusceptible (or relatively stable) ecosystems in relation to stock use is discussed.

Additional key words: Grazing, trampling, excretion, water balance, nutrient balance, soil stability, radiation microclimate, scalds, microenvironmental diversity, ecosystem stability

Introduction

Little research has been reported in Australia on the effects of stock on microenvironment. How-

ever, many studies exist from Australia and elsewhere from which the effects of stock may be inferred. These include reports on changes in vegetation and soils and on the end-products of stock-landscape interaction. This account attempts to draw together both published and new information to provide an outline of stock-micro-environment interaction of particular relevance to Australian rangelands.

Much of this account implies that stock generally affect the microenvironment adversely. This is not necessarily so. Adverse effects only show themselves in circumstances of mismanagement of domestic or wild stock in relation to the ecosystem used, particularly in the failure to realize that ecosystems vary considerably in their susceptibility to stock. An example of this is provided by one of the commonest observations on stock effects, that of change in vegetation composition. Thus, disclimax *Danthonia caespitosa* Gaudich.—*Stipa variabilis* Hughes² grasslands (44) on heavy Riverine clay have shown little change under grazing by sheep during 19 years of observation (71, 72). By contrast, shrub steppe dominated by *Atriplex vesicaria* Heward ex Benth. (bladder saltbush) growing on similar soils is moderately susceptible to variation in stocking rate of sheep, the most noticeable effect being elimination of the saltbush at stocking rates of 1.2 and 2.5 sheep per hectare (73) (figure 1). Finally, many shrub steppe communities variously dominated by *Atriplex vesicaria*, *Kochia astrotricha* Johnson (low bluebush), *K. pyramidata* Benth. (black bluebush), and *K. sedifolia* F.v.M. (pearl bluebush) growing on desert sandy loams or texture contrast soils have been seriously depleted by effects of both rabbits and sheep, sometimes resulting in complete de-

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²Most plant names follow Black (13) and Eichler (19).

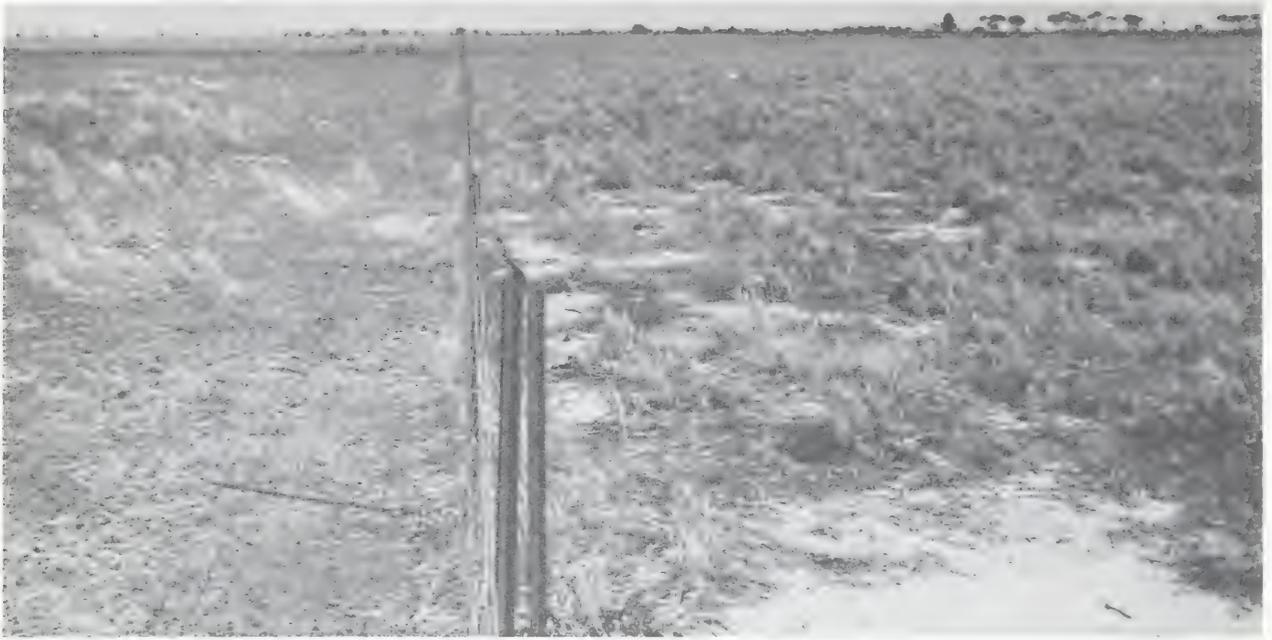


FIGURE 1.—Vegetation change as a result of variation in sheep stocking rate at "Emmet Vale", 49 km. N.N.W. of Deniliquin, N.S.W. The bladder saltbush (*Atriplex vesicaria*) on the right of the fence originally covered the entire area but was eliminated from the plot on the left of the fence after grazing for 5 years in 7 at a stocking rate of 1.2 sheep/ha. The plot on the right of the fence remained substantially unaltered after the same period of stocking at 0.6 sheep/ha. Details of the grazing experiment are given by Wilson and others (73). The condition of the vegetation is that under which the water-use results in figure 7 were obtained.

nudation (9, 16, 29, 49). Many of the more striking changes resulted from past failure to recognize inherent differences in susceptibility of the range added to which were the effects of drought, competition from rabbits, conditions of tenure, and financial pressures (1, 48).

Stock influence microenvironments as a result of their three basic activities: grazing, trampling, and excretion which here refers to both defecation and urination. Spatial variation in these activities, due to differences in stocking rate and to animal behavior, lead to effects on at least two scales: the former on a regional scale and the latter on a smaller, within paddock scale. Variation on a regional scale is evident at the State level from maps of stock numbers (18) while within paddock variation can arise from aggregation behavior concentrating effects around watering points (35, 45, 58), camping areas (26), and the tendency for some animals to graze into the wind.

Stock-Microenvironment Interactions

The ways in which grazing, trampling, and excretion influence the microenvironment can be considered in relation to the four microenvironmental components: water balance, nutrient balance, soil stability, and radiation microclimate.

Interactions between the three stock factors and these components are shown in figure 2. Of the twelve possible interactions only eight are obvious and reasonably direct. The interactions affect the components of the microenvironment in different ways but resolve themselves into three basic effects: reduction and changes in vegetation; modification of surface soil structure and modification in the availability of nutrients. The implications of these three effects of stock for water balance, nutrient balance, soil stability, and radiation microclimate are examined in the following sections.

Water Balance

Effects of stock on the water balance component are examined in terms of the water balance equation in which

$$P=R+\Delta D+\Delta M+\Delta U+fEdt \quad (1)$$

where P is rainfall; R is net surface runoff; ΔD is the change in surface water storage provided by dead and living plant material, and by surface hollows; ΔM is the change in soil water storage in the plant rooting zone; ΔU is the change in storage below the plant rooting zone and $fEdt$ is the total evaporation over the time, t, under consideration.

Reduction In Vegetation Cover

By reducing vegetation cover, trampling and grazing expose more of the soil surface to direct raindrop action. In shrub steppe communities, the shrubs may occupy over 33 percent of the ground area and, consequently, their removal adds substantially to the area of soil surface exposed. Further, the ground between perennial shrubs or tussock grasses is seasonally occupied by ephemerals which, when present, form a major component in the diet of sheep (36, 37, 52, 68). The duration of the ephemeral vegetation cover is consequently reduced. The additional area and duration of bare ground exposed to raindrop

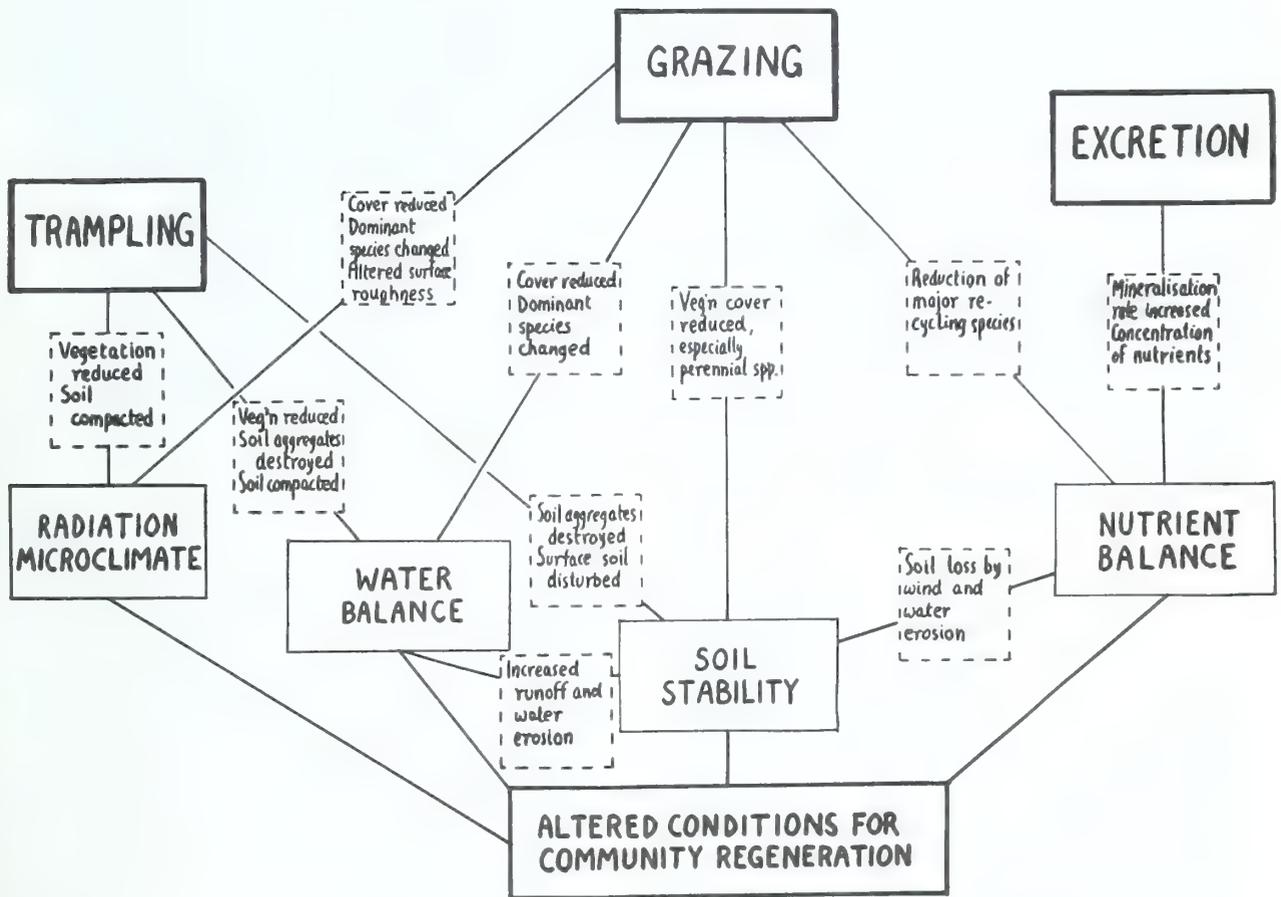


FIGURE 2.—Stock-microenvironment interactions. The direction of the interaction lines is from top to bottom for the stock-microenvironment interactions and from left to right for interactions between microenvironmental components.

action can be expected to result in more widespread deterioration of soil surface aggregates and structure (20) leading to an increase in net surface runoff, R (28, 62). A reduction in surface storage capacity, D , can also be expected, but this is unlikely to be of as great importance.

Soils in Australian rangelands vary considerably in their infiltration rate (I , equation 2). Rainfall intensities are such that runoff can be expected from some soils, even when initially dry, most of the time, while other soils, when dry, are capable of absorbing most of the rain-water received (fig. 3). Much variation in response of soils, due to increased direct raindrop action can therefore be expected, with soils (B in figure 3) of intermediate infiltration rates

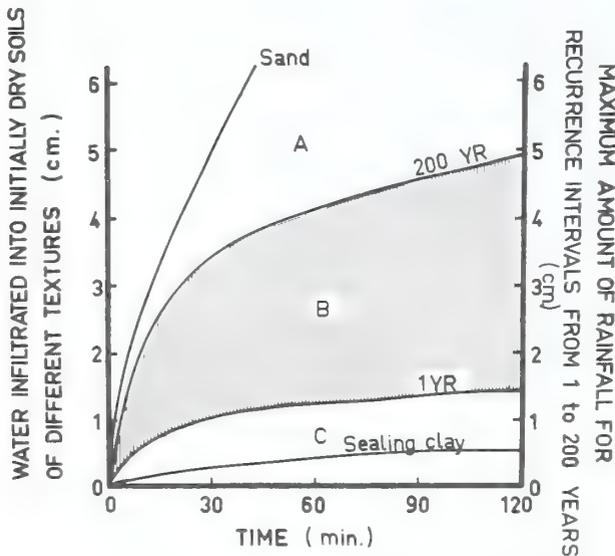


FIGURE 3.—Infiltration rate of water into rangeland soils of different textures and the maximum expected rainfall for recurrence intervals of 1 to 200 years. The cumulative infiltration curves refer to initially dry soils, using data from Jackson (28), Stannard (60) and Marshall (unpublished). The rainfall intensities refer to the average maximum intensities expected in the Western Division of New South Wales, using data from Stewart (61) and Wiltshire (74). Soils (A) are those capable of absorbing all of even the heaviest rains, soils (B) will absorb or shed water depending on rainfall intensity and soils (C) will shed water for all rains of the intensities plotted. For initially wet soils (data not plotted) most soils would, irrespective of texture, shed water from rainfall of intensities in the range plotted. (After Marshall, (43).)

relative to expected rainfall intensities probably showing the greatest response.

Modification Of Surface Soil Structure

By breaking down soil aggregates and by compaction of the surface soil, trampling can locally reduce the infiltration rate (I) of water into the soil and so influence runoff where the relationship between the two is

$$R = P - (fI dt + \Delta D) \quad (2)$$

Several other effects of trampling on surface soil structure have been noted including a reduction in pore space, soil penetrability, hydraulic conductivity and air permeability, and an increase in bulk density (3, 21, 24, 64). However, because of the prime importance of infiltration rate in the water balance of the soil a study was made of infiltration in terms of sorptivity, S , in relation to sheep tracks (fig. 4). Sorptivity and infiltration rate are related in the initial stages of infiltration by

$$I = St^{1/2} \quad (3)$$

The results obtained from the application of the ring infiltrometer method described by Talsma (63) are shown in figure 5.

The results in figure 5 show that sorptivity at first falls rapidly, at least on the desert sandy loam investigated, with an increase in trampling index and thereafter remains relatively unchanged. This implies that it is not so much the intensity of trampling that is important, but the proportion of the total area traversed by tracks.

The convergence of many tracks on watering points is an obvious example of an increasing proportion of trampled ground (fig. 6). An indication of the proportion of ground covered by tracks can be obtained using the track intensity to distance from watering point regression of Lange (35) and assuming a mean track width of 30 cm. when the tracks are found to occupy 16, 21, 24, and 25 percent of the ground at 1,600, 800, 200, and 100 m. respectively from the watering point.

Reduced infiltration due to trampling has also been shown by Lusby (38) at Badger Wash on the Colorado Plateau. There it was largely responsible for a 30-percent increase in runoff and



FIGURE 4.—Network of sheep tracks at Benilkie Ridge, 137 km. N.N.E. of Balranald, N.S.W., typical of the site on which variation of sorptivity with trampling intensity was investigated (fig. 5). A trampling index (T.I.) was assigned to the tracks depending on their prominence. Trampling indices illustrated include T.I. 0: soil between shrubs traversed by tracks; T.I. 0.5: track barely discernible (for example, track from bottom right to top left); T.I. 1: track clearly defined but with little or no difference in level with surrounding soil surface (for example, tracks in foreground from left to right); T.I. 4: track well defined with surface more than 2 cm. lower than the surrounding soil surface (for example, track in background from top left to top centre). In the study, intermediate and higher T.I. values were obtained at track intersections.

45-percent increase in sediment yield from grazed compared with ungrazed catchments over a 14-year-study period (39). The importance of reduced infiltration due to trampling has also been noted by Jackson (28).

Natural resilience of the soil is of some importance in its reaction to trampling. Thus, the high swelling and shrinking capacity of many of the sodic clay soils of the Riverine Plain of south-eastern Australia and possibly also the soils of much of the Mitchell grass (*Astrelba* spp.) country, in addition to their inherently low infiltration rates, are likely to reduce the effects of trampling. The more loosely aggregated, calcium rich, desert sandy loams have less natural resilience. In climates where frost heaving occurs, this can

reverse the effect of trampling by its seasonal effect on infiltration (55).

Change In Dominant Species

Efficiency in the use of water by vegetation depends in part on the soil volume exploited by plant roots, the plant rooting zone M in equation 1. The differential grazing treatments of Wilson and others (73) resulted in adjacent plots with and without *Atriplex vesicaria* (fig. 1). Changes in soil moisture down to 54 cm. were followed over a 33-day period in these plots after recharge of the soil profiles by rain during November 1970. The results shown in figure 7 indicate that the saltbush roots exploited the water in the

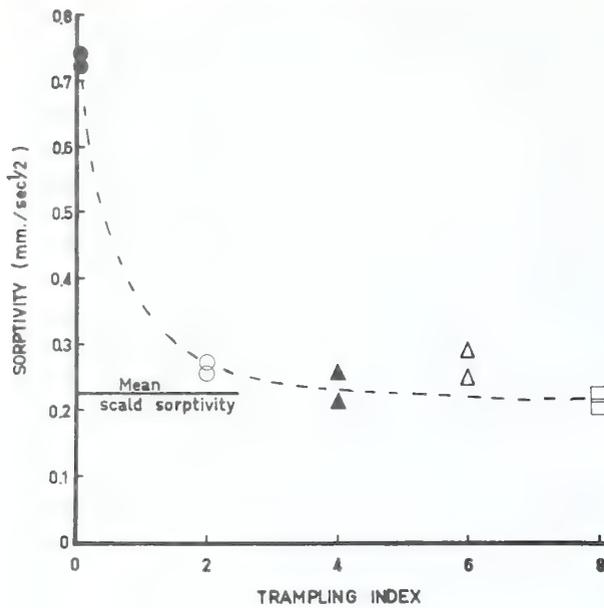


FIGURE 5.—Variation of sorptivity with trampling intensity. Trampling intensity was rated according to the trampling index defined in the caption of figure 4. The average initial moisture content of the soil was 4.6 percent by weight. The mean of four determinations of sorptivity for scald soils of similar moisture content is given for comparison. Scalds are near level, extensive, bare surfaces resulting from soil erosion (see Discussion and Conclusions, p. 180). They have characteristically low sorptivity values.

top 30 cm. of soil more effectively than the end-of-season growth of the annual, *Calocephalus sonderi* F.v.M., and the perennial grass, *Danthonia caespitosa*, which were present in both plots.

A similar example of this effect of grazing was shown by Jones (33). However, his results show in addition that moisture from the soil under the degraded community eventually evaporates, resulting in similar amounts of soil moisture in both profiles. The implication is that the soil water has been more efficiently used in the presence of the saltbush where more of it has been exchanged for dry matter production.

The main effects of stock on water balance are the reduction in water available for plant growth, largely by effects on infiltration rate, I, and hence runoff, R, but also by a reduction in the exploitable soil water by the vegetation, M.

The implications of the effects of stock for in

situ evaporation (J_{Edt} in equation 1) and for erosion are considered in the sections on radiation microclimate and soil stability, respectively.

Nutrient Balance

Effects of stock on nutrient balance have been studied less than those on water balance. Not only are such studies inherently more complex but there has prevailed the feeling that in arid environments water is likely to be the determinant factor. However, several reports (4, 14, 15, 22, 30, 33, 50, 51) have drawn attention to the existence of considerable variation in anion and cation concentrations horizontally and vertically in Australian rangeland soils. This variation may be important in the interpretation of some of the observed plant responses because of the low inherent fertility of the soil (27, 70) (see table 1).

Rate of Mineralization

Studies on sown pastures in more humid climates indicate that some plant nutrients eaten by sheep are more rapidly converted to mineral form than if the plant material had been allowed to decay in the soil (7, 8). Trumble and Woodroffe (65) recorded an increase in density and vigor of grazed pearl bluebush (*Kochia sedifolia*) compared with ungrazed controls during a period following a year of exceptional rainfall of about one in 16 years recurrence. They concluded that the increase was due mainly to: "an increased circulation of nutrients from the vegetation to the soil via the grazing animal and thence back to the plant," with urine returning approximately 75 percent of the nitrogen ingested and feces, 20 percent. Other factors may also have contributed. These include the pruning effect as suggested for the zone of increased vigor of *Atriplex vesicaria* which occurs at varying distances from watering points depending on grazing intensity (45). This effect is considered to result in the more effective use of soil moisture by the shrubs. There is also a possible reduction in competition by ephemeral vegetation which, when present, is preferentially grazed by sheep.

A dependency on rainfall of the response to grazing found by Trumble and Woodroffe (65) is indicated in their results by the absence of a



FIGURE 6.—Aerial view of sheep tracks converging on watering troughs at Caroombon, 62 km. N.N.W. of Deniliquin, N.S.W. Vehicle wheel tracks also appear in the photograph. The area of the photograph is 141 by 203 m. The vegetation changes from annual barley grass (*Hordeum leporinum*) within the 63 m. radius of the trough to the right hand side of the fence, through a zone of barley grass and annual saltbush (*Atriplex pseudocampanulata* Aellen) within the 123 m. radius, with perennial bladder saltbush (*Atriplex vesicaria*) and annual saltbush (*Atriplex lindleyi* Moq.) dominating beyond that.

response in the five poor to average rainfall years preceding the exceptional year. Also, while the most rapid recycling appears to occur by urination, this can contribute to losses in excess of 50 percent of nitrogen by volatilization from bare soil surfaces under summer conditions (67). Further, the rate of decomposition of sheep feces, which are strongly water-shedding once dry, is very slow in a semiarid environment (50), slower than the rate which can be inferred for the litter of many perennial and annual dryland species from its comparative lack of accumulation from year to year. These findings indicate only a lim-

ited beneficial role for the effect of stock on the recycling of plant nutrients in arid and semiarid rangelands by increased mineralization rates.

Concentration Of Nutrients

Concentration of plant nutrients occurs on a small scale with the localized deposition of individual urine patches and feces, and on a larger scale due to aggregation behavior in camping or in water seeking. Examples are provided by Hilder (26) of the effects of camping behavior on the redistribution of nutrients for sown pasture in the summer rainfall, northern Table-

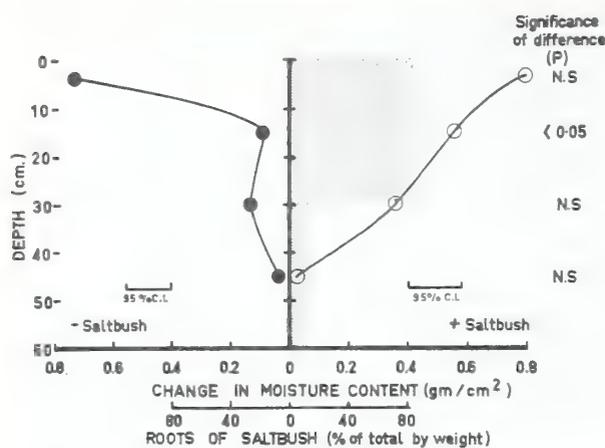


FIGURE 7.—Soil moisture use in adjacent sites with and without bladder saltbush (*Atriplex vesicaria*) at Emmet Vale, 49 km. N.N.W. of Deniliquin, N.S.W. (fig. 1) over the 33 days after November 19, 1970. Average initial moisture contents for the depths 0-7.6, 7.6-23, 23-38, and 38-54 cm. were 16.9, 20.2, 22.6, and 25 percent; 15.4, 19.5, 23.0, and 26.3 percent of soil oven-dry weight for the sites with and without saltbush, respectively. Average short-wave radiation over the period was 676.2 cal./cm.²/day. The water-use was equivalent to 1,009 cal./cm.² and 568 cal./cm.² in the saltbush and no saltbush sites, respectively (taking 1 g. water = 590 cal./cm.²). Light falls of rain over the period of measurement (totalling 1.24 cm.) have not been included in the calculations. The percentage of saltbush roots with depth was calculated from data of Jones and Hodgkinson (31).

lands of N.S.W., where one-and-a-half to one-hundred-fold concentrations occurred, depending on the particular plant nutrient. No similar study appears to have been conducted in the arid and semiarid rangelands, although Lange (35) had noted a concentration of sheep fecal pellets of greater than 4:1 between sites at 183 and 1,600 m. from a watering point. Evidence of the concentration of nutrients is also commonplace in the shade of trees, the corners of paddocks, or near watering points by the presence of pure stands of reputedly nutrient demanding species such as *Sisymbrium erysimoides* Desf., *S. irio* L. and *Hordeum leporinum* Link (barley grass).

Removal Of Major Recycling Species

Variation of organic carbon, nitrogen, and phosphorus, and of chlorides, sodium, potassium, calcium, magnesium, total soluble salts, and con-

ductivity is known to occur in the soils of many of the rangeland shrub steppe communities (4, 30, 33, 50, 51, Marshall and Tupper, unpublished). Many of the dominant perennials (*Atriplex* spp. and *Kochia* spp.) accumulate sodium and chloride in their leaves in the field and under glasshouse conditions and some are nutritionally favored by high concentrations of sodium (5, 12, 30, 76.)

These studies have implications for stock interactions which result in the elimination of species which predominate in the recycling and spatial transfer of plant nutrients. Jessup (30) showed that concentrations of chloride and total soluble salts under *Enneapogon ovenaceus* (Lindl.) C. E. Hubbard grassland, which had previously carried the shrub species *A. vesicaria* and *K. astrotricha*, were at levels more comparable with the inter-shrub soil rather than the higher concentrations below the shrubs. Charley (14) proposed that the pattern of redistribution of chloride following the destruction of perennial shrubs by grazing is a key factor in the sequence of species dominance as grazing intensity increases. Thus, the sequence of dominance from *A. vesicaria* to *Bassia* spp. to *Enneapogon* sp. with increased grazing pressure is related to a progressive decrease in salinity concentration of the depressions in which the vegetation he was studying grows, and an increase in concentration of the surrounding, un-vegetated shelves. Rixon (50, 51) showed that soil from mounds associated with *Atriplex vesicaria* before its elimination 5 years previously by grazing still exceeded soil from intervening areas in its capacity for mineralization of nitrogen but was significantly lower than the capacity of soil from below existing shrubs.

The emphasis on shrub steppe communities has been intentional because little of relevance has been reported for other Australian rangeland communities with few exceptions (11, 46, 54, 75). Gaps also exist in the understanding of the shrub-steppe patterns perhaps the most noteworthy of which is the comparatively little attention given to soil water movement in the distribution of the soluble anions and cations although associations between the two are evident in the work of Jessup (30) and Jones (33).

The possibility exists for addition of nitrogen to the rangeland ecosystem by direct fixation by

lichens, blue-green algae and other cryptograms (53) and by *Medicago* spp. and other N-fixing flowering plants (11). If the contribution turns out to be significant, then the interaction of trampling and these species may also be of some importance. It seems probable, however, that variation in this source of plant nutrient, along with income in rainfall (69) and its subsequent redistribution is likely to remain of minor importance in relation to other effects of stock.

Soil Nutrient Losses

The quantities of nutrients considered so far in processes of recycling and redistribution have been three to four orders of magnitude smaller than the bulk sources available in the soil and, where relevant, the atmosphere. Even the amount of nutrients contained in the standing crop of vegetation is small in comparison with these bulk sources. Thus, while the importance of the recycling portion of the total plant nutrients should not be underestimated, the comparative seriousness of losses from the bulk source of nutrients in the soil requires some emphasis.

Soil loss was considered in terms of nitrogen and phosphorus by Charley and Cowling (15). They indicate that Australian rangeland soils are low in these essential elements by world standards (table 1) and demonstrate from profiles examined in an *Atriplex vesicaria* shrub-steppe a marked decrease in concentration of available nitrogen

and phosphorus with depth (table 2). They also calculate that erosion of the top 10 cm. of soil would result in the loss of 27 percent of the total nitrogen, 21 percent of the total phosphorus and 38 percent of the organic matter contained in the soil to a depth of 45 cm. rising to 35 percent for nitrogen and 45 percent of organic matter when the available portions only are considered.

Soil Stability

Stock, by trampling and grazing, reduce soil stability and make soils more susceptible to erosion. Soil erosion resulting from wind action is considered here as a direct interaction of micro-environment with stock; erosion resulting from water is considered as an interaction of the water balance component with the soil stability component.

Reduction Of Protective Vegetation

Soil erosion by wind following the reduction of perennials in rangeland vegetation by grazing has been noted by several authors (9, 10, 16, 29, 49). The importance of perennial species in protecting the soil from wind erosion has also been recognized, because they alone persist when the covering of annual species on the intervening soil surface has disappeared (29, 41, 43, 49).

The role of perennial species on erosion susceptible soils is the maintenance of the rangeland re-

TABLE 1.—Comparison of Australian and overseas arid zone soils as the percentage of surface soil samples according to nitrogen and phosphorus contents

Soils	No. samples	Nitrogen (percent total)					Mean nitrogen (percent)
		<0.01	0.01-0.03	0.03-0.05	0.05-0.1	0.1-0.5	
Australian	77	4	22	23	41	10	0.06
Overseas	38	0	16	29	18	37	0.11

Soils	No. samples	Total phosphorus (p.p.m.)					Mean phosphorus (p.p.m.)
		0-100	100-250	250-500	500-1,000	>1,000	
Australian	70	24	39	30	7	0	240
Overseas	70	7	6	14	54	19	710

Source: From Charley and Cowling (15).

source. One of the effects of perennials is to reduce wind velocity. The smoother the surface, the lower the value of the roughness parameter, z_0 , and the higher the wind velocity, u , at a comparable height, given the same geostrophic velocity (table 3). Another effect of vegetation on the wind is to reduce the drag force on the intervening soil surface and so reduce soil particle movement. In table 3, drag, expressed as the shearing stress for the entire surface, τ_0 , is 6 times greater over the scrub covered ground than over bare ground. However, this is partitioned between the surface roughness and the intervening ground surface. In the example in table 3 the proportion of the total drag acting at the ground surface is negligible in the presence of the scrub covering

while over the bare ground surface it is all acting at the ground surface.

The proportion of the total drag exerted at the ground surface has been shown to depend both on the vegetation elements and their density (no./unit area) (40). An expression for appraisal of perennial plant cover for erosion prediction makes use of the product of the unobstructed drag coefficient of the vegetation elements, $C_f(z)$, and lateral cover, L_c , that is, the average frontal area of the elements/average surface area occupied per element. The product $L_c \cdot C_f$ is related to a constant for the condition at which the ground surface shearing stress, τ_0 , becomes negligible. Thus when

$$L_c \cdot C_f(z) \geq 0.0147^3 \quad (4)$$

TABLE 2.—Distribution of mineralizable nitrogen and available phosphorus with depth from *Atriplex vesicaria* communities in western N.S.W.

Depth	Mineralizable nitrogen ¹	Available phosphorus ²
<i>Cm.</i>	<i>P.p.m.</i>	<i>P.p.m.</i>
0 - 2.5	316	17.3
2.5 - 5	200	16.3
5 - 10	144	8.0
10 - 15	49	3.7
15 - 22.5	38	2.3
22.5 - 30	29	2.0
30 - 45	26	1.7

¹ Mineral nitrogen released in 9-wk. incubation.

² NaHCO₃ extraction.

Source: From Charley and Cowling (15).

TABLE 3.—Wind parameters over bare soil and scrub¹

Surface	Bare soil	Scrub
Roughness parameter z_0 (cm.)	0.1	100
Friction velocity u^* (cm./sec.)	57	138
Surface shearing stress τ_0 (dyne/cm. ²)	4	24
Wind velocity at 10 m. u_{10} (m./sec.)	13	7

¹ Calculated for geostrophic wind velocity $U_0=25$ m./sec.; latitude 43°. From Deacon (17).

no net soil loss from the area occupied by the vegetation elements is expected (40). The reference height, Z , here is 1.6H where H is the mean roughness element height. Field tests and comparison of predictions of erosion hazard for shrub steppe communities with the field assessments of Jessup (29) show good correspondence when a value of $C_f=0.4$ is assumed for the vegetation elements (43).

The results of prediction of erosion hazard in the field can be presented in terms of the value of $L_c \cdot C_f$ relative to the threshold value, or as the maximum average distance tolerable between shrubs (D) in terms of their height (H). A typical value of maximum tolerable D/H for Australian shrub rangelands appears to be about 3.5 (43) where H is the average of the maximum heights of the vegetation elements. Caution is required in extrapolation of this value to other situations, however, as it depends on the value of the unobstructed element drag coefficient, the openness of the vegetation elements, their general outline, their diameter to height ratio, and their behavior at different wind velocities.

³ A more accurate expression is

$C_f(u_{10}) = b/\sqrt{L_c + a}$ where,

for 1.6H, $b=0.1014$, $a=-0.0005$;

2.36H, $b=0.0918$, $a=-0.046$;

3.94H, $b=0.0799$, $a=-0.066$,

the derivation of which is given by Marshall (42). For the values of C_f expected for vegetation elements, however, the simpler expression is of sufficient accuracy for practical use.

Breakdown Of Soil Aggregates And Disturbance

Trampling influences soil stability in two ways. First, by breaking down soil aggregates, it provides a supply of particles more susceptible to movement by wind. Secondly, both rainfall and trampling are disturbing agents, with the latter particularly effective in mixing the heavier residual particles with underlying lighter particles thereby recreating a surface layer of erodible material.

Runoff And Water Erosion

The low percentage cover of vegetation in semi-arid and arid rangelands for much of the year makes their soils particularly susceptible to water erosion with the combination of direct raindrop impact and largely unimpeded runoff (43). Lack of rainfall itself becomes limiting in terms of

sediment yield produced from catchments covered by seminatural vegetation at the more arid extreme of rangelands. However, in semiarid rangelands, a combination of sufficient rain and inadequate vegetation cover has been shown to produce, for American conditions at least, a peak in sediment yields in an annual rainfall regime of between 10 and 20 inches (34). Those effects of grazing and trampling on the water balance component which increase runoff (see Water Balance, p. 169) further aggravate this already naturally severe problem of erosion of soils by water. Some of the worst gullies arise initially from cross-contour tracks, often leading to water holes (fig. 8). These tracks, acting both as areas of lowered infiltration rate and as channels for water shed from adjacent soil surfaces, become rapidly eroded.



FIGURE 8.—Gully erosion originating from cross-contour sheep and vehicle tracks leading to a watering point in black and pearl bluebush (*Kochia pyramidata* and *K. sedifolia*) country 64 km. N.N.W. of Balranald, N.S.W.

Radiation Microclimate

Very little information is yet available on the detailed effects of stock on radiation microclimate. However, a number of effects can be anticipated following the reduction in vegetation cover, a change in dominant species, and modification of the soil surface. The implications of these effects are examined in relation to net radiation, the partition of net radiation and diversity of microclimate.

Net Radiation

The albedo, or surface reflectivity a is known to be the main contributor to variations in net radiation R_N of similarly exposed surfaces (59) where

$$R_N = R_G (1 - a) + R_{NL} \quad (5)$$

with R_G the incoming shortwave radiation and R_{NL} the net longwave radiation.

Net radiation will then alter with changes in the proportion of ground occupied by vegetation, changes in the dominant species and modification of the soil surface depending on albedo differences between plant species and soil surfaces. These changes were examined in shrub steppe communities with the shrub species *Kochia sedifolia*, *K. pyramidata*, *Atriplex vesicaria*, and *A. nummularia* Lindl. present at a site 64 km. NNW. of Balranald, N.S.W. in December 1970. Summertime values of albedo were obtained for the shrub species, the perennial grass *Danthonia caespitosa*, samphire *Pachyornis tenuis* (Benth.) J. M. Black, and compacted and uncompact soil (table 4).

The albedos for the plant species in table 4 vary comparatively little. From this it can be inferred that stock-induced changes in species-dominance are unlikely to produce a marked shift in surface net radiation. The maximum possible change, that is from *Kochia sedifolia* to *K. pyramidata*, would result, given equal replacement of one by the other, in a local increase in net radiation of 4 percent. When the change in the net radiation of the entire surface is considered, this is likely to be lower because of the unchanging albedo of the intervening surface.

Changes in vegetation cover are likely to result in a still smaller change in surface net radiation, at least for the situations examined.

TABLE 4.—Summertime albedos of some rangeland plants and soils (solar elevation $\geq 30^\circ$)

Item	Sample No. ¹	Albedo	
		Mean	S.E.
Plant species:			
<i>Kochia sedifolia</i>	14	0.208	0.0229
<i>K. pyramidata</i>	11	.165	.0076
<i>Atriplex vesicaria</i>	8	.186	.0216
<i>A. nummularia</i>	7	.183	.0151
<i>Danthonia caespitosa</i> (50 percent dry leaves)	11	.179	.0132
<i>Pachyornis tenuis</i>	2	.174	—
Soils:			
Uneroded red sandy loam:			
Dry	14	.175	.0169
Wet	6	.135	.0108
Eroded compacted red clay loam:			
Dry	21	.276	.0289
Wet	6	.186	.0145

¹ 20 readings per sample.

Thus, the change expected from a reduction in the cover of *Kochia sedifolia* ($a=0.208$) from the commonly encountered value of 33 percent to a bare soil surface ($a=0.175$) would only be a 1.1 percent increase in surface net radiation.

The small change due to a reduction in vegetation can, however, be more than offset by changes in soil surface albedo due to compaction and surface erosion. The albedo of an uneroded red sandy loam was found to be much lower than that for an adjacent eroded red, compacted, clay loam surface (table 4). The expected net radiation over the eroded soil surface was consequently 10.1 and 5.1 percent lower for dry and wet conditions, respectively.

Reflection coefficients of several Australian rangeland species are reported by Sinclair and Thomas (56), but they are generally higher than the values obtained for the *in situ* measurements on whole plants in table 4 because they are for single leaves or mosaics of leaves.

Partition of Net Radiation

The partition of net radiation at a surface can be expressed, in the absence of advection and neglecting the photosynthesis term, as

$$R_N = LE + Q + G \quad (6)$$

where LE is the energy used to evaporate water, Q is that used in sensible heat transfer to the air, and G is that used in heating the soil.

The effect of stock on this partition of energy is complicated. First, stock, by reducing vegetation cover or inducing a change in dominant species, alter the surface roughness, and thereby influence the transfer process affecting the removal of heat and water vapor from the vegetation and soil surface. Thus, comparing a surface covered by well-spaced shrubs with a bare soil surface, the transfer of water vapor and heat is likely to be least efficient of all for the shrub canopies, more efficient for the bare soil surface, and most efficient of all for the shrub canopies. Secondly, the partition of net radiation depends on the availability of water for evaporation, an availability which depends mainly in the present context on the proportion of radiation intercepting plant surface and soil surface. The latter is a less controlled source of available water, unlike a plant surface with its stomata. Also, the soil surface usually shows an earlier decline in the availability of water because of the greater resistance to evaporation provided by the soil surface layer as it dries out.

The complications outlined make quantitative prediction of the differences in radiation microclimate difficult particularly when, in reality, the altered water balance due to stock further complicates the effects expected.

The findings of Aase and Wight (2) on energy balance components relative to percent plant cover in *Bouteloua-Carex-Stipa* rangeland near Sidney, Montana, are of interest as one of the few examples in which such an evaluation has been attempted in the field. They report a 40-percent reduction in evapotranspiration (LE in equation 6) from bare ground in comparison with 100-percent cover over a growing season of 113 days. Ground covers of 25, 50, and 75 percent yielded closely similar results, representing on average a 21-percent reduction in evapotranspiration compared with 100-percent cover. They also found differences in daily energy partition between different vegetation covers and for periods of different water availability. Thus, the ratios of sensible heat transfer (Q in Equation 6) to latent heat transfer (LE in equation 6) were, for a wet

period, 1.22, 0.49, and 0.18 and, for a dry period, 2.33, 1.95, and 1.88 for vegetation covers of 0 percent, mean of 25, 50, and 75 percent, and 100 percent, respectively. Their results reflect, for both periods, lower availability of water for evaporation the smaller the proportion of vegetation cover. What is not apparent from studies of this type, however, is the effect on details of the microenvironment between and within units of vegetation, that is on the spatial diversity of microclimate.

Spatial Diversity Of Microclimate

The most notable difference between areas which have lost their perennial plants and unaffected areas is the reduction of habitat diversity in the former. This results from the reduction in area of radiation intercepting surfaces above the ground surface. Considerable microclimatic contrasts exist as the air and soil are traversed from beneath vegetation units out into the open. At the time of the albedo measurements reported in table 4, summer midday soil temperatures at 2 cm. depth were found to differ by up to 16° C. between shrub shade and sun microhabitats. The measured soil temperature at similar depth on a denuded area was lower than the intershrub soil temperature by 3° to 6°, largely attributable to soil surface albedo difference. What appears more important, however, was the spatial uniformity of microclimate in this latter situation. Similar shade and sun soil temperature differences were noted in a natural community in a semihumid environment (57). Many other examples of contrasting microenvironments exist in the general literature on microclimatology (23). Further description of these is comparatively meaningless, however, without reference to some specific ecological problem. Instead, general aspects of microenvironmental diversity are discussed in the next section.

Discussion And Conclusions

Interrelationships Of Stock-Microenvironment Interactions

Stock-microenvironment interactions have been treated individually for the purpose of their definition and evaluation, as far as possible, of their relative importance. However, in the field, no

one interaction occurs separately. Interrelationships exist between practically all the interactions and certainly between all of them and the plant component of the rangeland ecosystem. At this stage of our poor knowledge of the interactions themselves, commentary on interrelationships would appear unjustified. Certainly, the more subtle interrelationships as they first affect the regeneration of the plant communities remain obscure. However, consideration of scald formation and the reduction of habitat diversity can serve to illustrate the complexity of actual stock-microenvironment interactions. Also, just as semipermanent degradation of the microenvironment can result from effects of stock so, also, can examples be found of resilience in microenvironments where, given apparently the same treatment by stock, the microenvironment has the capacity to recover. This forms the third topic of discussion.

Scalds—A Case Study Of Interacting Micro-environmental Responses To Stock

The term "scald" has been applied to practically level areas of ground which are denuded of

vegetation (9) (fig. 9) and the natural regeneration of which is slow (10, 32). A number of different types have been recognized by Beadle (10) and some controversy surrounds the precise stages of their formation (9, 10, 66). It is not the intention here to be concerned with the different types of scald or details of their formation but rather to present scalds as an end point in microenvironment degradation following interaction with stock.

Scald susceptible country usually has texture contrast soils in which layers of heavier texture underlie the top, light-textured layer, and are progressively poorer in their infiltration rates with depth (fig. 10). Scald initiation then involves interrelationships between stock grazing and trampling, the water balance and soil stability components, and, perhaps, the radiation microclimate component of the microenvironment. As a result, the grazed perennial species die. The water infiltrating into the soil is probably reduced at this stage by trampling and greater exposure to raindrop action, and some soil erosion by wind and by water is likely. Exposure of large areas unprotected by vegetation allows



FIGURE 9.—A scald 37 km. N.N.W. of Hay, N.S.W.

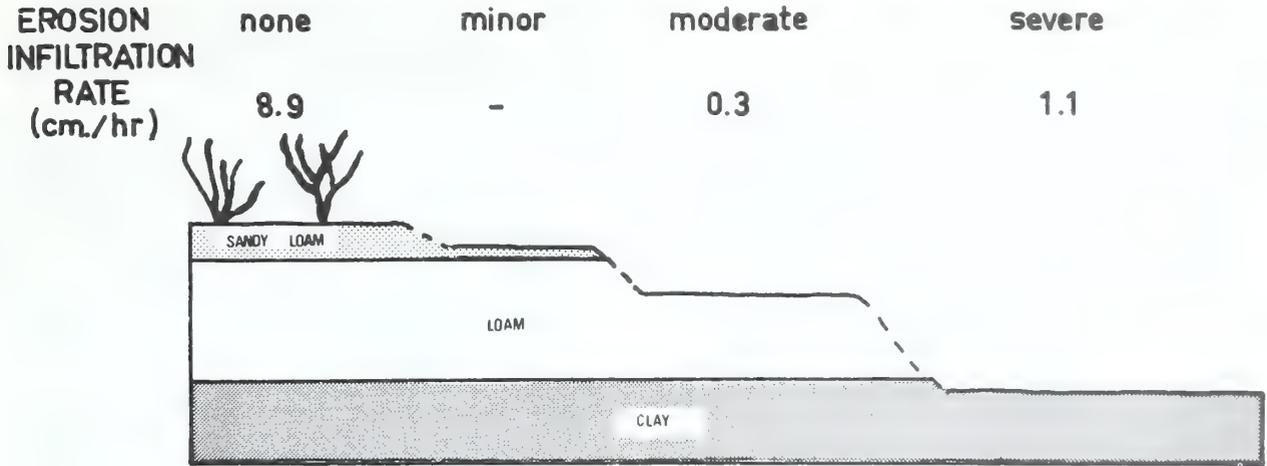


FIGURE 10.—Diagrammatic representation of changing surface infiltration characteristics and texture at different stages in scald formation on a red-brown earth, 32 km. W. of Condobolin, N.S.W. (Modified after Stannard (60).)

greater wind erosion to take place. As successive soil layers are exposed, the poorer infiltration rates lead to greater runoff and water erosion, and a more homogeneous and unfavorable habitat for annual plant growth. Finally, a near uniform surface of smooth, self-sealing, clay-loam soil with a low infiltration rate results. Little opportunity exists in this microenvironment for seed lodgment; maximum water penetration is about 15 cm.; and a high chloride content occurs near the surface. Thus, while erosion of soil is a fairly obvious feature, interactions of stock with other components of the microenvironment contribute at all stages of degeneration.

Maintenance Of Microenvironmental Diversity

Maintenance of microenvironmental diversity is important for the regeneration of plant communities and conservation of landscape stability for several reasons. The role of perennials is well recognized in creating diversity and thereby influencing community regeneration (25, 49) and conserving landscape stability (40, 41, 43). The combination of contrasting environments closely juxtaposed provides habitats for the growth and population maintenance of the ephemeral constituents of the community. In the absence of diversity in a uniform environment some, and occasionally (as with scalds) all, of the component

species of the plant community may disappear or be considerably reduced in their contribution.

Some of the contrasting factors in the perennial-between-perennial mosaic of environments have already been cited, including temperature, nutrient, and water balance differences. Soil texture differences can also occur with mounds of locally accreted mineral soil and organic material beneath shrubs providing more favorable seedbeds than the soil of intershrub areas. With stock trampling and grazing in the intershrub areas, these habitats can provide refugia for the growth and seeding of plants, the regeneration of which would otherwise be reduced in the community (6). Loss of such refugium environments can consequently represent an important stage in environmental degeneration.

Ability Of Microenvironments To Recover

Perhaps of prime importance in attempting to influence management of rangelands from the viewpoint of stock-microenvironment interaction is the ability to recognize those situations in which the soil-plant-animal complex has the capacity to recover from adverse stock-microenvironment interaction or even resist adverse interaction, and those situations where recovery is unlikely. It would be particularly useful to know, for any pastoral land-use situation, which stock-

microenvironment interactions, feeding back onto regeneration of the plant community, were likely to be of greatest importance in degeneration. However, much needs to be done before our knowledge of stock-microenvironment interactions can contribute fully to the scientific management of Australian arid and semiarid rangelands. In particular, many of the interactions identified in figure 2 need to be evaluated over a wider range of situations. The way in which the interactions are interrelated in particular situations requires further clarification. Most importantly, the implications of the altered microenvironment need to be examined not only in terms of plant and animal productivity, but also in terms of plant community and species regeneration.

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EFFECTS OF GRAZING ON MICROENVIRONMENT OF UNITED STATES RANGELANDS

By Russell J. Lorenz¹

Abstract

Some factors of the microenvironment have received considerable attention in relation to grazing in the United States. Change in species composition, invasion by undesirable species, mulch accumulation, and soil moisture status have been studied in relation to grazing season and grazing intensity. Generally, the adverse effects increase with grazing intensity, but differences in response are often not as great as are differences between no grazing and grazing. In many respects, interaction of the moisture regime or of energy and temperature factors with canopy height and density or with mulch accumulation appear to be similar for rangeland and for the more thoroughly studied cultivated crops. The effects of grazing on factors affecting infiltration and runoff are fairly well documented, but the effect of grazing on factors affecting evaporation, evapotranspiration, the energy balance, and nutrient cycling have been studied very little. Comprehensive information on the effect of grazing on all microenvironmental factors for a specific situation are lacking.

Additional key words: Species composition, mulch, infiltration, runoff, evapotranspiration, microclimate.

Introduction

Grazing is usually considered in terms of its effects on the vegetation as evaluated by species change or by change in plant productivity or vigor. Information concerning the effect of grazing on microenvironment is either lacking or restricted to a few easily evaluated factors. Dis-

cussion of these factors becomes rather involved, because it is the environment, both micro and macro, which largely determines the character of the vegetation of an area. Alteration of any environmental factor by grazing, or by other means, will be reflected by change in other environmental factors as well as by vegetational response. The cycle of cause and effect becomes endless.

It is obvious that grazing of any kind or intensity will affect the microenvironment, and that each situation is unique. A thorough understanding of all physical and biotic factors is necessary for proper evaluation of the impact of grazing on a particular ecosystem. The grazing animal can best convert the stored energy and nutrients of much of the land area of western United States to dietary protein. We must first evaluate what is known about the effect of grazing on the system, and then work toward understanding what is not known, so that efficiency of this conversion can be increased.

The most obvious contribution of the grazing animal to the ecosystem is of a mechanical nature—change in height and density of the canopy, trampling, and deposition of excreta. Defoliation is the major direct animal influence. Selectivity by animals for plant species or for plant parts, with changing season or with changing grazing pressure, complicates study of defoliation and of the final influence of grazing. The effects of grazing intensity on change in species composition, plant density, and ground cover have been reported for a variety of situations. The reasons for the change and the overall effect on the microenvironment have not been fully investigated.

Microenvironmental parameters include the microclimatic factors, soil and its related factors, and living organisms and their related factors. Much of the microclimatic data and some of the

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soils data have been gathered without the grazer because the uncontrollable influences of grazing complicate the study of these factors. However, there is considerable information available on the effects of various biotic factors on microclimate. The known influence of grazing on these biotic factors allows inference to possible effects of grazing on the microclimate. Plants themselves are a part of the microenvironment, therefore, any change in growth form, size or density, or in species composition of the community, induced directly or indirectly by grazing, has an effect on the overall microenvironment. Change in species composition produced by grazing has been described for many rangelands; however, only unique instances will be cited here when they serve to illustrate specific effects of grazing on the microenvironment.

Through the ages, the grazing animal has influenced the evolution of United States rangelands. In a summary of the history of grazing, Heady (25) considered grazing to be a force in natural selection long before man replaced wild with domestic animals. Plants and animals in central North America evolved in a grassland-grazing animal context. With the shift from wild to domestic animals, grazing intensity and selectivity changed the grasslands somewhat, but Heady concluded that this replacement, as such, did not destroy the grasslands. Most grasslands of the Great Plains survived change in grazers in spite of considerable mismanagement. However, deterioration of rangeland, accompanied by increased rate of soil erosion and increased sediment load, is often associated with immigration of livestock and ranchers. Grazing by domestic animals has been blamed for this situation, and in many cases, rightly so. It is easy to see the end result of poor grazing management, but to understand the reasons why certain changes occurred, and to develop methods for correcting old errors while avoiding new ones is far more difficult. Reed and Peterson (43) found extreme weather fluctuations, rather than grazing intensity, to be the major influence on mixed prairie range. However, the rate of vegetation change produced by weather fluctuations was influenced by grazing intensity.

Crocker (12) discussed the soil and ecological problems arising from chronic overgrazing. He

defined chronic overgrazing as an intensity of grazing which modifies plant cover so that productive capacity is seriously impaired. He emphasized the importance of assessing direct effects on the vegetation as well as those indirectly affecting production through soils effects.

Buffington and Herbel (7) attribute the conversion of the desert-grassland climax of southern New Mexico to a desert-shrub climax, dominated by mesquite (*Prosopis juliflora* [Swartz] D.C.) to grazing by domestic animals. They eliminated climatic change or fire as possible causes for the change, but found close correlation with beginning of the grazing industry. Islands of mesquite supplied seed which was disseminated through the digestive tract of the animals. In this case, grazing set off a series of events which resulted in conversion to a desert-shrub type in a relatively short time.

Some grasslands, such as the bunchgrass types of the Pacific Northwest and California, are very sensitive to grazing. It has been suggested (51) that low grazing pressure, due to lack of large herds of grazing wild animals in these areas, allowed the more sensitive bunchgrasses to survive. Introduction of domestic animals increased the grazing pressure which resulted in loss of the perennial bunchgrass in many areas.

Some aspects of the microenvironment have received considerable attention; others have been studied very little, although indirect inferences have been drawn. All microenvironmental factors are closely related, thus the following discussion is arbitrarily divided into categories.

Moisture Regime

No one environmental factor influences plants more than does water. Management practices can be employed which increase the efficiency of water use, but shortage of available water often remains as a limiting factor. Grazing has a definite effect on factors which contribute to the moisture regime—interception and redistribution of precipitation by the plant canopy; infiltration and runoff as influenced by standing vegetation, litter accumulation and trampling. Evaporation and evapotranspiration (ET) continually reduce the reservoir of available water. The most active region of the water regime extends from a few cm. in the soil to the top of the vegetation canopy.

Any disturbance or alteration of the components of this region greatly influence the water balance of the entire system.

Interception

Redistribution and loss of water through interception by the canopy is often overlooked. Collins (10) reviewed works in which 20 percent of the total rainfall was lost through evaporation of intercepted precipitation in forest vegetation in Wisconsin. Interception losses in conifer forests were found to be twice those of hardwood forests of equal canopy density. The conifers intercepted 40 percent compared with 20 percent for the hardwoods on an annual basis. Interception by crop plants was found to range from 6.9 to 35.8 percent of the total precipitation, depending upon density of the vegetative cover.

In a detailed study of interception by grassland vegetation, Clark (9) found density of Nebraska vegetation to be the major factor. Due to the smaller amount of surface exposed, low-growing, mat-forming species intercepted less moisture than did species of greater height. Stratification of vegetation, as in a true prairie complex, increased interception loss. The water intercepted by the prairie vegetation ranged from 84 percent of a 0.32-cm. rain in a 30-minute period to 51 percent of a 5-cm. rain in a 1-hour period. As would be expected, wind and other evaporation factors had a large influence. Duration and rate of precipitation was also found to be important, but the type and amount of vegetation was of most importance.

A spreading, semidesert shrub can collect a sizeable amount of water and channel it down branches and stems, thus improving moisture conditions in its own root zone (11). Redistribution by this means is an important survival mechanism for the shrub, but it increases the aridity of the areas between shrubs. Stemflow is also important in crop plants, such as corn (*Zea mays* L.), alfalfa (*Medicago sativa* L.), and soybeans, (*Glycine max* [L.] Merrill).

Removal of all or part of the vegetative cover, or change in species composition in response to grazing will surely influence interception and consequently various other aspects of the water regime. Cooper (11) reviewed work done in the California chaparral for which equations for

quantities of water involved are being developed. This information would be useful for other vegetation types, particularly if the effects of grazing were included.

Infiltration And Runoff

Consider first the soil factors which influence rate of infiltration. Duley (16) reported that a rapid reduction in rate of water intake by bare soils was accompanied by formation of a thin, compact layer at the soil surface. This layer was the result of a severe structural disturbance brought about by the action of raindrops. Although the rate of formation and degree of sealing depended upon soil type and structure, it was formed in all cases. He found that a thin covering of straw kept the intake rate constant over a 5-hour period. The straw was then removed while the water application was continued. The intake rate rapidly decreased to near zero. Removal of the 7.6-mm. compact layer of soil and protection of the newly exposed surface with burlap resulted in an intake rate near that of the originally protected surface. Duley (17) reported that a surface cover of either grass or crop residue increased the intake rate over the initial rate for bare soil. The intake rate 90 minutes after start of precipitation was 8.4 and 8.9 cm./hr. for native vegetation 46 cm. tall and for cultivated soil covered with 5,604 kg. straw/ha., respectively. At the same time, intake rates were only 1.7 and 1.2 cm./hr. for native grass clipped to the soil surface with all debris removed, and for bare cultivated soil, respectively.

Dee et al. (15) found a high positive correlation between water intake and the amount and species of standing vegetation, litter, and vegetation plus litter on Pullman silty clay loam on the High Plains of Texas. Infiltration rates varied under different plant communities. Over a 2-hour period, soil under blue grama (*Bouteloua gracilis* [H.B.K.] Lag. ex Steud) absorbed 21.3 cm. of water, compared with 14.2 cm. for windmill grass (*Chloris verticillata* Nutt.), 9.7 cm. for annual weeds, and 5.3 cm. for buffalograss (*Buchloe dactyloides* [Nutt] Engelm.). A comprehensive study on the Wasatch Front Range in northern Utah (33) showed that plant and litter cover accounted for 73 percent of the variance in the amount of water retained during a 30-minute

simulated rainfall. Organic matter content was found to be the most important soil factor influencing soil erosion, and soil organic matter was related to litter accumulation.

These studies emphasize the importance of vegetation and litter in maintaining infiltration rate and reducing runoff and soil erosion. Herbage and mulch yields were determined in connection with an infiltration study (38) on mixed prairie in North Dakota when grazed at three intensities for over 40 years. Total air-dry herbage yields were 815, 1,708, and 2,470 kg./ha. for the heavily grazed, moderately grazed, and ungrazed areas, respectively. Mulch weights were 383, 2,008, and 4,652 kg./ha., respectively, for these treatments. Intake rates were 3.76, 6.10 and 10.85 cm./hr., respectively, for the initial hour of precipitation. Total herbage and mulch accounted for 88 percent of the variation in water intake rate.

Mazurak and Conrad (31) compared intake rates on three soil types for pure stands of six cool-season and four warm-season native and introduced species. In general, the cool-season species maintained a higher level of water intake than did the warm-season species. This was attributed to their more favorable effect on soil structure. We can assume, therefore, that change in species composition through grazing management which changes a grassland from cool-season to warm-season species (47) may result in reduced water intake rate, without considering other effects such as trampling or reduction in mulch.

The inverse relationship between grazing intensity and infiltration rate has been reported by others (5, 18, 24, 26, 27, 32, 33, 37, 38, 39, 40, 41, 42, 43, 44, 50). A comprehensive study of intake rates on midcontinental rangelands (39) showed that water intake rate was more closely correlated with both new and old vegetation than with other variables studied. Vegetation factors influenced intake rate more than did soil factors on saline-alkali upland, dense clays, silty soils of various sites and on most sandy soils. The soil factors influenced intake rate more than did vegetation factors only on extreme sands and on overflow sites, while both factors were of equal importance on shallow range soils and on some clay soils. Structure was the most important soil factor whenever soil factors were of major concern.

Other factors have been found to affect infiltration. Some of these are animal induced, others are not. Thompson (50) suggested that changes in surface soil characteristics produced by the shrink-swell action of frost during the winter improves infiltration. Heavy summer thunderstorms often destroy this condition. He considers these factors to be more important to overall intake ability in many cases than are the grazing effects.

The physical trampling by grazing animals was discussed by Packer (34). Working in the Boise River Watershed in Idaho, he used two intermixed types of foothill spring-fall range. Part of the area was dominated by bluebunch wheatgrass (*Agropyron inerme* [Scribn and Smith] Rydb.) and another part by cheatgrass (*Bromus tectorum* L.). From an infiltration study, he established specific ground cover conditions for preventing water erosion during typical major summer storms. No more than 30 percent of the soil surface could be bare, and the other 70 percent had to be covered by either plant foliage or litter. The bare soil between the plants and the litter patches could be no larger than 10 cm. in diameter on wheatgrass range, and no larger than 5 cm. on cheatgrass range. However, he found these specifications to be inadequate if the range was subjected to trampling. Using a steel "hoof," he imposed simulated trampling disturbance on 0, 10, 20, 40, and 60 percent of the plot surface. All levels of trampling reduced the amount of ground cover and increased the size of the bare soil openings on both range types. He found that 60 percent trampling caused little more reduction in cover than did 40 percent, because the "hoof" impacts often occurred on litter that had been moved by previous impacts. This resulted in redistribution of litter with little additional reduction in soil surface cover. All levels of trampling increased the amount of overland flow and the amount of soil erosion. Thus, he recommended that more vegetation and litter should remain when trampling is involved.

Quinn and Hervey (36) compared forage loss from trampling by yearling steers under various intensities of grazing. Losses ranged from 1 percent under light grazing to 5 percent of the total production under heavy grazing, or from 22 to 67 kg./ha. Susceptibility to trampling loss varied with species, blue grama being less susceptible

than prairie sandreed (*Calamovilfa longifolia* [Hook.] Scribn.) or needle-and-thread (*Stipa comata* Trin. & Rupr.). The steers traveled an average of 2.4 km. per 15-hour period in a 22-ha. pasture grazed lightly, and 3.2 km. in those grazed moderately and heavily. Brown and Schuster (5) also reported detrimental effects of trampling by livestock on hardland soils in the southern High Plains. Comparison of penetrometer readings showed 6 times as much compaction on grazed as on ungrazed areas. They found the compaction to be indirectly influenced by reduction in organic matter in the surface soil brought about by prolonged heavy grazing. Bulk density of the surface soil was 0.996 gm./cc. on the ungrazed area and 1.180 gm./cc. on the grazed area. No difference in bulk density was found between grazed and ungrazed areas on a high elevation cattle range in Utah in early summer before grazing and in late summer after grazing (28). However, bulk density increased in both grazed and ungrazed areas during the summer. This was attributed to change in soil moisture. In early summer, soils were moist and swollen, thus they weighed less per unit volume than they did when dry late in the summer. Greater bulk density of grazed compared with ungrazed areas, with little difference due to intensity of grazing, has been reported by others (27, 32, 40, 43, 44).

Increase in runoff and erosion as grazing intensity increased has been reported (1, 29, 34, 46). Infiltration and runoff are closely related; the factors which restrict infiltration induce runoff. Lusby (29) studied four grazed watersheds on salt-desert range near Grand Junction, Colorado. He found that cover remained about the same over a 14-year period without grazing, but the amount of bare soil and rock increased and ground cover by vegetation decreased on the grazed watersheds. Runoff averaged 30 percent less from ungrazed than from grazed watersheds, and sediment yield was 45 percent less. He concluded that, within a physiographic area, runoff is directly related to the percentage bare soil.

Litter Accumulation

The effect of grazing on residue and litter accumulation is important to the moisture regime. Decrease in litter accumulation as grazing intensity increases has been reported by sev-

eral workers. Reed and Peterson (43) found 2 to 2.5 times as much litter following light grazing when compared with heavy grazing. Air dry weights of from 47 to 54 gm./m.² of interspace under heavy grazing contrasted with 83 to 142 gm./m.² under light grazing. Organic matter content of the surface 5 cm. of soil ranged from 1.64 to 2.61 percent under heavy grazing, and from 1.67 to 2.74 percent under light grazing.

Chandler (8) concluded that grazing was an undesirable practice in wooded areas of eastern United States because it reduced organic matter content of the surface soil through reduction in litter accumulation. The reduced organic matter content and the trampling by livestock reduced porosity of the surface soil, which resulted in reduced water-holding capacity. However, isolation from grazing, or light grazing, may also be detrimental to the vegetation (35, 54). Accumulation of excessive mulch was found to retard growth and hinder seedling establishment. Reduction in number of species present and reduced growth and flowering were also reported.

One of the most comprehensive reports on the effects of mulch on grassland environment was published by Hopkins (26). He studied the mixed prairie near Hays, Kans., to determine the amount of mulch, its rate of decomposition, and its effect on infiltration, soil temperature, evaporation and soil moisture. He found that under favorable moisture conditions, 3 to 4 years were required for the decomposition of vegetative material on the soil surface. By the second year from 40 to 60 percent of the initial weight had been lost, and the leaves of all grasses had disintegrated, leaving only a fibrous material. By the third year, the lower layer of mulch was intermixed with mineral soil.

Microbial activity in the mulch layer and the surface layers of soil are influenced by change in microenvironment. The rate of decomposition of the litter is therefore also affected. Witkam (55) studied microbial activity in oak, pine, and maple stands near Oakridge, Tenn. He followed bacterial and fungal counts, mycelial growth, microbial evolution of CO₂, and moisture and temperature changes in the litter at biweekly periods for one year. He found that microbial respiration was controlled in decreasing order by temperature, bacterial density, moisture and tim-

since leaf drop. He found that of the climatic effects, temperature was most important in areas where moisture was not limiting. During the early stages of litter decay, about 40 percent of the weight loss appeared to be independent of microbial activity. He concluded that leaching of leaf solubles and the physical and chemical breakdown of the vegetation accounted for the early weight loss.

There has been little research on litter decomposition in grasslands. Work on a fescue (*Festuca arundinacea* Schreb.) meadow by Malone (30) showed that vegetation type had a large influence on rate of organic matter decomposition, especially when species are present which produce bacteria-inhibiting compounds. Fescue was found to produce such a compound, and killing the fescue caused a rapid population increase of soil bacteria. High and low soil temperatures and moisture levels were found to affect some microorganisms. Manipulation of vegetation will, therefore, have a large influence on decomposition rate of organic matter, mineralization processes, and nutrient cycling.

Evaporation And Evapotranspiration

Published results from evapotranspiration (ET) studies on crop plants and intensively managed forages are plentiful. Little information is available on native vegetation of the arid and semiarid regions (23). Blaney (4) summarized the information for semiarid regions. Based on review of the few published papers and on his own field observations, he concluded that under normal conditions, seasonal precipitation of at least 30.5 cm. is necessary before water will penetrate below the grass root zone. Seasonal rainfall of less than 30.5 cm. is usually consumed by native grassland before deep percolation occurs. For brush and chaparral areas, at least 46 cm. of precipitation must fall during any one year before water will move below the root zone.

Collins (10) reported that ET losses in the United States as a whole are estimated to be 70 percent of the total 76 cm. of average annual precipitation received. The amount varies widely from region to region, ranging from 50 percent of the 119 cm. received in the Appalachian region to over 90 percent of the 25 to 38 cm. received in some areas of the west. Without vegetative

cover, rapid evaporation at the soil surface forms a dry layer of soil which restricts upward movement of water. This reduces the overall rate of water loss. Adding vegetation allows movement of soil water to the atmosphere through the plant. The only limit to this system is the water available and the depth and distribution of the root system. Potential ET is the amount of water loss that will occur if at no time there is a deficiency of water in the soil for use by the vegetation. This has been calculated to be 46 cm. annually in the northern portion of the short-grass prairie and 102 cm. in southern Texas (10). Potential ET varies throughout the year in response to the change in temperature. Seldom are the values for potential ET and actual ET equal in the western United States due to the lack of available soil moisture during at least a portion of each season.

Energy Balance

The microenvironment of any organism includes various aspects of energy exchange. Physiological response of the organism depends primarily upon energy flow in terms of temperature. However, all microclimatic factors—air temperature, relative humidity, wind speed, solar radiation, thermal radiation—influence the organism. At the same time, factors of the microclimate are closely associated with and highly dependent upon all factors of the microenvironment. In the case of plants, light intensity and quality are also important.

A discussion of all the energy exchange functions is not possible here. Gates (22) stressed the influence of microclimate and energy exchange on the individual organism. Decker (14) discussed the energy balance of a plant cover in the subhumid region of the United States, and Baumgartner (3) discussed the ecological significance of vertical energy distribution in plant stands. Factors of importance included air temperature, plant temperature, wind velocity, potential evaporation, net radiation, vapor pressure deficit, and carbon dioxide concentration. The canopy can be arbitrarily divided into zones or layers by consideration of these factors in a vertical profile. Energy gradients exist which are dependent upon canopy density and height as

well as upon interaction among factors within each zone.

Robertson (45) studied the spectral energy of light available to plants under several sky conditions, including bright sunshine, skylight, twilight, light from cloudy skies, and light within canopies of varying densities. The proportion of red and far-red energy increased as haziness increased or as solar elevation decreased. Transmission through a crop canopy resulted in a high proportion of far-red energy. He suggested that the spectral composition of light be considered as an environmental factor, particularly as it relates to species growing under an overstory of other species.

Decker (13) compared net radiation over a short-grass turf, an alfalfa field, and a corn plot. Net radiation represents the energy available for thermal and biological processes. Therefore, differences between canopies of different height are important to the entire energy exchange of the community. During daylight hours he found higher net radiation values for the taller vegetation types, an indication that more heat energy was available in the corn and alfalfa canopies than in the short-grass canopy. If the heat supplied to the soil and atmosphere were the same for all three covers, then the extra energy would have to be used in evaporational processes. Thus, ET would be greater for the taller crops than for the shorter ones.

In a study of the energy budget within a cornfield, Brown and Covey (6) found an exponential relationship with leaf area approximating extinction of net radiation within the crop. The largest leaf-air temperature differences were found to be near, but not at, the top of the crop. They found that 46 percent of the net radiation was used for transpiration in this corn crop, 13 percent for soil evaporation, 32 percent for sensible heat flux and 6 percent for soil heat flux. Thus, 16 percent of the net radiation reached the ground under the dense crop.

The effect of vegetative cover and mulch on surface temperatures and soil temperatures was reported by Hopkins (26). With an air temperature of 32° C., maximum surface temperatures were recorded on a west-facing grazed hillside, which had less mulch than any other area in his study. In an adjacent enclosure, surface tempera-

ture under 10 cm. of mulch was 29° C. At the same time, temperatures in the upland short-grass were 37 and 32 C. on the grazed and ungrazed sites, respectively. The ungrazed short-grass had 5,357 kg. mulch/ha. while the moderately grazed had 3,127 kg.

Vegetation Effects

Plant competition for various components of the microenvironment is greatly affected by grazing, particularly if grazing is of a selective nature. Competition for soil moisture has received most attention and is perhaps the most important factor in much of the United States. In specific instances, competition for light is also of major importance. Reproduction of most species is highly dependent upon these factors. This is substantiated by many reports of impaired reproduction of certain species under heavy grazing or with no grazing. Production of seed and suitable conditions for germination and plant establishment are necessary. Smith (49) described various disturbances which affected seed germination of annual plants in the Sierra Nevada foothills of California. Herbage removal, fire and soil disturbances significantly reduced the number of germinating seedlings of *Bromus mollis* L., *Bromus tectorum* L., and *Trifolium microcephalum* Hook. Burning or soil disturbance caused the largest reduction in the number of grass seedlings. However, the soil disturbance was perhaps more severe than would be encountered under most grazing conditions.

Penfound (35) studied the effects of protection from grazing of tall-grass prairie and of re-vegetated cropland in Oklahoma. He compared protected prairie, grazed prairie, protected cropland and grazed cropland. The protected prairie changed from midgrass through tall-grass prairie to tall-grass prairie with many woody species. He predicted that if protection had continued, this area would have been taken over by woody plants. The grazed prairie vegetation remained nearly constant in the midgrass stage. Protected cropland vegetation changed rapidly from annuals to forb-short grass to short grass-midgrass-tall grass; however, when cropland was grazed the successional changes were from annuals to short grass-midgrass to midgrass. In

an earlier report, concerning mixed prairie near Hays, Kans., Tomanek and Albertson (52) found that ungrazed areas were dominated by tall grasses while moderate grazing resulted in replacement of the tall grasses by midgrasses and short grasses. Heavy grazing nearly eliminated the tall grasses and reduced the midgrasses, while the short grasses increased proportionately. Total basal cover increased with increasing grazing pressure on all sites except the rocky breaks. This increase in basal cover commonly accompanies increase in blue grama under heavy grazing in the mixed prairie as described as Sarvis (47). He found that grazing effects resembled those of drought. A number of species that were adversely affected by drought were also injured by heavy grazing. Needle-and-thread (*Stipa comata* Trin. & Rupr.) and prairie junegrass (*Koeleria cristata* [L.] Pers.) were listed as examples. A change in species composition of this nature will certainly affect other elements of the microenvironment.

Halogeton (*Halogeton glomeratus* [M. Bieb.] C. A. Mey.) invasion of heavily grazed western ranges was discussed by Frischknecht (20, 21). It infested small areas in which the soils were high in both total soluble salts and exchangeable sodium in heavily grazed ranges. Then it invaded all heavily grazed units and heavily grazed spots in lightly grazed and moderately grazed units, particularly when they were spring grazed.

A species of considerably different stature, but also a problem in some areas, is small clubmoss (*Selaginella densa* Rybd.). Van Dyne and Vogel (53) found that high level of fertility, shading, and mulch accumulation reduced ground cover by small clubmoss in central Montana foothill grasslands. Decrease in cover was greater in areas grazed intensively than in areas protected for 4 years. Clubmoss stands on moderately grazed sites or in adjacent protected areas did not change during this period. In this case, the mechanical effects of grazing and trampling by sheep were more detrimental to small clubmoss than to other species present.

One of the undesirable effects of poor grazing management is conversion to a sagebrush dominated type. Data are lacking for change in microenvironmental factors during the conversion, however, in recent years efforts to convert back to more productive range are documented with

microenvironmental data. In general, removal of sagebrush improves soil moisture conditions, but each situation is unique. Runoff from a shrub-type vegetation will be increased if a layer of ice or frozen soil occurs on the surface during snow-melt. However, a layer of snow caught in the vegetation will prevent freezing at the surface which will improve infiltration and reduce runoff. Alley (2) reported this to be the case in a study on the Red Desert of Wyoming. Areas sprayed to control sagebrush were soon covered with perennial grasses. The grass cover improved infiltration by holding a uniform snow cover which kept the soil surface from freezing. Thus, less water ran off the sprayed areas than from the sagebrush areas. Fisser (19) followed soil moisture and temperature changes in sagebrush and sagebrush controlled areas, with and without grazing in Wyoming. Soil moisture accumulation during the spring was greater on a mesic foothill grassland than it was on an arid desert-shrub type, and the greatest accumulation was in the 2- to 5-foot depth in the shrub controlled area of the mesic site. Grazing did not influence moisture accumulation on the arid site, but did reduce spring recharge rate in the mesic site. Severe climatic conditions restricted revegetation, thus soil moisture released by brush control was not utilized. Soil temperature was warmest on an annual basis under the shrub-dominated areas, although the difference was only about 1° C.

Rowe and Reiman (46) evaluated the effects of conversion from brush to grass or from brush to grass-forb vegetation on evaporation, ET and surface runoff in the San Gabriel Mountains of California. They found that soil depth, mulch cover, vegetative growth and season had a large influence on the response to conversion from one vegetation type to another. Although grazing was not part of their study, it is reasonable to believe that changes in water regime due to change in vegetation type brought about by grazing management would be influenced by the same factors.

Conclusion

Comprehensive information concerning the effects of grazing on microenvironment of rangelands in the United States is scarce. This review brings together information on the effects of

grazing, with that on microenvironmental factors which has been obtained independent of the grazing animal. Much information is available pertaining to microenvironmental factors, particularly as related to cultivated crop production. This could not be covered here. Hopefully, this review will stimulate concern and interest in aspects of rangeland microenvironment which are influenced by or which have an influence on the grazing animal and will ultimately enhance proper management of the natural resource.

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EFFECTS OF PAST GRAZING IN DETERMINING RANGE MANAGEMENT PRINCIPLES IN AUSTRALIA

By J. C. Newman¹

Abstract

Grazing in arid Australia has been based on optimism rather than fact, resulting in loss of perennials, erosion and reduced productive capacity. The deteriorative trend can be halted if grazing pressure is adjusted to conform to available knowledge of land capability. The management principles which appear to be appropriate, from a consideration of past practice, experience, and research follow.

- Land type should govern grazing use and grazing pressure. Consequently, land types need to be identified, delineated, and described in terms of factors related to grazing use. Land type should be the basis on which all developments, such as fencing and watering, are superimposed.
- The basic premise in assessing arid land capability is that the long-term protection of the soil resource is vital.
- Grazing should not utilize the resource above a predetermined limit, the limit to be based on a species with a protective role.
- The landholder must be prepared to forego short term financial advantages and accept a long term investment.

There is need at the quantitative level for further knowledge to assist the scientist and pastoralist to measure the trend of pastures and to know the limitations of the pasture species, particularly those with protective roles. The advantages of spelling, establishment of waterspread areas, and the feasibility of special grazing practices aimed at restoration or increase in productive capacity, need to be assessed.

Range management implies manipulation, pref-

erably informed manipulation, of the grazing animal over the soil and vegetation resource. The aim of management is to attain maximum sustained use of the land without causing permanent damage to the vegetation or soil. In Australia, emphasis has been on livestock management rather than on pasture management. Australian pastoralists have developed a high degree of expertise in management of livestock. Pastures, however, receive only secondary consideration when stock movements or reductions are planned.

Additional key words: Land types, arid lands, land capability, grazing assessment, soil conservation.

History Of Development

The history of grazing use on arid and semi-arid lands in Australia is similar to that which has occurred in other parts of the new world. The Australian experience is telescoped into a shorter period. The result has been similar in all States of the Commonwealth, whether sheep or cattle or both were used.

A major collapse occurred in eastern Australia during the 1890's. The number of stock being carried in the pastoral areas had increased substantially, costs had been rising, and pastoralists met the situation by further increasing the number of stock they managed.

Rabbits, which had been introduced to the country as food animals, increased greatly and exerted a serious effect on the pastures. The period was marked by a series of drought years, and the price for greasy wool fell to 5 cents per pound. The effect extended beyond the arid areas, but the arid areas were affected most. Sheep flocks in Queensland fell by 60 percent, in N.S.W. by 53 percent, and in South Australia by 35 per-

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cent (28). Sheep populations in the rangelands have never fully recovered.

In New South Wales

Grazing by sheep began between 1850-60 in the Western Division, which covers most of the arid and semiarid pastoral areas of N.S.W. The sheep population rose from 6.5 million in 1879 to 15.4 million in 1891. The rainfall during this period was very favorable and well above the long-term average, particularly in the northern part of the Division. From the midnineties, the rainfall in the Western Division began to fall, and an extended drought period began. The period ended with a severe drought, 1901-02, by which time the sheep population had fallen to 4 million. During this latter period the reserve of perennial plants was greatly depleted, and soil erosion became a serious problem.

Since 1902, stock numbers recovered slowly to 6 to 7 million and remained around this number until the late 1950's. During the late 1950's and early 1960's, stock numbers rose to 9 million. A severe drought, 1965-67, led to a fall in sheep numbers to 6 million.

The increase in numbers during the late 1950's and early 1960's was a result of good seasons, a major reduction in the rabbit population and high wool prices, which led to considerable investment in additional watering points and fencing.

The drought in the midsixties, and consequent reduction in stock, indicate that the Division is still very susceptible to drought when stock numbers increase. However, at the close of the drought in 1967, most areas were in fairly good condition, although several areas which had carried very high stock numbers became seriously wind-swept, indicating that a repeat of the 1902 situation could occur again with unwise use.

During the period from 1900 to 1971, development, by way of additional fencing and provision of water, has increased so that the area available for grazing has increased markedly. Probably 80 percent of the pastures in New South Wales are now within 3 miles of water. Early droughts, as measured by livestock condition, appeared to be more frequent but were due to the paucity of water supplies. These droughts were water droughts and led to severe concentration of stock

around the watering points. Droughts of the present day tend to be feed droughts.

Experience was similar in Central Australia (6, 22), Western Australia (1, 23, 29), and South Australia (24).

Effect Of Grazing On The Landscape

All of the rangeland types described by Perry (23) have been significantly affected by grazing. Newman and Condon (20) described the effect on each of the six major rangeland types. The six major types are:

Grassland

Grassland, composed of mitchell grasses (*As-trebla* spp. on grey-brown cracking clays).

Shrublands

Shrublands, composed of saltbushes and blusbushes (*Atriplex* spp., *Kochia* spp., *Chenopodium* spp.) on a range of soil types.

The shrub lands are frequently associated with texture contrast soils, which are susceptible to serious degradation.

Low Woodlands

Low woodlands represent a wide range of vegetation associations depending upon the soils and climate.

The most important tree species in the rangeland type is the mulga (*Acacia aneura* F. Muell.), which occurs on red earths, red loamy soils, sandy soils, and texture contrast soils. Much of the deterioration in the mulga lands is attributed to the loss of palatable understory species (29) and their replacement by unpalatable species.

Some other woodland communities, such as cypress pine-box (*Callitris collumellaris* F. Muell. and *Eucalyptus populneum* F. Muell.), are affected by invasion of inedible scrub, and production has been seriously affected (18).

Flood Plains And Alluvial Fans

The soils and vegetation vary within this rangeland type which includes the well watered outwash plains adjacent to mountain ranges, the flood-out plains alongside ephemeral streams (both of which have coarse textured alluviums), and the broad plains of fine textured alluviums

associated with the large river systems. All of these situations are highly productive.

Spinifex Grassland

This characteristic grassland occurs extensively on sand plains and dune fields and to a lesser extent on sandy red earths. Spinifex consists of species of *Triodia* and *Plectrache*. All of the species are low in palatability, utilization, and productivity (26). Consequently, overgrazing is rare. Because of the low productivity, the range type is used only when it is adjacent to land with higher productive capacity.

Mountains And Hills

These areas are generally stony and steep, and are not important as a grazing resource. They support limited grass, herbage, and scattered timber and are occupied only because of proximity to better lands. Water is rarely provided within the hills. Where the hills are extensive, stock graze them only when temporary water is available. Localized deterioration has occurred as a result of timber cutting for fuel or mining purposes.

An estimation of the present condition of the Australian rangelands is presented in table 1. Broadly, the position is that the grasslands and the spinifex grasslands are in reasonably good condition in comparison with the pristine state. Damage is mainly a loss of palatable species without serious invasion by inedible species. Res-

toration appears to be relatively simple. The mountains and hills, the low woodlands, and the flood plains and alluvial fans are moderately degraded, with 10 percent of their total area being in a critical state of deterioration.

The shrublands have deteriorated to the greatest extent, due to the susceptibility to grazing of the perennial shrubs and to the erosive nature of the soil. Twenty-five percent of the total area has either lost the shrub layer or deteriorated to a scalded state. At the latter stage, production is nil and restoration is difficult and expensive. The major cause of deterioration has been excessive grazing pressure in the early years of settlement. Severe droughts have manifested the problem.

Past And Present Grazing Practice

Grazing practice throughout arid and semiarid Australia has been, and still is, simple. This applies where both sheep and cattle are grazed.

Sheep holdings are broken up into approximately 12 paddocks. Cattle grazing is more extensive, often with little more than boundary fencing. In sheep areas, the majority of the land is commanded by water, so that sheep do not have to travel beyond 5 to 6 kilometers for water. Cattle country is less well developed, and extensive areas are unwatered. During drought periods, relief has been obtained by establishing a new watering point on land that was previously beyond the grazing reach of cattle. This drought tactic obviously is limited.

TABLE 1.—*Percentage of rangeland types in particular degeneration classes*
[The present pastoral value in relation to expected pristine condition]

Rangeland types	Percentage of degeneration			
	Little or none (80-100 percent)	Minor (60-80 percent)	Moderate (40-60 percent)	Severe (<40 percent)
Grasslands	30	55	15	Negligible
Shrublands	10	25	40	25
Low woodlands	40	30	20	10
Flood plains and alluvial fans	40	30	20	10
Spinifex grasslands	70	20	5	5
Mountains and hills	50	20	20	10

Source: After Newman and Condon (20).

In cattle areas, some grazing control can be obtained by turning off water from a bore and moving cattle to another bore. Cattle normally graze about 8 kilometers from water in dry periods, so that when water is spaced more than 16 kilometers apart the herd is reasonably confined to one water.

Spelling is not normally carried out. Pastoralists claim that kangaroos utilize spelled areas, thus negating their value. Some unconscious spelling does occur in the summer rainfall zones during the rainy season. At these times, bores are not used, and livestock graze well away from normal waters and depend on temporary surface waters.

In general, there is no conscious attempt to manage pastures. The Australian pastoralist is essentially an animal husbandman and lacks an appreciation of the long term reaction of pasture and soil to grazing pressure. Stock manipulation is based on the condition of the animal rather than on the pasture or soil.

Cultivation is rare, but there are three main aims: 1, to produce a cereal or forage crop and eventually a better pasture. This occurs only on the fringe of the rangeland; 2, as an irrigation enterprise based on underground or river water. These schemes appear to be attractive only during drought periods; and 3, as a reclamation procedure, either on severely eroded land or on areas where use can be made of run-on for water-spreading purposes. These latter schemes have regional significance, but the profitability is marginal at present.

Land Tenure

Although not a direct management factor, the framework on which the pastoral enterprise rests is significant. Rangelands in Australia are almost wholly held under Crown Lease tenure. Leases were originally for short terms, up to 21 years and often less. Modern leases tend to be long term (99 years).

There is a limit to the area which any one individual can hold. The home maintenance area principle was established to ensure that subdivision did not proceed beyond a size which would give a landholder a return sufficient to support him and his family at a reasonable level. At

the same time it prevented an individual from acquiring a very large area. This concept is valid only when prices for produce are stable. Although the returns to individuals have varied from affluence to near poverty, the scheme appears to have encouraged a responsible type of lessee to settle and develop his lease.

Damage to the resource is likely when a lessee is in financial difficulty. In these circumstances, it is difficult to apply what may be considered necessary controls which further reduce income, at least temporarily.

The long term lease provides the lessee with sufficient incentive to wise management, yet protects the interest of the Crown. Occupation of the land on long lease with prospect of renewal appears to be the most desirable tenure basis on which to encourage both the maintenance of the resource and the best development of it in arid areas.

Future Land Management Policy

In the ultimate sense, soil erosion is the most important problem to be faced in an arid area. Although erosion generally occurs imperceptibly over a long period and proceeds through progressive stages of deterioration of vegetation, it can, on some land types, become irreversible over a lifetime.

Much of the rangeland in Australia is producing less than it has in the past. The degree to which production has been depressed varies with land type. The feasibility of restoring productivity to previous levels or better also varies with land type. From a consideration of past grazing and research experience, a number of basic attitudes for future application can be considered.

The Significance Of Land Type

Management has not varied with land type to any extent. Consequently, uneven utilization on a variable range has led to situations where areas of extreme erosion and negligible erosion occur side by side.

Improvements which concentrate livestock, such as water, shearing sheds, and holding yards, have been located without consideration to land type. In parts of western New South Wales, serious scald and wind-sheet erosion have occurred, be-

cause tanks or dams and shearing sheds coincided with texture contrast soils.

Charley and Cowling (4) have shown the hazardous nature of nutrients in Australian arid area soils. Many of the soils are polygenetic in nature, and have formed in more humid eras than the present. Small soil losses of 5 to 10 cm. truncate soils carrying perennial saltbush (*Atriplex vesicaria* Heward ex Benth) pastures, and critical amounts of nitrogen, phosphorus, and organic carbon are lost. They postulate that these losses can limit regeneration even where water is adequate, as on a furrowed area.

It is most important that the soils which are susceptible to near irreversible degradation be recognized. Consequently, the identification and description of the rangeland in terms of its land units or types are prerequisites to development and proper use. This inventory must then be expressed in terms of the practical capability and limitations of each land type. It provides a basic guide to fencing, water provision, and grazing management.

Examples of the value of land type surveys and grazing assessments are available in parts of Australia. In Central Australia an area of approximately 26 million hectares of arid pastoral land was surveyed, mapped, and described in terms of land systems (22) by a team of Commonwealth Scientific and Industrial Research Organization (C.S.I.R.O) scientists. A major drought followed, which led to erosion and a serious decline in production throughout the area. The administrators of the area requested advice on the matter, and the N.S.W. Soil Conservation Service was able to use the land system survey as a basis on which to recommend management practices and safe grazing capacities for each holding (6).

More recently, a land unit survey was conducted on a much smaller area of 1.2 million hectares in northwestern New South Wales. This area is more closely settled, and consequently required the greater detail of the land unit rather than the land system. A grazing assessment of each land unit and holding was carried out. The latter work was conducted on a cooperative basis between the University of N.S.W., C.S.I.R.O and the N.S.W. Soil Conservation Service.

Grazing Assessment

The major problem in the past has been excessive livestock numbers. As a first step in future development, grazing pressure must be reduced in a logical manner.

As a starting point, it is appropriate to determine the number of stock which can safely graze an area in the long term, under present management practice. Sophisticated grazing systems can be developed from this basis. Land type provides a realistic basis on which to assess grazing capability, the potential for development, and need for restrictions.

Condon (5) described a method of assessing grazing capacity of arid land in Australia. The method depends upon establishing a safe grazing capacity for a relatively large, uniform area of country, for which records are available. Each factor affecting grazing is then recognized, and rating scales are allocated for the factors, which include rainfall, soils, topography, tree density, drought forage, pasture type, condition or erosion, and barren areas. The assessments are made on each land system, land class, or land unit within a holding.

The accuracy of the method depends upon the reliability of the input data. Some obvious limitations will be apparent. In particular, interactions are not considered, for example, a group of land classes on the one holding as compared with a holding with one land class.

However, the method is an improvement over traditional methods, which are based solely on what similar country (a holding as a whole) has carried in the past. Adjustments are made after a deficiency has become obvious. Where an assessment has been too high, an adjustment is not made until obvious deterioration has occurred. Deterioration has often been critical and permanent.

An example of a holding with this experience occurs in central New South Wales. The holding is on the low woodlands range type, with long term, average annual rainfall of approximately 330 mm. It is being invaded by inedible scrub and is affected by sheet erosion. It covers over 40,000 hectares and was settled before 1880. An early survey (1919) reported that the holding was a very well grassed, open woodland. A report in

1959 indicated that pasturage was generally fair, with the balance sparse, and that considerable invasion by inedible scrub had taken place. A detailed survey in 1970 claimed that the ridges were seriously affected by water sheet erosion, and that up to 85 percent of this land class was unproductive; the level areas were in fair condition, about 20 percent being affected by sheet erosion; and the texture contrast soils, which occur on only a small area, were seriously scalded and wind-sheeted, about 70 percent of the land class being affected.

Only minor improvements have been undertaken on this holding since early in the century. These consisted of a small amount of subdivision and one tank constructed about 1949. Consequently, a similar area has been available for grazing throughout.

The following grazing assessments are on record.

1918—Estimated to carry 1 sheep to 2.6 hectares.

1932—Lessee estimated holding could carry 1 sheep to 6.5 hectares.

1934—A surveyor estimated holding could carry 1 sheep to 6 hectares, but the official estimate was given as 1 sheep to 4.3 hectares.

1948—Assessed at 1 sheep to 4 hectares.

1959—Assessed at 1 sheep to 4.5 hectares. Land Board assessed the holding at 1 sheep to 5.6 hectares.

1970—A Soil Conservation Service assessment was 1 sheep to 10.1 hectares.

The actual stocking record in 10-year means from 1940 reads: 1940-1949—1 sheep to 4.2 hectares actually carried; 1950-1959—1 sheep to 4.2 hectares actually carried; and 1960-1969—1 sheep to 8.9 hectares actually carried.

A perusal of the annual figures since 1937 indicates that fluctuations in stock numbers have occurred with rainfall, but recovery from droughts is poorer, and the level of recovery is becoming less with time, as pasture deterioration continues.

Traditional methods of assessing the ability of land to carry livestock are not effective in this situation. A method based on land inventory and state of the vegetative resource is essential as a

basis on which to develop restorative management systems.

However, serious repercussions can follow when the assessed carrying capacity of a holding is altered significantly. For example, if an overutilized and deteriorating holding is in debt, a reduced carrying assessment may seriously aggravate the landholders financial position. It is understandable that the bodies charged with the responsibility of administering the land do not welcome sharp changes in concepts of land capability, because the whole economic structure of the enterprise can be upset.

A significant error in the overestimation of grazing capacity can have, and has had, serious effects on management. Overassessments have occurred where the assessment has been based on experience during a short period of above average rainfall. Inevitably, dry periods follow, the landholder continues to hold high stock numbers, hoping for a return to normal seasons, and serious deterioration results. When land sales result from overassessment, the incoming tenant is forced to abuse the land in order to obtain the returns he was led to believe would result.

A method of assessing grazing capacity, based upon an inventory of biological factors and related to past grazing experience, is valuable in a number of ways. It can be used by land administrators who need to know the grazing capacity of specific areas of land so that settlement can take place on an equitable basis, the risk of deterioration of the resource is reduced, and a fair rental can be placed on the land. It can be used by the range manager and advisor in determining development policies, such as water placement and fencing and grazing programs.

The system can also be used when new lands are opening up, provided that reasonable affinities can be established with lands for which some grazing history is available. If livestock numbers are controlled and restricted to a number considered appropriate, the trend to deterioration will cease.

To attempt erosion control or erosion prevention and simultaneously continue with overpopulations of grazing animals is unrealistic.

Provision Of Water And Fencing

It is logical that sufficient water and fencing be provided so that the range can be fully utilized.

In the assessment of the ability of a holding to carry stock, the basis should always be based on watered area and not the total area. Most deterioration becomes evident during drought. At these times, stock tend to graze nearer to water than during periods of good rainfall and abundant feed. Water and fencing should be arranged on the basis of grazing behavior in drought if full utilization is to be obtained.

Water and fencing should be based on land type. Land types often vary over a short distance. In these cases, grazing needs to be related to the land type most susceptible to damage. Separation of land types by fencing provides for greater flexibility in grazing management, fuller utilization of the environment, and for the deliberate manipulation of pastures.

Centers of livestock concentration such as water and shearing sheds and yards should be located on land types tolerant of erosion.

Trend

It is difficult to know on many of the Australian rangeland types whether the trend of long term productive capacity is upward or downward. The high variability in rainfall and the variability in seasonal occurrence leads to great variation in pasture response, irrespective of grazing pressures. It is important to be able to recognize the effect of a particular grazing pressure or management system on the long term health of the range.

Valentine (27) described the use of the key zone concept in determining correct use. The key zone is the area immediately beyond the sacrifice zone. The sacrifice zone is the area immediately surrounding a watering point or other point of livestock concentration and which is subject to gross overuse by trampling. He claimed that the correct stocking rate coincided with proper use of the species within the key zone.

Osborn, Wood, and Paltridge (21) showed the effect of grazing in relation to water, and recog-

nized that moderate grazing was more beneficial to perennial saltbush than light grazing. Barker and Lange (2) extended the work and endeavored to find a trend. Their work indicated the complicated nature of the grazing pattern and the lack of definitive data, which prevented a full interpretation of the trend of the pasture.

In an endeavor to measure trend, the critical importance of the browse shrubs needs to be appreciated. Goodin and McKell (11) stressed the value of the browse shrubs compared to the value of perennial grasses. They were mainly concerned with production, but Australian browse, although having an important productive role, has only low to moderate palatability (16). The major role of the shrub and tree is in protecting the resource and maintaining the long-term production. Marshall (17) drew attention to the importance of the shrub stratum in protecting the soil, and sought a minimum shrub requirement.

Tree density is important in the same way. Burrows and Beale (3) quoted densities of 247 mulga trees per hectare and 173 trees per hectare as necessary to assure regeneration and drought reserve, respectively, in different parts of Queensland. In New South Wales, specific requirements are laid down for the retention of trees for grazing purposes and cultivation purposes in the Western Division.

Accurate monitoring of selected environments is necessary to ascertain trend under different management pressures.

Drought Policies

Much of the overutilization in arid Australia has occurred because droughts have been regarded as abnormal. The first requirement in management policy is to accept that drought is a normal experience in the rangeland. Grazing practice must be adjusted to this fact.

Ideally, stock should be removed from the area during drought. The ability to move stock has improved in recent years, but it is clear that there is a practical limit to the flexibility that can be obtained in this regard.

Carrying only the number of stock that can be supported through a drought of up to 12 months reduces the impact of drought. Some

holdings have opportunities of drought evasion by supplementary irrigation, cutting of edible scrub and runoff farming. Individual holdings need to explore the possibilities of their own environment. Each holding must adopt a rigid policy of reduction in stock numbers in extended drought.

Type Of Animal

Under current land use practice, sheep and cattle grazing are the alternatives. Mostly, they are regarded as alternatives. It appears that advantages in production and ability to manipulate pasture accrue from joint use.

In special situations, goats appear to offer some advantages when run in conjunction with sheep. On areas which have been invaded by shrub, goats are capable of utilizing species which are inedible to sheep. From observations in New South Wales, goats appear to favor browse above grass, and they could be used to restore grasses to an area.

Grazing Systems

Virtually no work has been carried out on the effect of practices such as spelling, rotation, seasonal grazing, and periodic intense grazing. Assessment at this stage is on theoretical grounds and on scattered landholder experience.

There is little practical evidence to suggest that more production will accrue from specialized grazing systems, as compared with set stocking patterns. However, there is considerable evidence to show that pastures can be modified by grazing at particular times and by spelling. Heavy grazing for a short period can cause the loss of perennial saltbush and its replacement by perennial grass in a very short time (16). This can increase production in the short term at least. It also demonstrates the susceptibility of the pasture to mismanagement. This work was carried out on a fine-textured alluvium which is not easily eroded.

Observations are being made on a method of periodic intense grazing, followed by spelling, on a fine-textured alluvium which carries a dense growth of weedy shrubs, such as *Bassia* spp. Heavy grazing removes all plant growth, and there is some evidence that more palatable species reappear during the period of spelling. How-

ever, the landholder adopting this grazing method has an area of improved pasture, irrigated from bore water, which enables him to assure himself of reserve feed when dry periods prevent regeneration of the intensively grazed areas.

When eroded areas have received reclamation treatment, benefit has followed the practice of periodic grazing and spelling. On a bare scald which was reclaimed by furrow treatment, a landholder obtained value by spelling during seasons of adequate rainfall and grazing during periods of drought. The furrow treatment enabled the paddock to respond better during drought than uneroded areas, because of the run-on effect after small rains. The area has become a special purpose pasture.

The role of grazing systems appears to lie in manipulations of pastures to produce special purpose pastures, to encourage or discourage particular species or groups of species, and for reclamation purposes. It is important to set a specific target when a grazing system is contemplated.

Special Practices

The practices include edible scrub cutting, irrigated pasture, water spreading, and species introduction. None of these practices has wide application, but each can be significant over a small area.

The economics of these ventures vary from time to time and situation to situation. Provision of regular green feed by irrigation, waterspreading, or ponding can enable cattle to be carried or sheep to breed where otherwise they would be marginal. Small areas of green feed may have value, beyond the apparent amount of production, where it can be used for flushing ewes, carrying rams, or holding lambing ewes.

There appears to be little scope for successful introduction of exotic species, except in the favored niches or artificial sites created by waterspreading. The chances of finding suitable exotics is remote because of the low fertility of the soils and the low moisture availability.

Williams (31) suggested that some species have been lost to our pastures. It is doubtful whether this has happened to any extent. It is more likely that regeneration is more difficult because of a change in local environment. Refuge areas still exist. After a major, 8-year drought in Central

Australia, response (in species numbers) to rain was spectacular. At Cobar in central New South Wales, an initial survey of species on a seriously eroded red earth recorded 12 grasses and 8 herbs. After spelling from grazing for 7 years and treating with furrows, 27 grasses and 75 herbs were recorded, none of which were introduced. After water ponding on a bare scald at Nyngan, N.S.W., a species count rose from zero to 22 grasses and 33 herbs in 3 years. There appears to be an ample range of native species available, and number of species is not limiting in production or protection.

Restorative Programs

There have been many attempts by individuals and government to restore eroded lands to production. Most of the effort has been directed toward the seriously degraded situations, such as the spectacular scald. It is normal for an ephemeral response to be obtained, but permanent restoration is difficult. However, reliable techniques have been developed for most of the eroded situations which are encountered. They are not always economically attractive in the short term.

The basis for all restoration programs is manipulation of the soil moisture by way of furrowing, ploughing, diversion, or ponding in some form. These techniques have been adequately described by Cunningham (7, 8) Fitzgerald (9, 10), Jones (12, 13, 14, 15), and Newman (19). Other factors, such as seeding, nutrition and stock exclusion, are often included in the treatment.

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INFLUENCE OF GRAZING ON THE MICROCLIMATE OF MIXED GRASS PRAIRIE¹

By Warren C. Whitman²

Abstract

On a Northern Plains mixed grass prairie in the 1970 season, grazed vegetation had 78, 13, 32, and 37 percent as much standing crop, standing dead material, litter, and total aboveground plant material, respectively, as ungrazed vegetation. Air and soil temperatures, to a depth of 120 cm., were higher on the grazed site throughout the season. Wind movement near the ground surface on the grazed site was three times that on the ungrazed site. Soil moisture to the full profile depth was somewhat greater on the ungrazed site until after midsummer. Atmospheric moisture and vapor pressure deficits were only slightly different over the two grazing treatments.

Additional key words: Microenvironment, Northern Plains grassland, temperature, soil moisture, humidity

It has been generally accepted that grazing has a rather profound influence on the microenvironment of native grassland, but surprisingly little factual data are available regarding the exact nature of this influence. Ellison (9) stated that grazing reduces both standing herbage and the accumulation of mulch, with the result that evaporative losses are encouraged, and a lighter, warmer and drier microenvironment is created.

Rice (17) studied the growth and develop-

ment of several tall grass prairie dominants in Oklahoma and recorded some microclimatic factors. He found that the more mesic grasses were reduced in abundance by high air and soil temperatures and high evaporation. Hopkins (13) found that the mulch layer in Kansas grassland reduced soil temperatures, retarded evaporation from the soil surface, and increased the amount of available moisture in the soil.

Since fire removes accumulations of vegetation and litter, it might be expected that burning would have microenvironmental effects similar to grazing. Dix and Butler (7), Aikman (1), Robocker and Miller (18), Ehrenreich (8), Kucera and Ehrenreich (14), Hadley and Kieckhefer (11), and Anderson (2) studied the influence of burning on grasslands in the tall grass region, and evaluated some microenvironmental effects. In general, these studies have shown that the microenvironment of the burned plots was more severe than that of unburned plots. Dix's study (6) is the only one which deals directly with the influence of burning on the Northern Plains mixed grass prairie. Daubemire (5) has reviewed extensively the studies of fire influences on grassland, including microenvironmental effects. Old (15) has published a detailed study of microclimate, fire, and plant production in Illinois tall grass prairie. She developed an interesting microclimatic index for the comparison of the microenvironment of different burning regimes.

Whitman and Wolters (23) characterized microclimatic gradients in ungrazed mixed grass prairie in western North Dakota. Soby (19) examined the utilization of radiant energy by mixed grass prairie in the same area. Whitman (22) has discussed the general role of microclimate in the grassland ecosystem. These studies, however, do not provide an adequate evaluation of graz-

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ing influences on the microenvironment of the Northern Plains mixed grass prairie.

In the 1970 season, a study for comparing microenvironmental factors in grazed and ungrazed native mixed grass prairie was begun on a 35-acre piece of native grassland at the Dickinson Experiment Station in southwestern North Dakota.³ The area included a 4-acre enclosure that had not been grazed since 1961; the remaining grassland had been grazed heavily in late fall every year since 1957, usually leaving 3-7 cm. of stubble. The grazing history of the area before 1957 is unknown, but it apparently had been subjected to moderately heavy summer grazing for a number of years.

The study area is situated on an upland ridge at an elevation of approximately 2,500 ft. (762 m.). The top of the ridge rises about 300 ft. (91 m.) above the surrounding land. The surface materials of the study area and its surroundings are part of the Tongue River member of the Fort Union formation of Paleocene age. The soil of the area is mainly Flasher loamy fine sand, but minor differences in the soils may be present due to the effects of slope and exposure of parent materials.

The Northern Plains mixed grass prairie has been described by Weaver and Clements (21). Hanson and Whitman (12) have given detailed descriptions of grassland types in western North Dakota. On the study area Goetz (10) found a total of about 130 plant species. The principal grassland type is needle-and-thread-blue grama-sedge. The major grasses in this type are needle-and-thread (*Stipa comata*), blue grama (*Bouteloua gracilis*), and western wheatgrass (*Agropyron smithii*). The sedges, needleleaf sedge (*Carex eleocharis*), and threadleaf sedge (*Carex filifolia*) are also important. These grass and sedge species make up about 80 percent of the total cover of the type. Plains reedgrass (*Calamagrostis montanensis*), prairie Junegrass (*Koeleria cristata*), green needlegrass (*Stipa viridula*), prairie sandreed (*Calamovilfa longifolia*), and Sandberg bluegrass (*Poa secunda*) are important

secondary grasses. They make up about 15 percent of the cover.

The broadleaved plants (forbs) native to this type of grassland make up about 5 percent of the cover under undisturbed conditions, but these plants increase considerably under heavy grazing with a consequent reduction in the percentage of grasses in the cover. There are virtually no shrubby plants on the study area, and normally the woody plants are of little importance in this grassland type.

The climate of the Northern Plains is characterized as continental, semiarid, and subject to the extreme range of variability detailed by Thornthwaite (20), Borchert (3), and Coupland (4). The longtime climatic averages at the Dickinson Station (78-year record) show an average annual precipitation of 15.42 inches (39.17 cm.), with April-July precipitation averaging 9.21 inches (60 percent of the total), and April-September precipitation 12.11 inches (78 percent of the total). Snowfall is generally light. Open-pan evaporation during the growing season has averaged 31.90 inches (81.03 cm.).

The average annual temperature at the Dickinson Station is 44° F. (6.7° C.), with the January average 11.0° and July 69.0° F. The December-February mean is 13.8° F., and the June-August mean is 65.7° F. The average total wind for the April-September period has been about 16,500 miles (26,553 km.). Wind velocity is generally greatest in the spring period of March, April, and May, although tornadic winds of high velocity are experienced occasionally in the summer period.

Vegetation And Soil Influences

Grazing greatly reduces the total amount of plant material above the ground surface, as contrasted to the ungrazed condition, and results in a substantial change in relative proportions of the species in the cover (tables 1 and 2). To obtain yields, twelve 0.25-m.²-quadrats were clipped every 2 weeks during the growing season. Current season's material was hand separated from the previously produced, standing dead material. Litter from each plot was collected with a vacuum cleaner, oven-dried, ashed, and reported on an ash-free basis. Vegetation on the grazed site was

³The experimental area is situated in the SE $\frac{1}{4}$ NW $\frac{1}{4}$, sec. 32, T. 140 N., R. 96 W., 2 miles northwest of Dickinson, Stark County, N. Dak.

TABLE 1.—*Standing crop, standing dead material, litter, and total plant material above ground on grazed and ungrazed sites at the end of the major growth period in the 1970 season (Aug. 18)*

Treatment	Dry weight yield (g./m. ²)			
	Standing crop ¹	Standing dead ²	Litter	Total plant material
Grazed	196	36	209	441
Ungrazed	252	272	662	1,185

¹ Current season's production.

² Material produced prior to the 1970 season.

not subjected to grazing until after the end of the growing season. Consequently, all measures of plant materials and microclimatic observations were made on an area which was not disturbed by grazing at the time the measurements were being made.

The standing crop of vegetation (current production) on the grazed treatment was about 78 percent as much as on the ungrazed treatment, while standing dead material and litter were 13 and 31 percent as much on the grazed as on the ungrazed site (table 1). Total aboveground plant

material at the end of the major growing period in the 1970 season was 441 g./m.² on the grazed treatment, 37 percent of the 1,185 on the ungrazed treatment. The reduced mass of plant material on the grazed site could be expected to have substantial microenvironment influences.

Evidence of such effects is shown in the species composition of the standing crop (table 2). The taller grasses, such as needle-and-thread, western wheatgrass, and prairie sandreed, decreased under grazing, while the shorter blue grama grass increased. Selaginella, which has an average height of about 1 cm., produced 12 percent of the dry matter on the grazed site, but almost nothing on the ungrazed site. Apparently it was the victim of litter accumulation, which frequently averaged over 3 cm. in depth. Point analyses have shown the actual basal cover of the grazed vegetation to average about 38 percent without *Selaginella* hits included and up to 70 percent with these hits included. Basal cover on the ungrazed site determined on the same basis averages less than 25 percent.

Not only does the grazed vegetation have a higher proportion of shorter species in it than does the ungrazed, but grazed leaf heights and approximate canopy heights are less throughout the season (table 3). Measurements were made of each species on each plot at the time of clipping.

TABLE 2.—*Species yields and percentage composition of yields of vegetation on grazed and ungrazed sites at the end of the major growth period in the 1970 season*

Species	Grazed		Ungrazed	
	Yield	Composition	Yield	Composition
	G./m. ²	Percent	G./m. ²	Percent
<i>Stipa comata</i>	45.0	22.9	105.1	41.7
<i>Agropyron smithii</i>	19.8	10.1	33.8	13.4
<i>Calamagrostis mont.</i>	15.3	7.8	—	—
<i>Calamovilfa longifolia</i>	—	—	16.6	6.6
<i>Koeleria cristata</i>	16.8	8.6	—	—
<i>Bouteloua gracilis</i>	59.9	30.5	28.9	11.5
<i>Carex elcocharis</i>	11.5	5.9	10.3	4.1
Miscellaneous grasses	0.4	0.1	3.3	1.3
Perennial forbs	22.5	11.5	48.9	19.4
Other forbs	5.2	2.6	5.0	2.0
Totals	196.4	100.0	251.9	100.0
<i>Sclaginella densa</i>	25.9	—	0.2	—

The grazed vegetation averages between 30 and 50 percent shorter than the ungrazed vegetation throughout the season.

Below ground biomass and soil bulk density also are affected by grazing. Five 1-inch cores were taken on each clipped plot immediately after clipping, a total of 60 cores at each date representing 12 individual samples. The results of this sampling were remarkably consistent and showed that at all dates of sampling the weight of subterranean material (roots and rhizomes) was appreciably greater on the grazed site than on the ungrazed site (table 4). For the season, underground plant material averaged 2,519 g./m.² on the grazed site and 1,643 g./m.² on the ungrazed site, a little over 53 percent greater weight of material occurring under grazing.

The compacting influence of animal trampling under grazing had altered the bulk density of the soil to a depth of about 20 cm. (table 5). The increase in bulk density under grazing was especially marked in the first 10 cm. of the soil profile. Bulk density values were determined from small cores (2.5 cm. diam.) and were highly variable. The core values obtained in the 1970 season do, however, correspond closely to values obtained with larger cores (6.35 cm. diam.) in previous years. No attempt was made to assess directly the significance of either the greater bulk of root material under grazing or the increase in soil

bulk density in relation to microenvironmental influences.

Microenvironmental Influences

Air Temperatures

Air temperatures were determined with shielded thermocouples mounted at various heights above the grazed and ungrazed grassland; temperatures were recorded hourly by a strip-chart recording potentiometer. The thermocouples were mounted at heights of 2.5, 7.5, 15, 25, 55, 75, and 120 cm. above the ground surface on both areas, with an additional unit at 130 cm. on the grazed area, and at 145 cm. on the ungrazed area. On both sites, greatest height of measurement above ground was considered to be mature canopy height plus 1 meter.

Temperatures above the grazed grassland averaged 1.5° C. higher than the temperatures above the ungrazed vegetation on the season—long basis, and, in general, showed about the same difference in each of the summer months (table 6). Highest average air temperatures occurred in July, with temperatures above the grazed and ungrazed sites averaging 23.7° C. and 22.0°, respectively.

The nature of the gradients in air temperature that exist above the grassland in the Northern Plains have been discussed by Whitman and Wolters (23) in some detail. The gradients found

TABLE 3.—Average leaf heights of major species and average canopy heights of grazed and ungrazed vegetation at approximate monthly intervals during the 1970 growing season

Species	Leaf heights in cm. at different dates							
	Grazed				Ungrazed			
	5/24	6/22	7/22	8/18	5/24	6/22	7/22	8/18
<i>Stipa comata</i>	6	12	14	21	11	25	33	35
<i>Agropyron smithii</i>	9	25	25	27	16	32	34	35
<i>Bouteloua gracilis</i>	2	7	9	9	4	13	16	16
<i>Carex cleocharis</i>	6	9	9	10	8	15	17	16
<i>Calamagrostis mont.</i>	10	13	18	17	—	—	—	—
<i>Calamovilfa long.</i>	—	—	—	—	—	30	42	47
Average	7	13	15	17	10	23	28	30
Approximate canopy ht. ¹	9	25	32	35	12	32	47	53

¹ Combined leaf and stalk heights of all standing vegetation—estimated.

TABLE 4.—*Below ground biomass to a depth of 1 meter on grazed and ungrazed sites at different sampling dates during the 1970 season (ash-free, oven-dry weights—g./m.²)*

Treatment	Sampling dates						
	May 26	June 15	June 25	July 9	July 30	Aug. 10	Aug. 19
Grazed	2,772	2,301	2,908	2,581	2,370	2,362	2,342
Ungrazed	1,454	1,489	2,168	1,688	1,474	1,532	1,693

on the grazed and ungrazed sites in this study are shown in table 7. Weekly average temperatures for the week of July 12-18, 1970, are given for the hours of 4:00 a.m. (daily minimum), 2:00 p.m. (daily maximum), and 10:00 p.m. (approximate greatest increase with height).

During the night the trend of the temperature profile is generally warmer upward, while during the day the trend is warmer downward. Gradients are similar over grazed and ungrazed vegetation, with the temperature at 2:00 p.m. increasing 5-6° C. from the top of the profile to the maximum temperature, usually at 2.5 or 7.5 cm. Since these temperatures are weekly averages, they do not show the full range that might be expected on any one day. Such ranges might be twice as great as the averages.

The average temperature for the whole profile at any specific hour was generally greater above the grazed vegetation than above the ungrazed vegetation. However, all temperatures in the profile above grazed vegetation would not be expected to be higher than all temperatures in the gradient profile above ungrazed vegetation.

TABLE 5.—*Soil bulk density values on grazed and ungrazed sites for the 1970 season*

Depth	Bulk density values	
	Grazed	Ungrazed
<i>Cm.</i>	<i>G./cc.</i>	<i>G./cc.</i>
0-10	1.16	1.03
10-20	1.35	1.27
20-30	1.40	1.40
30-40	1.40	1.40
40-120	1.50	1.45

At 2.5 and 7.5 cm., air temperatures exceeding 32° occurred on more days above ungrazed vegetation than above grazed vegetation (table 8). Above a height of 15 cm., maxima over 32° C. occurred more often over grazed vegetation. Higher maximum temperatures close to the ground in the ungrazed vegetation probably were caused by the reduced air movement through the large accumulation of vegetation, in contrast to the much smaller accumulation on the grazed area.

Soil Temperatures

Soil temperatures were measured with thermocouples 1.2, 2.5, 7.5, 15, 25, 55, 75, and 120 cm. below the soil surface, with the values recorded hourly, as for air temperatures. Soil under the grazed vegetation averaged 2-4° C. warmer than under the ungrazed vegetation (table 9).

Substantial gradients in soil temperatures existed under both grazed and ungrazed conditions, with the general tendency for the gradients to be cooler downward in the months of June, July, and August and cooler upwards in September (table 10). Except for some variation in the upper 2.5 cm., temperatures at all measured depths under the grazed vegetation were appreciably higher than under the ungrazed vegetation. Differences of 4° to 6° C. between grazed and ungrazed treatments were not uncommon for the same soil depths. By mid-September, the soils on both sites had cooled significantly throughout the measured profile.

Diurnal temperature fluctuations were not marked below a depth of 15 cm. under either of the treatments. The range of diurnal variations in the upper 15 cm. of the soil was considerable greater on the grazed site than on the ungrazed

TABLE 6.—Average air temperatures (C.) by months above grazed and ungrazed grassland during the 1970 season¹

Treatment	Average temperatures by months				Seasonal average
	June	July	Aug.	Sept.	
	<i>Degrees</i>	<i>Degrees</i>	<i>Degrees</i>	<i>Degrees</i>	<i>Degrees</i>
Grazed	20.7	23.7	22.9	15.2	20.6
Ungrazed	19.2	22.0	21.7	13.7	19.1

¹ Average of all temperatures measured at various heights above the ground.

site. For example, during the week of August 9-15, the average range between maximum and minimum values at a depth of 7.5 cm. was 8.2° C. on the grazed site and only 4.8° on the ungrazed site. Similar ranges in extremes at this depth occurred on most days throughout the season.

Wind

Wind movement was measured by means of small rotating-cup anemometers supported at 15, 30, 90, and 130 cm. above the soil surface on the grazed site, and at the same heights on the ungrazed site, except for the uppermost unit which

was at 145 cm. (canopy height plus 1 meter). Counters which recorded the number of revolutions of the anemometer rotors were read daily.

Wind velocity at a height of 15 cm. averaged 2.1 km./hr. on the grazed site and only 0.6 km./hr. on the ungrazed site (table 11). Wind velocity increased rapidly on both sites as height above the ground increased, reaching an average of 8.7 km./hr. (5.4 m.p.h.) at 130 cm. on the grazed site and 8.4 km./hr. (5.2 m.p.h.) at 145 cm. on the ungrazed site. Wind velocity at these points, equidistant above the vegetation canopy, were nearly equal, as expected.

The development of the vegetation during the

TABLE 7.—Profiles of average temperatures (C.) at different heights above the ground surface at 4:00 a.m., 2:00 p.m., and 10:00 p.m. for the week of July 12-18, 1970 on grazed and ungrazed sites.

Height above surface	Grazed			Ungrazed		
	4 a.m.	2 p.m.	10 p.m.	4 a.m.	2 p.m.	10 p.m.
<i>Cm.</i>	<i>Degrees</i>	<i>Degrees</i>	<i>Degrees</i>	<i>Degrees</i>	<i>Degrees</i>	<i>Degrees</i>
145 ¹	--	--	--	15.0	30.0	19.4
130 ²	16.1	30.6	19.4	--	--	--
120	16.7	30.0	20.0	14.4	27.8	18.9
75	16.7	31.1	20.0	13.9	28.3	17.8
55	15.6	30.6	19.4	13.9	28.3	17.8
25	15.6	31.1	18.3	12.8	29.4	16.7
15	15.0	32.2	17.8	11.1	32.2	14.4
7.5	13.9	31.7	16.7	11.1	36.1	13.9
2.5	15.0	35.6	17.2	14.4	34.4	16.7
Average	15.6	31.6	18.6	13.3	30.8	16.9

¹ Height of canopy (45 cm.) + 1 meter.

² Height of canopy (30 cm.) + 1 meter.

season influenced wind movement near the ground on both sites (table 12). The average wind movement on the grazed site at a height of 15 cm. was 2.7 km./hr. in June, as the vegetation began its early development, and decreased to 1.6 km./hr. in August when the vegetation was at its maxi-

mum peak of development. By the end of August, the vegetation had dried considerably, seed had been shed, and fragments of stalks and leaves were being broken off, mainly by wind action. Consequently, wind movement at the 15 cm. height increased, reaching an average velocity of

TABLE 8.—*Number of days on which maximum temperatures exceeded 32° (90° F.) at different heights above grazed and ungrazed grassland during the 1970 season, June-September*

Treatment	Height above ground surface—cm.								
	2.5	7.5	15	25	55	75	120	130	145
Grazed	66	49	50	39	33	35	30	26	--
Ungrazed	76	87	54	34	19	21	17	--	19

TABLE 9.—*Monthly average soil temperatures (C.) to a depth of 120 cm. on grazed and ungrazed grassland during the 1970 season. (Average of all points measured.)*

Treatment	Average soil temperatures—°C.				Seasonal average
	June	July	Aug.	Sept.	
Grazed	19.1	23.5	23.6	19.2	21.4
Ungrazed	16.0	19.8	20.2	15.4	17.9

TABLE 10.—*Weekly average temperatures (C.) at different depths in the soil for selected weeks during the 1970 season under grazed and ungrazed grassland*

Depth below surface	Grazed				Ungrazed			
	June 14-20	July 12-18	Aug. 16-22	Sept. 13-19	June 14-20	July 12-18	Aug. 16-22	Sept. 13-19
	<i>Deg.</i>							
1.2	19.4	26.1	25.6	14.4	19.4	23.9	22.2	12.8
2.5	17.2	23.9	22.2	11.7	18.9	23.9	22.2	12.8
7.5	21.1	26.7	25.0	14.4	18.3	22.8	21.1	12.8
15	20.6	26.1	25.0	15.0	17.8	22.2	20.6	12.8
25	19.4	24.4	23.9	14.4	16.7	20.6	20.0	13.3
55	17.8	23.3	23.3	16.7	14.4	18.3	18.9	14.4
75	17.2	22.2	22.8	17.8	12.8	16.7	17.8	15.0
120	13.9	18.9	20.0	17.8	11.1	14.4	16.1	15.0

TABLE 11.—Average seasonal¹ wind velocity (km./hr.) at different heights above the ground surface under grazed and ungrazed treatments

Treatment	Wind velocity (km./hr.) at heights above ground				
	15 cm.	30 cm.	90 cm.	130 cm.	145 cm.
Grazed	2.1	3.9	7.9	8.7	--
Ungrazed	0.6	2.4	7.1	--	8.4

¹ Wind measured from June 6-Sept. 30, 117 days.

2.4 km./hr. during September. On the ungrazed site, the average wind velocity in June at the 15 cm. height was 1.1 km./hr. It decreased to 0.3 km./hr. For the season, wind velocity at 15 cm. on the grazed site was 3½ time that on the ungrazed site.

Soil Moisture

Soil moisture samples were taken at approximate weekly intervals throughout the season from May 25 to October 5. Four samples were taken on each site to a depth of 120 cm. with a 1-inch sampling tube. Soil moisture was determined gravimetrically, expressed as percent, and then converted to cm. of water in the profile by 10-cm. segments.

The precipitation pattern in the 1970 season was not entirely favorable. A total of 14.58 cm. of rain in May combined with moisture already in the soil resulted in 20 to 25 cm. of moisture in the soil to a depth of 120 cm. on May 27, when the first soil moisture sample was taken. In June 8.00 cm. of rain were measured, in July 11.33, in

August 0.99, and in September 4.06 cm. After the May rainy period, the principal rains which occurred were: June 2—26.16 mm.; June 13—19.81 mm.; July 14—22.86 mm.; July 23—18.54 mm.; and July 29—46.48 mm. The soil moisture pattern reflects the general precipitation pattern to a considerable extent.

There was somewhat more moisture in the soil under the ungrazed treatment than under the grazed treatment from the beginning of the study period until about the middle of August (table 13). Soil moisture conditions appeared to be essentially similar under both treatments for the balance of the season. Pressure plate determinations at 15 atmospheres indicated that soil moisture would become unavailable in the upper 50 cm. of soil on both sites at approximately the same moisture level—4.46 cm. on the grazed site and 4.36 cm. on the ungrazed site. Thus, soil water in the upper 50 cm. of soil became unavailable for plant use under both the grazed and ungrazed treatments on or before July 6, and remained so until sometime between July 20 and July 28, after which soil moisture in this layer

TABLE 12.—Average wind velocity (km./hr.) by month at 15 cm. above ground surface on the grazed and ungrazed sites, 1970 season

Treatment	Average wind velocity by months—km./hr.			
	June	July	Aug.	Sept.
Grazed	2.7	1.9	1.6	2.4
Ungrazed	1.1	0.5	0.3	0.6

TABLE 13.—*Total cm. of water in the 0-50 and 50-120 cm. soil layers on the grazed and ungrazed sites at sampling dates from May to October, 1970*

Date	Grazed			Ungrazed		
	0-50	50-120	Total	0-50	50-120	Total
5/27	9.43	10.78	20.21	10.88	13.97	24.85
6/15	9.30	12.52	21.82	10.59	13.51	24.10
6/22	6.63	8.65	15.28	7.84	15.77	23.61
6/29	11.51	20.19	31.70	6.94	14.10	21.04
7/6	3.95	8.07	12.02	4.03	13.81	17.84
7/13	3.16	7.47	10.63	3.56	8.77	12.33
7/20	3.04	5.95	8.99	3.52	7.58	11.10
7/28	5.11	5.40	10.51	5.09	7.21	12.30
8/4	6.94	5.49	12.43	8.21	7.48	15.69
8/11	5.13	6.52	11.65	6.50	8.60	15.10
8/18	3.63	6.21	9.84	3.45	5.95	9.40
8/24	6.10	6.10	12.20	3.19	7.69	10.88
8/31	2.46	4.76	7.22	2.55	5.29	7.84
9/8	2.93	4.87	7.80	2.71	5.79	8.50
9/14	3.24	5.00	8.24	3.19	4.98	8.17
9/21	3.56	4.86	8.42	3.52	4.95	8.47
9/28	4.75	5.17	9.92	4.65	5.61	10.26
10/5	3.61	5.12	8.73	3.57	5.19	8.76

was alternately available to a limited extent and then unavailable for most of the rest of the season. Except for late forbs, plant growth was practically complete by the end of July.

It might be thought that the large mass of plant material, including litter, on the ungrazed site would protect the upper soil layer on this site from drying as rapidly as the upper soil layer on the grazed site. The data in table 14 show the status of total and available soil moisture in the upper 10 cm. of soil under the grazed and ungrazed treatments. There seems to be little evidence that soil moisture from the upper 10 cm. of soil was lost more rapidly on the grazed site than on the ungrazed site.

Atmospheric Moisture

Relative humidity values were recorded hourly at 15 cm. above the soil and 1 m. above the canopy on both the grazed and ungrazed areas, using psychrometric elements operating on the Dunmore principle. These readings and air temperatures, recorded at the same time, were used to calculate vapor pressure deficits.

On both sites, weekly average maximum (5:00 a.m.) and minimum (4:00 p.m.) relative humidity values were generally higher 15 cm. above the ground than at 1 m. above the canopy (table 15). At the 15 cm. height during the week of June 14-20 average maximum, average minimum, and average weekly relative humidity values were higher on the grazed site than on the ungrazed site. During the week of July 5-11, relative humidity values at this height on both sites were practically the same. For the week of Aug. 23-29, average maximum values at this height on both sites were practically the same, and average minimum and weekly average values were somewhat higher on the ungrazed site than on the grazed site. As conditions became more severe with the advance of the season, the influence of the larger vegetation mass on the ungrazed site seemed to become increasingly important in modifying the atmospheric moisture regime near the ground. At 1 m. above the canopy (130 cm.—grazed, 145 cm.—ungrazed), relative humidity was appreciable higher over the grazed treatment

TABLE 14.—*Total cm. of water and cm. of available water in the upper 10-cm. layer of soil on the grazed and ungrazed sites at sampling dates in the 1970 season*

Date	Grazed		Ungrazed	
	Total cm.	Available cm.	Total cm.	Available cm.
5/27	1.97	1.23	2.29	1.63
6/15	2.90	2.16	2.65	1.99
6/22	1.60	0.86	1.55	0.89
6/29	2.11	1.37	1.18	0.52
7/6	0.54	0.00	0.61	0.00
7/13	0.46	0.00	0.63	0.00
7/20	0.69	0.00	0.75	0.09
7/28	1.78	1.04	1.63	0.97
8/4	1.77	1.03	1.93	1.27
8/11	0.68	0.00	1.10	0.44
8/18	0.57	0.00	0.55	0.00
8/24	1.10	0.36	0.47	0.00
8/31	0.34	0.00	0.47	0.00
9/8	0.55	0.00	0.56	0.00
9/14	0.93	0.55	1.06	0.40
9/21	1.10	0.36	1.07	0.41
9/28	1.71	0.97	1.67	1.01
10/5	0.97	0.23	1.03	0.37

TABLE 15.—*Average maximum, average minimum, and weekly average relative humidity values at two heights above the ground surface on the grazed and ungrazed sites for selected weeks in the 1970 season*

Season dates	Heights above ground	Grazed			Ungrazed		
		Weekly average maximum	Weekly average minimum	Weekly average	Weekly average maximum	Weekly average minimum	Weekly average
June 14-20	15 cm.	96	56	77	95	51	73
July 5-11	do.	76	32	52	76	33	52
Aug. 23-29	do.	69	26	45	69	29	48
June 14-20	Canopy + 1 m ¹	95	53	74	92	47	69
July 5-11	do.	70	34	52	69	30	48
Aug. 23-29	do.	67	28	46	63	25	41

¹ On grazed site canopy + 1 m. = 130 cm.; on ungrazed site canopy + 1 m. = 145 cm.

than over the ungrazed treatment during all 3 weeks reported.

Average vapor pressure deficits at the 15 cm. height were slightly greater on the grazed area than on the ungrazed area during each week (table 16). Prasad (16) demonstrated a strong correlation between vapor pressure deficits at this level and the status of water in grass leaves. At 1 m. above the canopy, vapor pressure deficit values were slightly higher on the ungrazed site than on the grazed site in June and July, and slightly lower in August. The differences in average relative humidity and vapor pressure values between the treatments are not great, taken as a whole, but the results illustrate that evaporative conditions near the ground on the grazed site were somewhat more severe than on the ungrazed site.

TABLE 16.—Average weekly vapor pressure deficits (mm. of mercury) at two heights above the ground surface on the grazed and ungrazed sites for selected weeks in the 1970 season

Week of season	Height above ground	Vapor pressure deficit on	
		Grazed	Ungrazed
		<i>Mm. Hg.</i>	<i>Mm. Hg.</i>
June 14-20	15 cm.	3.63	3.60
July 5-11	do.	12.15	10.58
Aug. 23-29	do.	11.98	11.67
	Canopy		
June 14-20	+ 1 m ¹	3.75	4.25
July 5-11	do.	12.17	12.25
Aug. 23-29	do.	12.87	12.18

¹ On grazed site canopy + 1 m. = 130 cm.; on ungrazed site canopy + 1 m. = 145 cm.

Summary And Conclusions

Microenvironmental conditions in heavily grazed Northern Plains mixed grass prairie were found to be appreciably different than conditions in similar ungrazed grassland when compared in the 1970 season. The observed differences appeared to be primarily the result of differences in vegetation bulk on the two sites. Total vegetation mass, including standing crop at maximum seasonal development, standing dead, and litter was 441.3 g./m.² on the grazed area and 1,185.2 g./m.²

on the ungrazed area. Underground biomass was greater under the grazed than under the ungrazed treatment, averaging 2519 g./m.² and 1643 g./m.², respectively.

Air temperatures over the grazed treatment averaged 1.5° C. higher than temperatures over ungrazed vegetation, although at a height of canopy plus 1 m. the temperatures averaged about the same on the two treatments. Soil temperatures to a depth of 120 cm. were also higher under the grazed treatment, averaging 21.4° C. for the season, while the average on the ungrazed treatment was 17.9° C. Wind movement at 15 cm. averaged 2.1 km./hr. on the grazed area and 0.6 km./hr. on the ungrazed. At canopy height plus 1 m. wind movement was about the same on the grazed and ungrazed areas averaging 8.7 and 8.4 km./hr., respectively.

Soil moisture was slightly greater under the ungrazed than under the grazed treatment until after midsummer, but available moisture was exhausted about the same time on both areas. Relative humidity and vapor pressure deficit differences were relatively small between the two treatments, but the results indicate that evaporative conditions near the ground were somewhat more severe on the grazed than on the ungrazed area.

It would be highly desirable to obtain information about several other microenvironmental factors to increase the validity of comparisons between grazed and ungrazed vegetation. A refinement of techniques involving soil moisture tension measurements, to make possible a more precise evaluation of water balance under the two treatments, seems indicated. An evaluation of the moisture stress status of the plant tissues in relation to microenvironmental stresses on the grazed and ungrazed areas, accompanied by precise growth and production measurements of the major species, would contribute substantially to understanding just how the microenvironmental influences directly affect grassland yield. Preliminary measurements of net radiation and soil heat flux indicate that there are differences in the energy budgets under the two treatments. More information on plant responses could be developed by additional studies in this area. A comparison of evaporation potentials throughout the growing season on the two areas could provide useful data on relative severity of plant stress conditions.

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EFFECTS OF LIGHT AND PHOTOPERIOD ON MORPHOGENESIS

By Frank B. Salisbury¹

Abstract

Photomorphogenesis in plants includes virtually all aspects of plant development: germination, etiolation, growth via photosynthesis, phototropism, phototaxis of chloroplasts, opening and closing of leaflets, entrainment of circadian rhythms, pigment formation, plant form, light damage (including ultraviolet), flower formation, bud dormancy, and many other responses. Action spectra implicate protochlorophyll, chlorophyll, carotenoids or flavins, phytochrome, and unknown pigments. The High Energy Reaction (HER) may be phytochrome-mediated and is of interest to those dealing with natural ecosystems. Photomorphogenetic responses may be direct photoconversions (photosynthesis), triggered (germination), triggered amplified quantitative (most phytochrome responses), or triggered amplified quantitative time-related (primarily photoperiodism). Phototropism involves a redistribution of auxin, but the mechanism is not yet understood. Complications include failure of reciprocity for negative and second positive curvatures, and effects of red light on subsequent sensitivity to blue light. Photoperiodism is a widespread phenomenon in plants (and animals), including both vegetative and reproductive responses. There are numerous flowering response types and interactions with temperature. The night interruption phenomenon is a phytochrome response, but time measurement (the central feature of photoperiodism) cannot be explained in terms of phytochrome conversion. Although characteristics of the photoperiodism clock are similar to those of the circadian clock, current evidence indicates that the two clocks are not identical.

Additional key words: Photomorphogenesis.

phototropism, phytochrome, high energy reaction, biological clocks, circadian rhythms.

Introduction

A plant growing on the range, be it grass or forb, is the product of the morphogenetic or developmental events that produced it. Virtually all of these are sensitive to light. Photomorphogenesis is a highly complex process involving numerous integrated events, each of which may be influenced or even dependent upon light. Hence, the initial task of cataloging morphogenetic responses to light is a formidable one. I have tried to organize the principal responses into 14 categories, beginning with germination and going to reproduction and dormancy. Some are broad while others are more specific. It is not possible in the limited space to review the entire topic of photomorphogenesis and still reach the depth of specific research papers, but the subject has been broadly reviewed in several books (2, 9, 14, 22, 28, 30, 35, 36, 42, 44, 48, 53, 54), and numerous reviews have appeared in the Annual Review of Plant Physiology (see References at end of this paper). A few technical papers are cited in relation to some topics, although most citations are to review articles and books.

Photomorphogenetic Phenomena

Germination Of Many Seeds And Spores (33)

It has long been known that germination of many seeds, fern spores, and so forth, is promoted, or inhibited, or not influenced by light. Study of seeds promoted by red light (some are promoted by blue) led to discovery of the phytochrome pigment system (see below). Some seeds are influenced in their germination by photoperiod rather than by exposure to a given quality and quantity of light (13). There are long-day

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seeds (for example, *Begonia evansiana* Andr.) and short-day seeds (*Veronica tournefortii* C. C. Gmel.).

The Etiolation Syndrome

Dark-grown plants differ in several important and easily recognizable ways from plants grown in the light (fig. 1).² Internodes of dark-grown seedlings elongate more, while leaves and roots are reduced in size, although monocot leaves are somewhat less inhibited than dicot leaves. Coleoptiles of grass seedlings elongate rapidly in the dark and are inhibited by light — adequately serving their function of protection for the leaves of the emerging grass seedling. Several dicot seedlings have a hook near the tip of the epicotyl, which straightens out upon exposure to light. The symptoms of the etiolation syndrome extend

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to the microscopic level, where chloroplasts develop in response to light. Red light and the phytochrome system are effective in converting an etiolated plant to a light-grown plant, but other systems may also be involved.

Plant Growth

When the angiosperm seedling is exposed to light, its protochlorophyll is converted photochemically to chlorophyll (another feature of the termination of the etiolation syndrome), and the plant becomes autotrophic. Photosynthesis is not usually thought of as a photomorphogenetic process, but it supplies the energy for such processes and thus strongly influences the forms and sizes of range plants and others.

Phototropism

Plant organs typically become oriented in relation to the direction of incoming light, stems

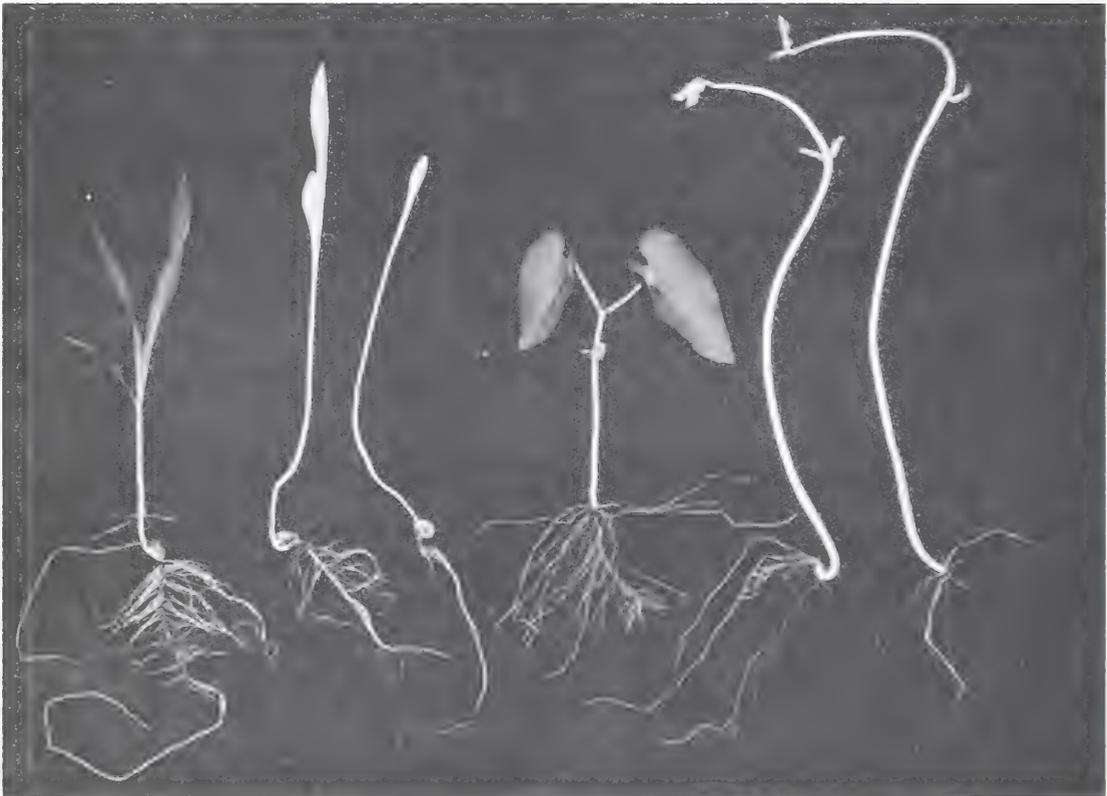


FIGURE 1.—Etiolation in corn and beans; greenhouse-grown (left) vs. 8 days darkness (right). Note the following in etiolated plants: Pale color, elongated stems, reduced leaves and roots, and hooks on bean seedlings.

bending toward the light and roots of many species away from it. Leaves may be oriented so that their surfaces are normal to the incoming light rays, or in a few cases (for example, the compass plant, *Silphium* sp.), leaf surfaces are mostly parallel to the sun's rays at noon. Flowers may also be oriented in relation to light.

Phototaxis Of Chloroplasts

Chloroplasts tend to lie along cell walls that are parallel to the sun's rays when intensities are high, and along walls normal to the sun's rays when intensities are low.

Opening And Closing Of Leaflets (22)

Leaflets of many species, particularly *Albizia* and *Mimosa*, fold up when plants are transferred to the dark—depending upon the quality of light preceding the darkness. The phytochrome system is again involved.

Entrainment Of Circadian Rhythms (2, 9, 15)

Many plants (and animals) exhibit circadian rhythms, in which functions vary with a periodicity approximating 24 hours. These include growth rates, petal opening and closing, concentrations of various substances such as starch, and leaf positions. The sleep movements of leaves have been most intensively studied. Typically, leaves are in a vertical position during the night and a horizontal position during the day. When plants are placed under constant conditions of temperature or light (total darkness or light of some constant intensity), the sleep movements continue. Under normal conditions, the movements are entrained to the daily cycle of light and darkness, but under constant conditions the rhythms become free-running, having periods typically shorter or longer than 24 hours. Entrainment is a response to the change from darkness to light (dawn) or light to darkness (dusk), so it is another example of photomorphogenesis. Under constant conditions, the rhythms can be phase-shifted by light perturbations.

Pigment Formation (27, 30)

In addition to the synthesis of chlorophyll referred to above, many other pigments depend

upon the presence of light for their synthesis. Good examples are the anthocyanins of apple or turnip skins and the carotenoids of tomatoes. A high-energy phase, depending typically upon blue light, is often followed by a low-energy phytochrome phase dependent upon red light.

Plant Form, Branching, And Elongation Of Stems (31, 32)

Plant form is often strongly influenced by light quality, intensity, or both. Cocklebur plants, for example, have a single unbranched stem when grown in the greenhouse but branch profusely in the field. Plants grown under fluorescent light are typically shorter and more branched than those grown under incandescent light (rich in far-red) or under a mixture of fluorescent and incandescent light. There is an interesting interaction between intensity and light quality. At low intensities, red light is more effective in inhibition of stem elongation than blue light, but at high intensities, blue light is more effective (31, 54). Plant form is also strongly influenced by photoperiod (44, 48). Strawberries on long days, for example, form numerous runners but do not form these on short days, flowering profusely instead. Even a tomato plant, day-neutral in its flowering response, is strongly influenced in its form by day length, as shown in figure 2.

Sun And Shade Leaves

Leaves developing under high light intensities frequently have more than one layer of palisade tissue, and their photosynthetic process is saturated at higher light intensities than leaves developing in the shade (4, 18). (This response could easily be a subcategory under Plant Form.)

Damage Due To High-Intensity Light

It is known that chlorophylls tend to bleach out when light intensities reach very high levels (for example, 12,000 foot-candles), a process known as photooxidation. Ultraviolet light will also damage plants, typically causing a bronzing of surfaces or death with sufficient exposure (48). The damage caused by ultraviolet light may be prevented if plants are subsequently exposed to high intensities of blue light, a process known as photoreactivation or photoreversal.



FIGURE 2.—Morphological response of tomato to photoperiod. Both plants have flowers and young fruit.

Flower Formation (14, 29, 44, 49)

In a very few cases, flowers form in response to light intensity (52), but in many cases, flower formation is controlled by photoperiod. Short-day plants flower in response to decreasing day lengths, while long-day plants flower in response to increasing day lengths. Some plants are day-neutral, flowering independently of day length.

Bud Dormancy (55)

Many deciduous trees become dormant in the fall in response to shortening days. A few of these resume activity in the spring in response to lengthening days. Some trees also exhibit a period of dormancy in midsummer in response to long days. These responses are invariably strongly modified by temperature. Winter dormancy, for example, can often be induced by exposure to low temperatures, regardless of day length, and it is frequently broken by prolonged exposure to cold. The interaction of light and temperature, though particularly striking in this case, is typical of virtually all photomorphogenetic responses.

Other Phenomena

This category is included to emphasize the point that the above categories are only representative and not exhaustive. Numerous examples could be mentioned, such as the production of foliar embryos on *Bryophyllum* under long days (54), the replication of chloroplasts, and the conversion of fern protonemata into prothallia.

Pigments

The first law of photochemistry states that light, to be effective, must be absorbed. Hence, in any photomorphogenetic investigation, we might attempt to discover the pigment absorbing the light in a given process. The approach is to determine an action spectrum, in which response is plotted as a function of wavelength, and then to compare this action spectrum with the absorption spectra of suspected pigments (10). This has been done for many of the processes listed above, sometimes with satisfying and important results. We will now reclassify the above responses according to the pigments known or suspected to be in control.

1. Protochlorophyll.—The conversion of protochlorophyll to chlorophyll is a straightforward photochemical reaction, and the action spectrum for the process closely matches the absorption spectrum of protochlorophyll.

2. Chlorophyll.—The action spectrum of photosynthesis also matches, rather closely, the absorption spectrum of chlorophyll, but as anyone knows who has attempted to keep up with the burgeoning literature, the situation is far from straightforward. For example, there is the Emerson Enhancement Effect, brought about by the interaction of photo-processes I and II and a collection of energy to a reactive center of the photosynthetic unit (3, 21).

3. Carotenoids or flavins. — These pigments absorb blue light, and phototropism is known to be a response to blue light. Nevertheless, as shown below, this is an unsatisfying example. Although most evidence implicates riboflavin as the absorbing pigment, conclusions remain ambiguous. There are also other plant responses to blue light for which pigments have not been determined.

4. Phytochrome (11, 28, 51).—In 1937, Flint and McAllister (20) determined an action spec-

trum for germination of Grand Rapids lettuce seeds. Relatively low intensities of red light were most effective in promoting germination, but seeds exposed to far-red light germinated even less than dark controls. In 1952, Borthwick, Hendricks, Parker, Toole, and Toole (6) tested to see if exposure to far-red light would overcome previous exposure to red. It did. When lettuce seeds that had properly imbibed water were illuminated by an alternating series of red and far-red light, they germinated when the last exposure was red and failed to germinate when the last exposure was far-red. Action spectra (fig. 3) for many photomorphogenetic processes were similar to those for promotion of germination by red light, so it seemed reasonable to test these other phenomena for photoreversibility. In a large number of cases, far-red light did overcome the effects of red light. Apparently exposure of some pigment to red light converted it to a form that most efficiently absorbed far-red light, and conversions might occur metabolically in the dark:



Synthesis Metabolic conversion Destruction

The feature of photoreversibility at once suggested an approach to isolation of this pigment but at the same time posed a difficult problem (10). The idea was to search for a pigment system that was converted from one form to another by exposure to red or far-red light, but determination of red light absorption required exposure to red light, and this converted the pigment to the form that most effectively absorbs far-red light. The problem was solved in 1959 by construction of a special spectrophotograph in which beams of red and far-red light were alternated 16 times per second, and differences in absorption were measured. The pigment system was named phytochrome. Its detection (12) *in vivo* (dark-grown corn coleoptiles) was followed by its detection *in vitro* (ground-up coleoptiles, cauliflower florets, and so forth), and finally its purification and virtual isolation. The pigment proves to be a protein with an allophycocyanin chromophore and a molecular weight estimated at about

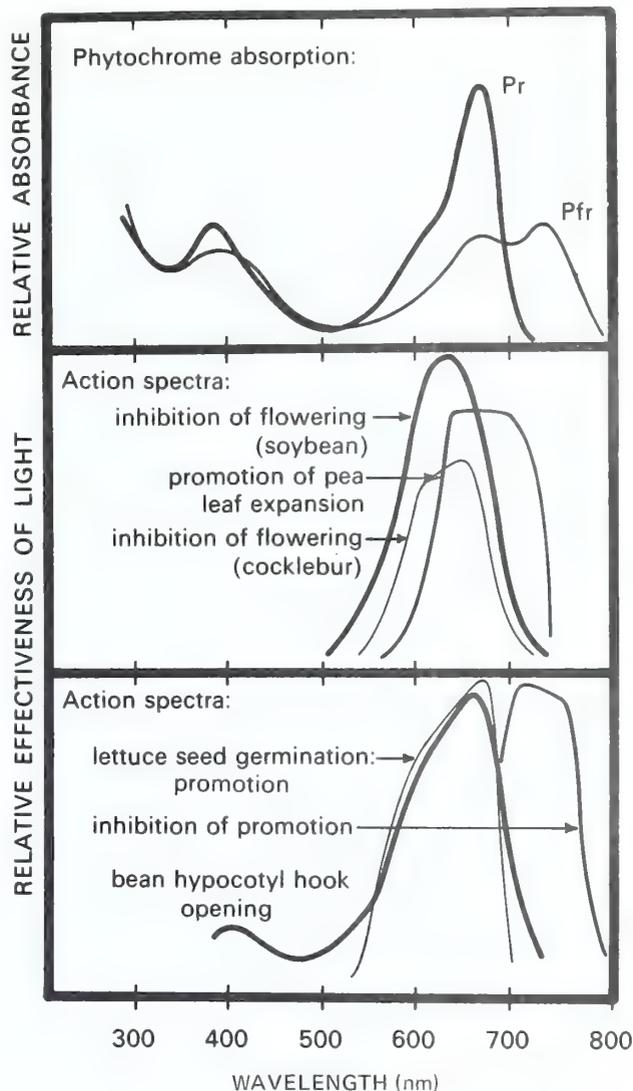


FIGURE 3.—Absorption spectra of both forms of phytochrome (13), and action spectra for several physiological responses (26, 41, 56).

60,000 grams per mole. The phytochrome system has been studied now in many plant responses, including germination, etiolation, phototaxis, opening and closing of leaflets, entrainment (this is in doubt), pigment formation, plant form, sun and shade leaves, flower formation, and winter dormancy.

5. The High Energy Reaction (30, 37).—It was noticed that several photomorphogenetic events were elicited by illumination with high light intensities applied for extended times, as

contrasted to the low intensities for brief periods effective in phytochrome responses. Blue and far-red wavelengths were most effective, and no sign of photoreversability could be detected. The control system, whatever it is, was referred to as the High Energy Reaction (HER).

For several years, it was thought that the HER must be controlled by a separate pigment system, but many workers now feel that it is a special manifestation of the phytochrome system. There are three principle lines of reasoning: First, absorption spectra of the two forms of phytochrome overlap (fig. 3), so when a plant is illuminated with far-red light, although most of the phytochrome is immediately converted to the red-absorbing form (Pr), some of this pigment absorbs far-red light (although much less efficiently), being converted in the process back to the far-red-absorbing form (Pfr). Pfr then absorbs far-red light and is converted back to Pr, but Pfr is continually being supplied. The end result is that when plants are illuminated with far-red light, most of the pigment exists as Pr, but some (on the order of 10 percent, depending upon the exact wavelength of far-red light) always exists as Pfr. Most physiological studies have indicated that Pfr is biologically active. If a brief exposure to far-red is given, the small percentage of Pfr will be metabolically destroyed in a fairly short time, but if long exposures to far-red are given, the small quantity of Pfr is maintained over a long interval of time. It can be as effective as a large quantity present for only a short time.

Second, the various forms of phytochrome are undergoing continual metabolic synthesis and destruction, this itself being influenced to varying degrees by the high-intensity light environment. Third, it is now known that Pr and Pfr have a number of intermediate forms. Some of these may exhibit photomorphogenetic activity.

Typically, the responses controllable by the HER are similar or identical to those controllable by the phytochrome system, which is strong evidence that the HER is really a special case of phytochrome action. Examples include germination of some seeds, etiolation effects, formation of anthocyanins and carotenoids, and perhaps effects upon plant form (including differences between sun and shade leaves) and flower formation. Much study on the HER has been

carried out by Hans Mohr and his colleagues at the University of Freiburg (36, 37). They have documented numerous interesting examples, including many changes in metabolites. In one case, the plumular hook on a lettuce seedling may be caused to form by exposure to low intensities of red light (phytochrome system) and caused to straighten by long exposures to high-intensity far-red light (the HER). These responses are especially important to plants in nature (for example, range plants), since they are typically exposed to high-intensity illumination for long durations, but seldom to the conditions typical of phytochrome experiments.

6. Unknown pigments.—We emphasized the difficulty of determining specific pigments in phototropism. It is easy to find many other ambiguous examples. We are not certain of the pigment system involved in the HER, although phytochrome provides the most fashionable current explanation. Entrainment of circadian rhythms is influenced by red and far-red light, but in some experiments, other wavelengths were equally effective. Probably DNA absorbs the ultraviolet light damaging to leaves, but protein may also absorb ultraviolet, and the photo-reactivation brought about by blue light is quite ambiguous. Apparently, in bacteria an enzyme is directly activated by the blue light, but this remains to be studied in higher plants.

Response Mechanisms

Once the pigments have been identified, then we are interested in how they act. What are the further mechanisms of a photomorphogenetic response? Most of this remains to be learned, but we can classify the responses into at least four broad categories:

1. Direct energy transformations.—Protochlorophyll conversion, photosynthesis, light damage, and probably photoreactivation provide examples. The illuminating energy drives the photochemical process directly.

2. Triggered responses: On-off.—In a few cases, exposure to a suitable quantity of light triggers a response, which is then of an all-or-none character. Usually we think of a seed as either germinating or not germinating, so this may provide a good example. Circadian rhythms are probably either being exhibited or not being exhibited.

These responses are certainly unusual, since one can almost always find some quantitative response to a light exposure. Even in these cases, careful studies might reveal seeds that began to germinate with threshold exposure but then stopped, or anomalous rhythms caused by threshold exposures.

3. Triggered, amplified, quantitative responses.—These are much more common. Light triggers the response, but exposure determines the level of response. The energy required for the response is usually much greater than the energy of the light absorbed, so the light rechannels metabolic energy, rather than providing energy as it does in photosynthesis. Examples are etiolation, phototropism, phototaxis, opening and closing of leaflets, pigment formation, plant form, and development of sun or shade leaves.

4. Triggered, amplified, quantitative, time-related responses.—In these cases, not only exposure is important, but the time that the exposure is given. In photoperiodism, an interruption of the dark period inhibits flowering in short-day plants, and the extent of inhibition is strongly a function of the exact time when the light interruption is given. Some of the responses known to be controlled by photoperiodism are germination (a few species), plant form, flower formation, and bud dormancy. Entrainment of circadian rhythms is also strongly time-dependent.

Phototropism

Virtually all of the processes mentioned so far have been investigated in considerable detail. To provide examples, we shall introduce phototropism and flower initiation. Plants in the field are responding to light in all the ways mentioned above, but for most of these this is of little consequence to the range manager. Phototropism is a good example, but flower initiation in response to photoperiod is important in several ways.

A coleoptile (or true stem of either monocots or dicots—although less work has been done with stems) bending toward a light source does so due to differential cell elongation rates: the cells on the dark side elongate most rapidly. Darwin found that the coleoptile tip responds to the light, although bending occurs well below. Went later showed that there is a lateral transport of auxin toward the dark side. For a while, investigators

considered the possibility that auxin was destroyed on the light side, but recent research has confirmed Went's original measurements, indicating that as much auxin exists in plants exposed to light as in plants kept in the dark, but there is a redistribution to the dark side (8). How does this happen? The actual mechanism remains almost a complete mystery. Figure 4 compares an excellent action spectrum for phototropism with the absorption spectra of carotene and riboflavin. The match is very good for riboflavin in the ultraviolet part of the spectrum, and perhaps a little better for carotene in the visible part of spectrum. Rather recently, mutants were found with 80 percent less carotenoid than normal plants (1). These respond phototropically as well as their normal counterparts. Nevertheless, it has not yet been possible to completely eliminate carotenoids as the photoreceptor pigments in phototropism.

The picture is complicated by the fact that curvature does not always increase with increasing light exposure (fig. 5). Above a certain exposure level, coleoptiles bend less and finally bend in the opposite direction, giving a negative curvature. With increasing exposure, this is followed by a second positive curvature.

Figure 5 assumes that the law of reciprocity holds. Long exposures at low intensities should be

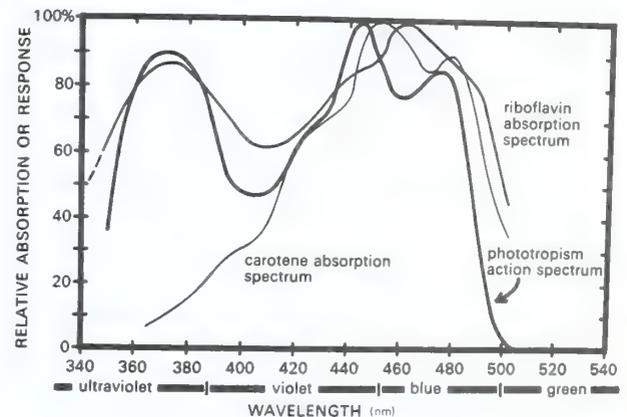


FIGURE 4.—Action spectrum for phototropism and absorption spectra of riboflavin and carotene (50).

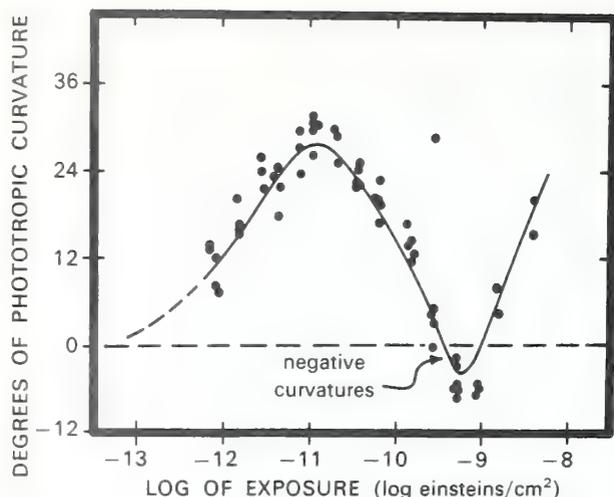


FIGURE 5.—Phototropic response of oat coleoptiles to various quantities of blue light (435.8 nm) applied at constant intensity (1.4×10^{-22} einsteins cm^{-2} sec^{-1}) for various duration times (57).

equal to short exposures at high intensities, providing the total quantity of light is the same in both cases. Reciprocity does hold over an enormous range of exposure times and intensities for first positive curvature, but this is not true for second positive curvature (51), where duration of illumination appears to be more important than total exposure. There are other complications. Previous exposure to red light greatly reduces the sensitivity to blue light for the first positive and negative curvature—but sensitivity of second positive curvature is increased. And we still don't know how the auxin moves in response to unilateral light.

Flower Initiation

Flowering in response to photoperiodism was discovered by Garner and Allard in 1920 (23). Responses to day length prove to be of widespread occurrence in both plants and animals, and there is typically a great variety of response, depending upon species. We now know that there are plants that flower not only in response to short days and to long days, but also in response to long days followed by short days or to short days followed by long days. Some plants are insensitive to day length, but flower in response to prolonged low temperatures. Others require such

a vernalization treatment followed by exposure to long days (typically) or to short days (in a few cases). Some plants are quantitative in their response, flowering under virtually any conditions but being promoted in their flowering by exposure to short days, long days, low temperatures, and so forth. Other species are absolute in their requirements, remaining vegetative until suitable conditions have been provided. There are numerous interactions between day length, temperatures, and other factors. Some species, for example, flower in response to long days at one temperature but are day-neutral at another temperature. Age of the plant is often important. A *Chenopodium* seedling can respond as a minute organism on filter paper in a petri dish, but many other plants must have several mature leaves before they will respond to suitable environmental conditions.

Virtually all of these responses are known among range plants. They are extremely important whenever a plant native to one region is moved to another where daylengths may be different at given times of year (if latitudes are different), or where different temperatures or other factors might influence flower initiation, development, or both. Olmsted (40) showed in pioneering studies with range grasses that varieties within a species (especially *Bouteloua curtipendula* [Michx.] Torr.) differ greatly in their responses to photoperiod, depending upon where samples are collected. Southern varieties exhibited a short-day response, while northern varieties were long-day plants. Both flowering and vegetative growth of each variety seemed well adapted to the region where the plant was native. These studies were subsequently confirmed and greatly extended by McMillan (34), who used 12 species of grasses in his work.

The modern analytical approach to a study of photoperiodism was initiated in 1939 by Hamner and Bonner (25). Among many other things, they carefully investigated the relationship between critical day and critical night, using *Xanthium strumarium* L. (cocklebur). This short-day plant responds to a single inductive cycle. On a 24-hour cycle, flowering occurs if the day is less than about 15 hours and 40 minutes (critical day). Hamner and Bonner found that if the night is longer than about 8 hours and 20

minutes (critical night), flowering occurs even when day-length varies considerably (cycle *not* necessarily equal to 24 hours). This indicated the importance of the dark period. They also interrupted the day with an interval of darkness and the night with an interval of light. Day interruption was without effect, but night interruption inhibited flowering. This discovery of the night-break phenomenon opened up numerous possibilities for research. What intensities and durations were required? When was the night break most effective? What qualities of light worked best?

The time of interruption is an important factor. Plants reach a maximum sensitivity to the light break at some set time after the beginning of the dark period, more or less independently of the dark period's total duration (fig. 6). It is important to note that night interruptions inhibit flowering in short-day plants but promote flowering of long-day plants.

Reciprocity holds, as an approximation, over a relatively narrow range of intensities and durations. Since the time of interruption is so important, reciprocity would not be expected to hold with long durations. If light is given at low intensity during the entire dark period, intensity of moonlight is often nearly sufficient to inhibit flowering of some short-day plants. When light is given at extremely high intensities (for example, from an electronic photoflash), durations of a fraction of a second are effective.

The most productive studies have involved light quality. Red light is most effective in the night-break phenomenon, with an action spectrum similar to those of other phenomena we have been discussing. Immediately after Borthwick and others (6) discovered the reversible nature of the light reaction in germination, they investigated the light-break inhibition of flowering in cocklebur, finding again that far-red reversed the effects of red and, thereby, implicated the phytochrome system (5). The key question in photoperiodism is how time is measured. Hamner divided the flowering response into a series of component or partial processes that have since been further elaborated. First, the dark period, to be effective, must be preceded by light. Second, the reactions of the dark period first involve a pigment shift from predominant Pr to Pfr. This apparently occurs in a brief interval of time, and

the critical night must therefore be accounted for by some subsequent time-measuring mechanism. Following the critical night, flowering hormone (florigen) synthesis is initiated in the leaf. Third, florigen is translocated to the bud, where it causes a redirection of growth from the vegetative to the reproductive form.

It was suggested that time measurement is a matter of the time required for phytochrome pigment shift (26). There are problems with this hourglass concept of timing. We have mentioned that pigment shift is apparently complete in a much shorter time than the critical night. Furthermore, time measurement is relatively tem-

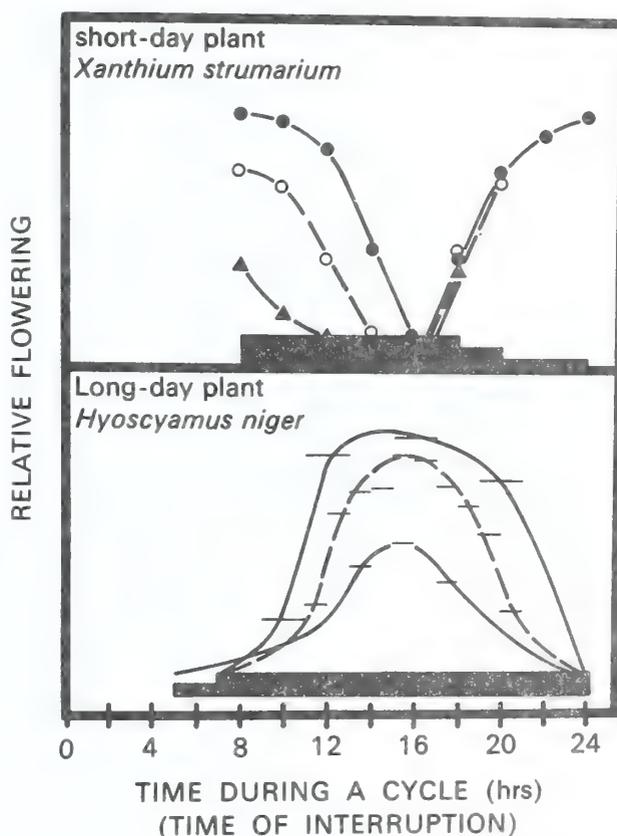


FIGURE 6.—Flowering responses of a short-day (46) and a long-day (15) plant to dark periods of various lengths (indicated by bars above the abscissas) that were interrupted at various times by light breaks (60 sec. for *Xanthium*, 1 or 2 hr. for *Hyoscyamus*—indicated by the length of the horizontal lines). *Xanthium* is maximally inhibited about 8 hours after beginning of the dark period, regardless of its length, and *Hyoscyamus* is maximally promoted by a light interruption near the middle of the dark period.

perature insensitive, as it is in the circadian rhythms. Phytochrome shift would be expected to be more responsive to temperature. It was shown (43) that the critical night, as well as the time of maximum sensitivity to a light break (39, 48), was not affected by threshold light of intensities capable of inhibiting flowering (fig. 7). If this light inhibits flowering by converting the phytochrome system, then time measurement can clearly not be a matter of phytochrome changes.

Hamner and his students (24) have found that various short-day and long-day plants exhibit

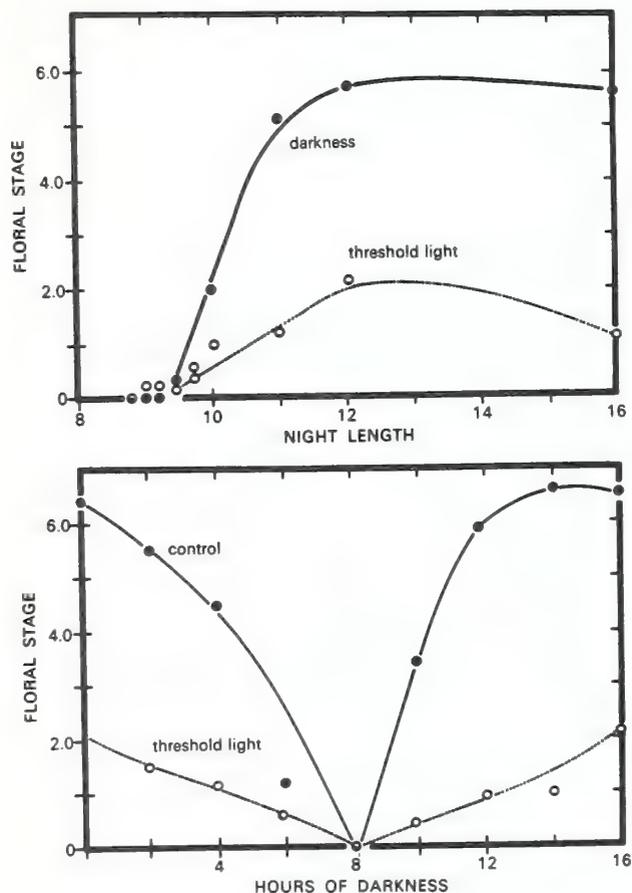


FIGURE 7.—Flowering response of cocklebur to length of night (top, 43) and time of light break (bottom, 48), as affected by threshold light ($10 \mu\text{w cm.}^{-2}$) during the dark period. Floral stages represent increasing levels of flowering nine days after treatment (for example, 0=vegetative, 3=first visible flower primordia, 6=flower primordia covering all but tip of inflorescence primordium).

alternating periods of sensitivity to light (fig. 8) in a manner reminiscent of circadian rhythms. He and others suggest that time measurement in photoperiodism is more closely related to oscillating time measurement in the circadian rhythms than it is to an hourglass mechanism of timing, such as pigment shift.

We have investigated this problem for several years (40, 43). When experiments were set up as in fig. 9, critical day could be studied. It was found that flowering would not occur unless an intervening light period exceeded about 5 hours. The experiment of fig. 9 indicates an increase in

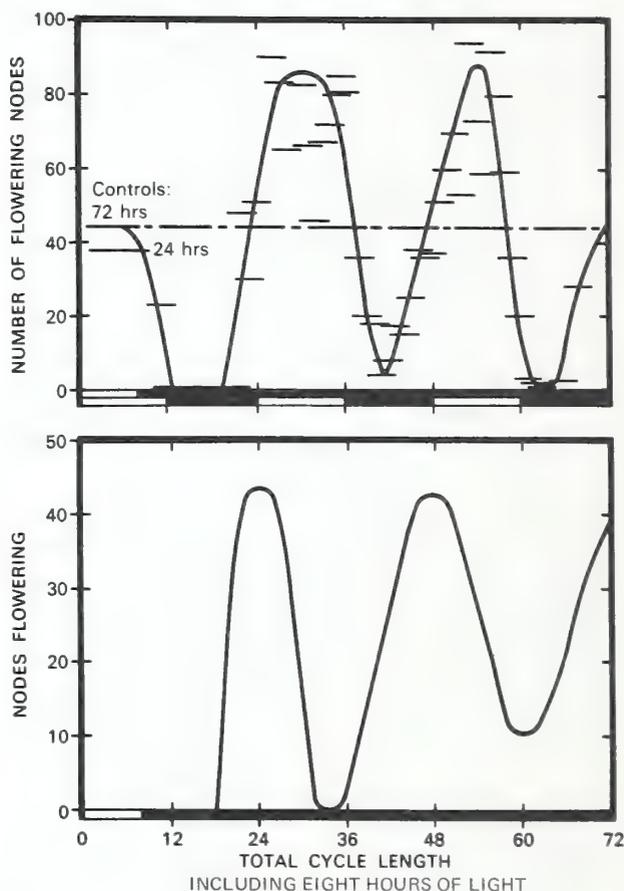


FIGURE 8.—Rhythmical flowering responses of Biloxi soybean after 7 light-dark cycles (44). Top: Effects of time of 4-hour interruptions of a 64-hour dark period. Upper bar on abscissa shows plan of experiment: 8 hours light, 64 hours dark; bottom bar shows postulated photophile (white) and skotophile (black) phases. Bottom: Effects of length of dark period, following 8-hour light period.

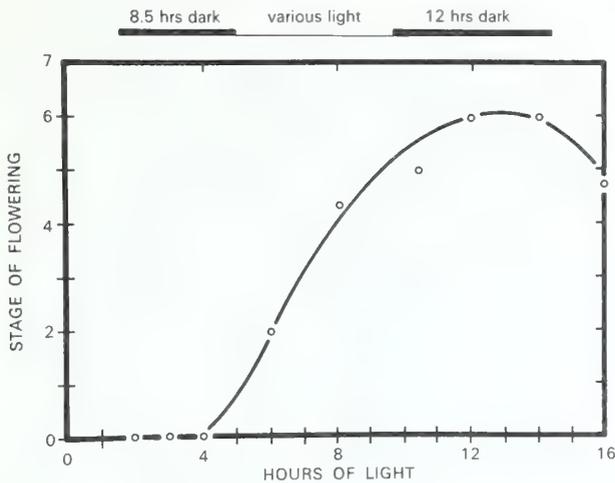


FIGURE 9.—Flowering response of cocklebur as a function of length of the intervening light period in an experiment symbolized by the bars above the figure (45). Floral stages as in figure 7.

flowering in response to increasing day length—a long-day response. Thus, cocklebur is a short-day plant when days are constant and longer than 5 or 6 hours (a shorter time than originally used by Hamner and Bonner) but a long-day plant when nights are constant and long enough, and days are around 5- or 6 hours. Using this experiment, it was possible to investigate the light requirements during the light period. Red light strongly promotes flowering under these conditions, and far-red inhibits—responses exactly opposite to those of the night-break phenomenon. Thus, the plants are alternating in their sensitivity to light, red promoting at one time and inhibiting at another, and far-red acting in an opposite way. This is another feature not unlike those observable in circadian rhythms.

In further studies, we were able to investigate resetting of the photoperiodism clock. As figure 10 indicates, a light interruption given 2 or 4 hours after the beginning of a long inductive dark period does not influence the time of maximum sensitivity to a second light break. When the first interruption is given at 6 hours, however, the time of maximum sensitivity to the second interruption is qualitatively changed—shifted about 10 hours. This is also known from studies on circadian rhythms. Thus, the photoperiodism clock exhibits many of the same features as the clock controlling circadian rhythms.

With this idea in mind, Alice Denney and I have investigated circadian rhythms in cocklebur, comparing their characteristics with those of the photoperiodism clock (17, 47). We have had to conclude that the two clocks, while having similar characteristics, differ extensively in detail so that they cannot both be direct manifestations of a single clock. Significant differences are as follows: (A) There is no evidence in the circadian rhythms for the interesting 6-hour shift mentioned above. (B) The flowering clock can be suspended. When plants are placed in the dark, they flower about equally well in response to equal dark periods, regardless of the length of the preceding light period, providing it is longer than 5 or 6 hours. No such phenomenon could be observed with the leaf movements, which are not suspended during long light periods. (C) We had thought that the extent of leaf movements might be an indication of sensitivity to floral induction, extensive leaf movements during the inductive dark period implying high sensitivity (high subsequent levels of flowering). When this was investigated over a wide range of day and night lengths, however, no relationship could be observed. (D) Most recently we have found that light intensities well above those required to inhibit flowering do not upset the circadian leaf movements. (E) In all of our experiments, we

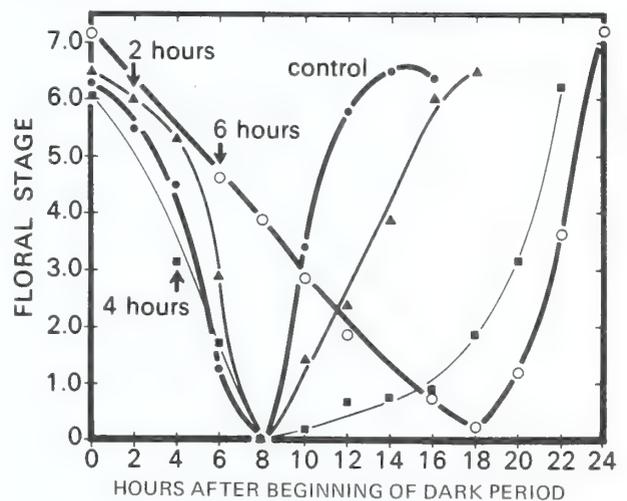


FIGURE 10.—Flowering response of cocklebur to a second interruption of the inductive dark period, following a first interruption at 2, 4, or 6 hours after onset of darkness (40). Interruptions were 60 seconds; floral stages as in figure 7.

have never been able to predict flowering by the leaf positions at any time in relation to an inductive dark period. All of these things seem to indicate that the photoperiodism clock and the circadian leaf movement clock are quite separate.

If time allowed, further details of the flowering process could be discussed. Interest in the possible extraction of a flowering hormone is high at present, after more than 30 years of failures in attempts to extract it. Dr. Denney and a graduate student of mine are presently working on this problem with a higher level of success than has previously been reported. We are quite excited.

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