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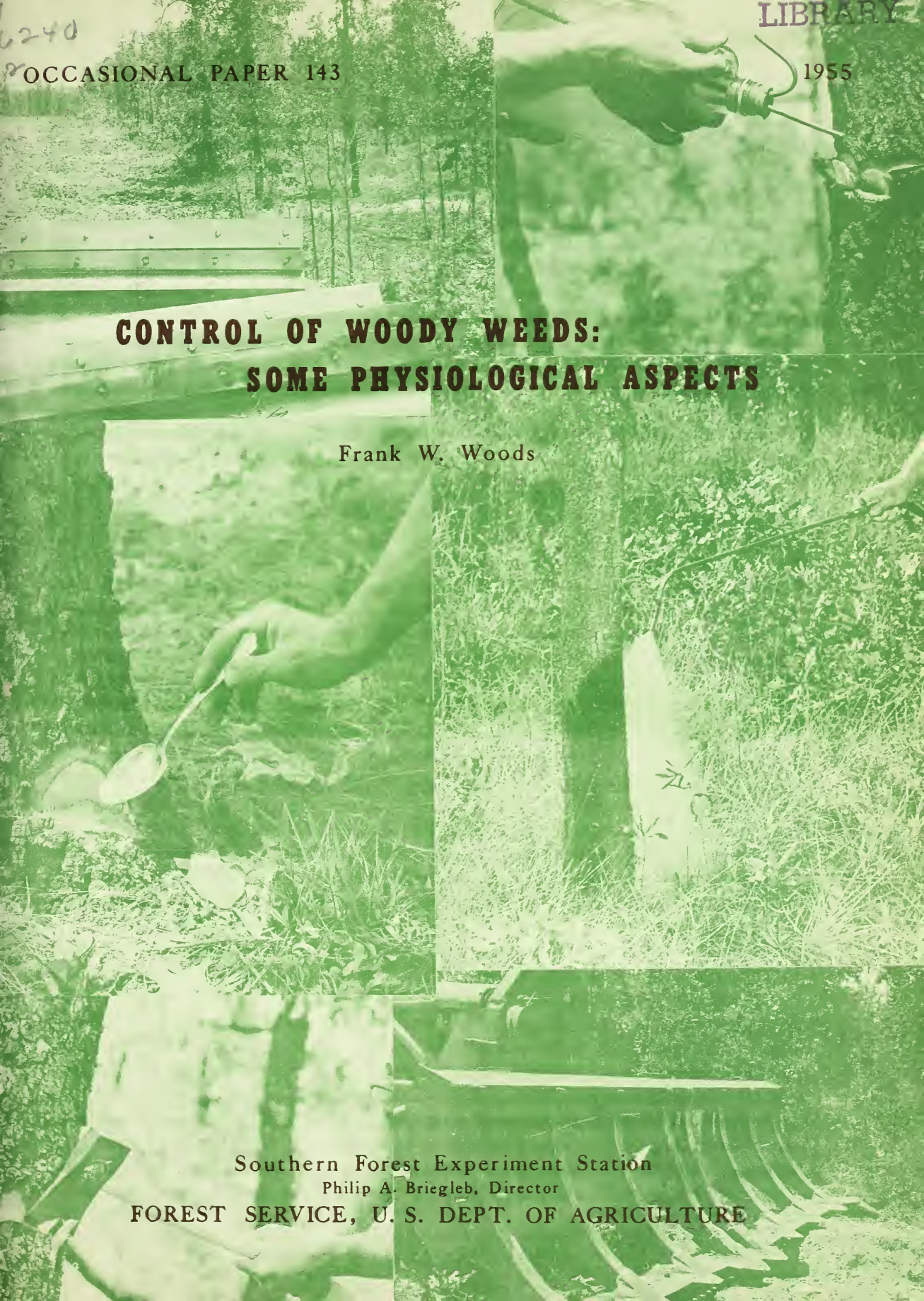
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CONTROL OF WOODY WEEDS:
SOME PHYSIOLOGICAL ASPECTS

Frank W. Woods

ACKNOWLEDGEMENT

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"In June and in August, as well doth appeere,
Is best to mowe brakes, of all times in the yeere."

Five Hundred Pointes of Good Husbandrie

Thomas Tusser, 1557

CONTROL OF WOODY WEEDS:
SOME PHYSIOLOGICAL ASPECTS

Frank W. Woods
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Recent advances in the knowledge of basic physiological processes, coupled with the discovery of the growth-regulator type of phytocides, have stimulated tremendous interest and work in methods of controlling weed plants. New advances are being made so rapidly that it is difficult for foresters to keep abreast of developments.

It seems desirable, therefore, to bring together some of the fundamental concepts of plant physiology as related to weed control. The field worker familiar with basic physiological processes can make most effective use of available tools and methodology. An understanding of the natural annual cycles in reserve foods of weed trees can make control methods more efficient. Information about the fluctuations induced by treatment may be equally as useful. This knowledge can be applied whether the control method is mechanical, chemical, biological, or pyric. Usually, treatment is most effective when the amount and location of reserves render the plant most susceptible to the particular method chosen.

While foresters are primarily concerned with the control of woody weed plants, herbs and grasses also occupy forests and must be dealt with in the course of management. Too, most basic physiological processes are similar in all plants, and information obtained by studying one group may often be useful in interpreting the reactions of another. Because of their small size and the fact that they can easily be grown throughout a life cycle under controlled environmental conditions, herbs have been studied more often than trees and other woody plants.

This discussion does not pretend to be a complete review of the literature on weed physiology. It should, however, give the reader an insight into several of the more important causal factors underlying plant response to control measures, with emphasis on changes in carbohydrate metabolism.

RESERVE CARBOHYDRATES OF ROOTS

Fire, chopping, or chemicals may entirely destroy plant parts or may kill all meristematic tissues above ground. Broad-leaved woody plants generally respond to such treatment by sprouting from the root collar. The source of energy and building material for the initial burst of regrowth comes from the food stored in roots. If these reserves are low, the initial sprouts will be weak; if reserves are high, response will be proportionately vigorous.

Reserve food is accumulated only when the rate of photosynthesis exceeds the rate of respiration plus the rate of assimilation of food into non-reversible forms, such as cellulose. Anything that affects these three processes affects the amount of food stored. If the leaf area of a tree is reduced, if the rate of respiration is increased, or if more photo-synthate is used in vegetative growth, storage is decreased.

Reserve foods of plants are mainly carbohydrates stored in roots, stems, and twigs. The location and form of these reserves varies great-ly among species. While some annuals like potatoes and corn are im-portant for their storage capacity, storage is generally most highly de-veloped in perennials and biennials.

Measurement of food reserves presents difficulties. Among the storage products used as indicators of total reserve food are soluble starches, dextrins, sugars, hemicellulose, available carbohydrates, fructosan, fructose, reducing sugars, invert sugar, and hydrolyzable carbohydrates (115, 69, 150, 33, 218, 202, 133). Some of these carbo-hydrates are immobile storage forms, such as starch, while others may be transitional from sucrose to non-reversible, non-available forms like cellulose. Still others may be protein precursors. Since the chemical composition of any plant is related to the stage of growth (216, 117, 215, 133), and since various carbohydrate components can vary among differ-ent parts of the same plant (198), a single carbohydrate fraction may not be a reliable indicator of the total available carbohydrates (hereafter called TAC).

For example, Preston and Phillips (172) showed that in some species of trees sugar may increase in spring while starch decreases. Fischer (66) found that starch in conifers disappears in winter while fat increases; in spring this relationship is reversed. Similar relationships may hold in herbaceous species and grasses. McCarty (133), working with clipped grass of several species, found hemicellulose to decrease while starch increased. In plants the starch-sugar conversion can take place repeatedly with a very small loss of carbohydrates. While starch

was one of the first-used indicators of TAC (138), it has never been generally acceptable. A satisfactory method for determining TAC has recently been developed by Weinmann (219) and will probably be used with increasing frequency in the future.

The physiology of grasses, herbs, and woody plants is basically similar. However, the balance of these processes may be quite different, so that the plants may respond variously to identical stimuli. Differences in plants, organs, tissues, and methods of investigation used in each group make extrapolation of data from one group to another possible and profitable. Voids of knowledge in one group may often be bridged by observation of another group.

Woody Plants

Seasonal Variation

Knowledge of seasonal trends in the reserve food accumulation of trees and shrubs has found immediate application in sprout control (40, 32, 180), interpretation of wood structure (85), and the pruning of apple trees (173).

Food reserves of trees have usually been found more abundant in roots than in stems, but their importance is not always evident in the initial spring growth. Twigs and branches store much of the reserve foods of some species (173). Also, if root growth precedes shoot growth (100, 76, 180), root reserves may be depleted by root growth and misinterpreted as having been used in shoot growth.

Seasonal periodicity of reserve carbohydrates has been noted in apple (34, 88), maple (101), pear, quince (185), sycamore (41), black locust (191), and cactus (197). These reserves are nearly always greatly decreased in spring while shoots and leaves are developing (15, 185, 172). Then, carbohydrates accumulate until fall dormancy sets in (149, 101, 185). Accumulation apparently begins after maturation of the leaves and after diameter growth is largely complete.

With fall dormancy there is generally no further accumulation of reserves in deciduous species. Instead, a period of depletion begins and lasts through the winter (149, 185, 19). This depletion is not great, and, as with grasses and herbs, may be attributed to respiration.

The classic description of seasonal variation in carbohydrate reserves of trees by Sablon (185) is worthy of repetition (author's translation):

Carbohydrate reserves of roots and stems. The roots of
deciduous trees act as reserve organs where carbohydrate
materials accumulate. At the beginning of autumn, at the
time when it is known that starch grains are very abundant,
reserve carbohydrates attain their maximum. Then during
autumn and winter, when starch disappears or at least be-
comes less abundant, the reserves diminish, but relatively
slightly. The largest part of the starch that disappears seems
to be transformed into reserve cellulose, which can be
found in the determination for starchy materials. In April
and May, the root reserves diminish rapidly and are con-
sumed by the formation of new branches and new roots.
From June to October, reserves increase steadily. During
this time, in fact, growth of the tree has slowed on the one
hand, and on the other, the rate of [carbohydrate] assimi-
lation has become intense because of the development of
leaves.

In a general manner, from the point of view that concerns
us, stems act in the same manner as roots, but their charac-
ter as a reserve organ is less accentuated. Their reserves
are less abundant than in roots, and particularly the differ-
ence between the maximum and the minimum is less. The
maximum of autumn is much smaller than in the roots and
the minimum of spring is sometimes greater than the min-
imum of roots. At the beginning of spring an increase in the
reserves of the stem can be verified in certain cases. This
is due to the fact that the reserves of roots have moved into
the stem.

Anderssen (6) and Kikuya (106) were able to demonstrate a large
increase of soluble carbohydrates in xylem elements during certain
seasons. Curtis (54) offers evidence that it is the phloem through which
upward translocation takes place. In either case, it is now well es-
tablished that there can be an upward movement of soluble carbohydrates
through stems.

However, no single rule will apply to all species of woody plants.
Bews and Vanderplank (19) were able to detect only a slight spring de-
crease in root reserves of Portulacaria rooperi, a small shrubby tree
native to Natal, indicating an absence of translocation. They said, "The
starch stored in the species studied did not seem to be used to any ap-
preciable extent during periods of renewed growth...." Apparently,
the new leaves became self-sufficient at a very early age. Wieler (226)

was not able to correlate the amount of reserve foods with the width of the annual rings in Robinia pseudoacacia or Pinus sylvestris.

In some evergreen trees, the yearly cycle of storage and depletion is reversed from that of deciduous trees. Although reserves of evergreens seem to accumulate at a slower rate than those of deciduous species, carbohydrate accretion continues throughout the winter and reserves are at a maximum just before spring growth starts. Unlike deciduous trees, evergreens seem to have no intensive late summer period of accumulation (92, 186). Juniperus virginiana seems to be an exception and can be cited as an evergreen having a yearly carbohydrate cycle similar to that of deciduous species (172).

Bews and Vanderplank (19) found that there can be 14 to 31 percent more usable carbohydrates on one side of the tree than on the other, with a gradient from north to south. This is apparently due to different rates of photosynthesis on sunny and shady sides.

In summary, the following relationships seem to hold true: After the winter dormant period, there is a sudden burst of growth in spring during which trees refoliate and herbs and grasses send up new shoots. This initial, vigorous, spring growth takes place at the expense of reserve foods stored the previous growing season. After refoliation has produced a sufficiently large photosynthetic area, reserves once again accumulate until shortly before fall dormancy. With the onset of dormancy and continuing throughout the winter, there is a small but consistent loss of TAC resulting from respiration. An inverse relationship between the annual march of carbohydrate reserves and the growth of tops seems to be the rule rather than the exception. So long as tops are growing rapidly, there is little or no accumulation.

Top Removal

Eradication of woody plants by cutting or burning is usually most effective if done at the time of the year when carbohydrate reserves are lowest. Aldous and Zahnley (3, 4) found that burning in late April increased the number of buck-bush stem sprouts, while a burn in May, only 23 days later, resulted in fewer sprouts per acre than were originally present. The reason appeared to be that the starch reserves of the plants had been practically used up before the May burn. In tests with sumac, Aldous found the least sprouting from stems cut in June, when starch reserves were at their lowest ebb. His test for starch consisted of a simple microscopic examination of wood sections stained with iodine. Huberman (97) found more reserve starch in unburned (defoliated) seedlings than in burned ones.

Clark and Liming (40) said, "Trees treated in June had fewer trees sprouting, higher mortality of sprout clumps, fewer sprouts per tree, and smaller sprout clumps than trees treated during any other month." Buell (32) also found that sprouting of dogwood was closely related to the season of cutting. Cuts made in late June and early July resulted in fewer and smaller sprouts than cuttings made in any other month. Little and Mohr (119) noted that "The use of summer fires proved superior to the use of machinery." Lotti (121) obtained a good kill of understory hardwoods with successive annual summer fires. Mid-June girdling of undesirable species gave less sprouting than girdling at any other season (7). Cutting Ostrya virginiana between June and September resulted in less sprouting than cutting at any other time of year (61). While vitality of pasture shrubs was found to generally decrease under repeated heavy clipping (74), control measures in July were found to be particularly effective (30).

Girdling large trees has many obvious advantages. It is more economical than cutting and leaves less litter on the ground as a fire hazard. Results of seasonal girdling tests closely parallel those of cutting experiments. Clark and Liming (40) found that trees girdled in June sprouted less than those girdled at any other time. Grano (80) found that girdling trees in spring, just after they had reached full leaf, produced the best kill and least sprouting.

However, girdling necessitates consideration of factors that are of no importance when tops are entirely removed, as by cutting. Under normal conditions, terminal buds produce auxins which move down the stems, inhibiting the growth of dormant buds and the initiation of adventitious buds. Food manufactured by leaves moves downward only through the phloem, while the transport of auxins takes place in both bark and wood through the phloem and the parenchyma (163).

Destruction or removal of the terminal buds stops production of these auxins, thereby permitting sprouts to develop. Because girdling does not destroy the terminal buds immediately, it may be more effective in killing weed trees than total destruction of tops. Girdles cut off the supply of food to the roots, while the auxins continue to move down through the wood parenchyma and prevent the formation of new leaf-bearing sprouts. Under these conditions the roots eventually starve to death.

Since the main avenue of downward auxin movement is through the phloem and adjacent wood, the depth of the girdle may be of great importance. A shallow girdle (so long as it completely severs the phloem for a width sufficient to prevent healing over) causes a maximum

of inhibiting action. Peeling the bark either removes the phloem or exposes it to the air, thereby causing it to die quickly. Clark and Liming (40) found a peel girdle more effective than any other type.

There may be reasonable doubt as to the source of the reserve foods used in initial spring growth. These foods may come from roots or from stems, depending upon the species under consideration. However, there can be no doubt as to the source of food when plants send up new shoots after tops are removed or the trunk is girdled. Roots are the only possible source.

Herbs

Seasonal Variations

Knowledge of the nature and amount of reserve carbohydrates in roots of perennial herbs has contributed directly to the eradication of such weeds as Canada thistle (212), regulation of mowing practices (228), and the determination of grazing capacity (25). Even though herbs often have the bulk of their carbohydrates in roots (112, 150), there may be considerable variation between species according to the season, root type, and root depth (69). Environmental factors, such as soil moisture, may also exert a strong control (230). While variability must be recognized (12), the over-all pattern is fairly uniform.

The phenology of plants may provide a guide to internal physiological conditions. Numerous investigators have shown that the quantity of reserve carbohydrates in roots of perennial dicots can be correlated with a growth stage (115, 25, 224, 69, 192, 12, 9, 193, 79). Annual herbs usually have small storage capacity and variations are relatively unimportant (159).

Graber et al. (79) found that new top growth of alfalfa in spring is largely initiated at the expense of root reserves. This has been corroborated by other workers (228, 87, 78, 116, 193) including Arny (9), who noted "sharp declines from late April through the first of May in the percentages of total sugars and total readily available carbohydrates in the underground storage organs [of some perennial weeds].... " Leukel (115) found that vigorous top growth during spring reduced the carbohydrate reserves of alfalfa plants by 50 percent. The flush of spring growth generally sends reserves to their lowest level of the entire year. If reserve carbohydrates are low, spring activity will be less vigorous than if reserves are abundant. The amount of top growth in spring has been correlated with the amount of food reserves stored during the previous growing season (193, 228, 2).

Depletion of reserves stops only when the photosynthetic tissue is sufficient to supply all food used in respiration and growth. Phenologically, this generally is soon after leaves mature (2). Accumulation continues until fall dormancy sets in and tops die or leaves are shed (115). Under these conditions top growth may alternate with root growth (130). After dormancy begins, there is no further accumulation of TAC until the following summer. During the dormant period, however, there may be shifts in basic carbohydrate components from one compound to another (13). TAC losses during winter are almost entirely due to respiration.

Environmental factors strongly influence the rate of accumulation during summer. High nitrogen contents in the soil may increase the vegetative growth and decrease the rate of carbohydrate accumulation (110). Dry weather (115, 154) may result in increased carbohydrate accumulation due to smaller use in growth processes, while the actual increment is decreased. Recurrent droughts may seriously deplete starches and sugars (230).

Top Removal

Responses of herbs to defoliation are numerous and varied. Among the more easily measured changes are depletion of reserves (193), decrease in the number of stolons (206), changes in species composition (140), reduction in dry weight of roots (228, 171), and lessening of hay yield (102, 114).

After a plant has been clipped, new top, stem, and root growth is initiated at the expense of previously deposited root reserves (193, 228, 155). Moran et al. (150) showed that "defoliation caused a depletion of [carbohydrate] reserves from both stolons and roots."

The more often plants are defoliated, the greater the depletion of reserves (206). Conversely, the amount of new foliar growth produced immediately after defoliation is directly related to the carbohydrate level at the time of defoliation (150, 155, 171).

The depletion period that results from cutting tops late in the growing season may last longer than the one following earlier cuttings. Smith and Graber (193) found that cuts made in mid-September depleted reserves for a month, while cuts in mid-August caused only a two-week depletion period. Wilkins and Collins (227) found that 5 percent of their sweet clover survived April plowing, while only 1 percent survived May plowing.

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The length of the depletion period is important if follow-up treatments are to be made. For phytocidal purposes, follow-up is most effective when reserves are lowest, and before the photosynthetic area of leaves is great enough to provide the food used in growth. Timmons (207) found that depletion of bindweed root reserves continued for 12 to 14 days after top removal, and he was later able to show that 2 weeks was the longest effective interval between shallow hoeings for the eradication of this weed (208).

Moran et al. (150) found that cutting caused relatively less depletion in plants with low carbohydrate supplies than in those with ample amounts. Apparently, depletion of the remaining reserves becomes progressively more difficult as the supply diminishes.

Partially defoliated plants recover more rapidly than those entirely defoliated (206). Any photosynthetic tissue left on the plant will contribute to its recovery by supplying carbohydrates used in growth.

When top removal on a sustained-yield basis is desired, as in production of hay, careful timing of cuts is essential. Salmon et al. (186a) found that cutting alfalfa at full bloom failed to injure the plants, while cuts made at the succulent stage were definitely harmful. The results of cutting at the wrong season may not be seen until later, when crop production is lowered. Too frequent cutting also can lower subsequent growth. Kudzu plants harvested four times during the growing season made practically no increased growth during the second year of treatment and also lost root weight (171). Time must be allowed for plants to replenish their reserves.

Plants cut frequently or late in the growing season may enter winter with low reserves and a high moisture content. Such plants are more susceptible to winter injury than those cut less frequently (115). When top removal has been excessive, reserves may not be great enough to allow respiration throughout the winter (206, 228), and the plant may die during the dormant season, the period when reserve requirements are least.

Grasses

Seasonal Variation

Grasses, like trees and herbs, have pronounced seasonal variations in carbohydrate reserves (117, 215, 132). The variations may

be associated with different developmental stages (151, 218 134, 188).
The literature on seasonal variations of reserve foods in grasses has
been summarized in an excellent review by Weinmann (220). Such in-
formation has been useful in the eradication of weed grasses (201), im-
provement of watershed values (99), and regulation of grazing practices
on permanent ranges (133). Productivity of grasses seems to be directly
related to root reserves (78): the greater the reserves, the more
vigorous the top growth.

        The periods of root and shoot growth of grasses do not neces-
sarily coincide. In many species, roots characteristically grow after
plants mature and when top growth is a minimum (201, 218, 188). Root
growth may also alternate with herbage growth (133). Since root growth
also requires carbohydrates, depletion of reserves cannot be attributed
to top growth alone. Tops may have completed growth and be actively
manufacturing and translocating carbohydrates to roots, yet, if these
carbohydrates are being used in root growth, there will be no build-up
of reserves.

Top Removal

        Response of grass roots to top removal by cutting, grazing, and
burning has been carefully studied. Specific anatomical changes, such
as smaller root diameters and smaller steles may result (168, 20). Other
effects include lower resistance to competition (78, 53), lower vigor
(214), decreased top growth (179, 87), smaller root quantity and lower
quality (184, 51), increased susceptibility to freezing and winter injury
(20, 78), lowered drought resistance (78), increased insect injury (77),
and death (33, 187, 86). Ultimately, the differential response of plants
to top removal may change the direction of succession and composition of
a region (45, 91, 53).

        The height of cutting is closely related to the depletion of reserves:
high cuts, leaving more photosynthetic tissue, are less exhausting than
low cuts. Harrison and Hodgson (87) state, "In general, the shorter a
given grass was cut, the less top growth it produced." Orchard grass
clipped to within an inch of the soil used nearly all root reserves while
ample amounts remained in plants cut to three inches. Sullivan and
Sprague (203) observed that larger plants gave greater yields of aftermath.

        Roots of perennial ryegrass were never completely exhausted as
long as defoliated plants were kept in light. However, in darkness re-
serves were depleted and protein hydrolysis took place (202). This
helps confirm the suggestion that endogenous respiration can take place

after carbohydrate reserves are exhausted (50, 161). In this process the proteins of the protoplasm are broken down into their constituent parts and utilized in respiration.

Robocker and Miller (181) found that a single time for burning or cutting tops did not affect all species of grass in a like manner. For example, cutting at the hay stage was harmful to big bluestem, Indiangrass, and switchgrass, but caused little bluestem to increase. At the same time, Canada and Virginia wildrye were injured by burning, while Indiangrass increased.

Frequency of cutting is also very important. Cassady (37) found that in the bluestem grass type of Louisiana "the ill effects of close repeated harvesting may last for several seasons, even under complete protection." Gernert (75) wrote that "the lowest production of roots by weight came from plots clipped most frequently."

Low yields of herbage can generally be correlated with a low rate of food accumulation (20, 78). Ellett and Carrier (63) found that grasses cut every seven days produced about half as much air-dry substance as plants cut once a year. Cassady (37) found the same relationship when plants were cut every two weeks. Both investigations agree closely with the work of Sullivan and Sprague (202), who showed that root reserves in perennial ryegrass were lowest about the eleventh day following clipping. Parker and Sampson (167) found the period of depletion to last 8-10 days. If reserves are not allowed to build up in the intervals between successive cuts, the result is nearly always harmful. Cutting too frequently may reduce the stored plant food and hence the growth during the following season (133, 78). Crowder et al. (52) found that clipping at 8-week intervals gave higher yields of dry matter than did harvesting at shorter intervals.

McIlvanie (137) found that 45 percent of the height growth of bluebunch wheatgrass was produced before reserves ceased to decline. The interval of time required to produce 45 percent of the top growth would therefore be of great importance in determining the interval between successive cuts, either for forage production or as an eradication measure.

Fertilization does not compensate for a lack of top growth (86). In fertilization, mineral elements are supplied, but carbohydrates can only be manufactured by the plant itself, except under extraordinary circumstances (such as by the application of sugar solutions to foliage).

Diurnal Variations in Carbohydrates

The difference between afternoon or morning cutting or burning of vegetation on the same or succeeding days is of little importance, so far as the total amount of root reserves is concerned. Changes in the amount of total carbohydrates during the night are probably slight, and the day-to-day loss or gain is normally small.

There are, however, pronounced diurnal changes in the carbohydrate content of the leaves (39, 131). During the day the products of photosynthesis accumulate in leaves as starch. Both sugars and starch are highest from 3 to 6 p.m., after which the concentration drops (111, 55). This lowering of concentration occurs when starches are transformed to sugars and translocated from the leaves. Concentration is lowest in the morning, just before photosynthesis starts (19, 55). More than half of the available carbohydrates in leaves have been found to disappear during the night (58). Curtis (56) found "a carbohydrate content 83 percent higher and a dry matter yield 19 percent higher in afternoon cutting than in morning cuttings [of alfalfa]."

While there is some dispute as to the magnitude of diurnal changes in the carbohydrates of leaves (55, 231, 56), these changes are of interest in that they may give a clue to the distribution of systemic phytocides.

Carbohydrate-Nitrogen Balance

There is a balance of carbohydrates to nitrogen best for both vegetative growth and carbohydrate accumulation. When the proportion of carbohydrates is high, accumulation is favored; when nitrogen is high, vegetative growth is favored. The classic study of Kraus and Kraybill (110) showed that tomato plants high in nitrogen were usually low in stored carbohydrates, and that when such plants were cut off near the base they rooted without producing new shoots. Tomato plants low in nitrogen sprouted vigorously when cut near the base. Foster (68) also associated nitrogen deficiency with starch congestion in tomato stems. The increased accumulation of carbohydrates when nitrogen is low has been attributed to the reduced use of these foods in protein formation (199, 122). Intensive protein formation is characteristic of fast-growing plants.

Harrison and Hodgson (87) withheld nitrogen from grass plants for several weeks so they would become relatively high in carbohydrates. Clipping these plants to three inches in height resulted in a better immediate growth than clipping to either six inches or one inch. Apparently the three-inch plants had the best C/N balance for immediate use in vegetative growth.

The C/N balance most favorable for extensive top growth may not be the most favorable for root growth. Harrison (86) found that "the addition of nitrogen brought about an increase in top growth, but the weight of roots was not increased over that of the roots of the un- fertilized grass." Reid (177) showed that root growth sometimes takes place when conditions are not favorable for top growth. Sprague and Sullivan (198) stated, "While final dry weight yields of tops and stubble were higher under high nitrogen nutrition, root weights were greater under low nitrogen nutrition." Apparently, high carbohydrates and low nitrogen favor root growth in some species.

Repeated clipping may exhaust roots faster in fertile than in poor soils (78, 124). Plants growing in poor soils store more carbo- hydrates and use less in vegetative growth; they can therefore sustain a larger number of cuts before becoming exhausted.

The C/N balance of a plant may change from time to time during the year. Weaver (216) found that the proportion of carbohydrates to nitrogen becomes greater as the growing season progresses. Pierre and Bertram (171) showed that the nitrogen content of kudzu roots is high in the spring, decreases during the period of vigorous vegetative growth, and increases once again after this period ends. Nitrogen has also been shown to disappear from the leaves of some plants after maturation and prior to abcission (43, 152). It is presumably trans- located to the twigs and stems.

Cutting the tops may mobilize carbohydrate reserves. In this process, the reserves are changed from an insoluble to a soluble form, and an increase in the amount of soluble nitrogen is apparent as early as 3 to 7 days after cutting (203). This agrees with findings that nitro- gen root reserves of red clover are depleted by spring growth as well as by regrowth following cutting (192, 228).

Not all investigations have revealed a correlation between the depletion of carbohydrate reserves and the depletion of nitrogen reserves. Bakke et al. (12) found the total nitrogen reserves of certain prairie grasses independent of the annual trends shown by carbohydrates. Bukey and Weaver (33) tried several different clipping methods and found that "the percentage of nitrogen was almost constant under all conditions of growth studied." Even though the nitrogen level might not change ap- preciably, a lowering of carbohydrates will bring a change in the C/N balance and result in conditions more or less favorable for vegetative growth and food storage. Under any circumstances, it seems as if the the variation in nitrogen is not so great as that in carbohydrates (44).

The general relationship between carbohydrates and nitrogen may be summarized as follows: Low carbohydrates and high nitrogen give the plant high resprouting capacity. Thus, to minimize resprouting of hard-to-kill weeds, nitrogen fertilization in advance of eradication measures might sometimes be advisable--at least from a physiological standpoint.

For those interested in nitrogen sources of seed plants, the interpretive review by Shields (190) will prove useful.

WEED CONTROL WITH GROWTH REGULATORS

Excellent reviews of work with growth-regulating phytocides such as 2,4-dichlorophenoxyacetic acid (2,4-D) and 2,4,5-trichlorophenoxy-acetic acid (2,4,5-T) have been prepared by Overbeek (164), Audus (11), Blackman et al. (21), Mitchell and Marth (148), Overbeek (166), Tukey (209), Norman et al. (160), Ahlgren et al. (1), Crafts (49), and Nickell (158). Such reviews are invaluable to the field worker with access to a limited library.

Kraus (109) has pointed out that the term "growth regulator" is applied to chemicals of widely varying characteristics. This term is not entirely satisfactory, because many of the effects of these chemicals are not growth responses. However, it has come into such general acceptance that it will probably continue to be used. The report of the committee on plant regulators, American Society of Plant Physiologists (211), and the minority report (113) are of great interest in this respect.

A partial list of growth regulators and their effects helps to clarify the meaning of the term (109):

Indoleacetic acid--causes cell enlargement, parthenocarpic development, root formation, starch digestion, and mobilization of carbohydrates.

Indolebutyric acid--very similar to the above.

Naphthaleneacetic acid--induces parthenocarpic development, cell enlargement, root formation, starch digestion, and suppresses development of abscission layers and lateral shoot development.

Iso-propyl-N-phenyl-carbamate--used principally as a herbicide on grasses.

2, 4-dichlorophenoxyacetic acid--brings about cell enlarge-
ment, cell proliferation, rooting, parthenocarpy,
starch digestion, increased respiration, and carbo-
hydrate mobilization.

2, 4, 5-trichlorophenoxyacetic acid--causes cell enlargement,
cell proliferation, root formation, tumor formation,
starch digestion, fruit ripening, and nastic movements.

Maleic hydrazide--results in dwarfing, prolonged dormancy,
retarded flower primordia, and decreased vegetative
growth.

New chemicals are constantly being developed and discovered.
One of the more recent, 2, 4, 5-trichlorophenoxypropionic acid, shows
promise on woody plants.

Differences in season, hour of application, soil type, micro-
flora, microclimate, carrier and formulation of the herbicide, and
weather conditions make every use of a chemical a unique problem.
Generalizations are necessary but risky.

Reactions of Plants to Treatment With Growth Regulators

Plants react to growth-regulator phytocides in various ways,
some readily observable and others measurable only by biochemical tests.
Curling and twisting of leaves and stems, the most obvious response, is
often used to evaluate the effects of minute quantities of growth sub-
stances. I. e., a measured amount of the phytocide is placed on a leaf or
petiole and the resulting petiolar curvature is measured in degrees. The
larger the departure from normal, the more effective the chemical (57, 95).

The phytocides may also destroy or interrupt the phloem (62, 210,
196). Meristematic tissues are often affected (204). Stem tissues may
proliferate (123). Disorganization and rupture of the cortex of roots (210)
may permit the entry of bacteria into the plant tissues and thereby hasten
death. Interference with native auxin, and with physiological and enzymatic
processes, is probably the factor underlying many gross morphological
responses (27, 233, 166, 221). Increase in respiration, lowering of
carbohydrates, and drop in fresh weight (210, 147, 84, 141) are also
characteristic.

Chemical concentrations too low to curl the leaves or affect respi-
ration may destroy chlorophyll (210), and disrupt photosynthesis (217, 123).

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It is also thought that these herbicides may kill by the production of toxic substances, thereby acting as toxin precursors (165).

The outstanding characteristic of the growth-regulator phytocides is their relationship to metabolic activity. They are generally most effective under the environmental conditions best for plant growth. Bausor (16) pointed out that "growth substances are not very effective in the epidermis, and the lack of influence on the hydrolysis of starch may be related to ... general inactivity in this tissue." Physiologically, the epidermis is comparatively inactive. Gallup and Gustafson (72) found that radioactive 2,4-dichloro-5-iodo-131-phenoxyacetic acid was translocated to and accumulates in the rapidly growing regions of the plant.

Since the selectivity of growth-regulator phytocides is relative (47), it is not possible to predict the exact reaction of a plant species to treatment. In some, the internal physiological balance (as indicated by phenology) may be favorable for response to treatment, while others, under the same conditions, may respond poorly. Rossman and Staniforth (183) showed that different strains of maize reacted differently to treatment with 2,4-D. Fribourg and Johnson (71), working with 2,4-D and 2,4,5-T, found similar variations in strains of soybeans.

Factors Affecting Growth-Regulator Activity

Since a plant's internal physiological condition is partially a reflection and integration of all its environment, a brief consideration of some of the environmental factors is appropriate. For more intensive review, the reader should consult the references mentioned on page 14.

Light

When light values are continually low, as in shade, photosynthesis and food accumulation are slight, and nearly all food manufactured may be utilized within the leaves. Since translocation of growth regulators takes place in association with organic foods made in photosynthesis (142, 48, 57), reduced light may inhibit the translocation of growth substances by decreasing the movement of organic foods (142, 143).

Light may also affect growth-regulator activity by acting as a source of heat. When air temperatures are low enough to become critical for plant metabolism, internal leaf temperatures may be raised by solar radiation. Growth regulators, generally effective only when plants are

physiologically active, may thus function even when air temperatures are below the critical level.

The diurnal cycle of light is also important. As pointed out above, photosynthesis takes place all day, food accumulates in leaves, and movement of this food away from leaves to other plant parts begins late in the afternoon. On this basis, afternoon should be the best time of the day to use growth regulators, which, as has been noted, are translocated in conjunction with organic foods.

Temperature

Growth-regulator activity increases with temperature up to about 90°F (26, 93, 143), whereupon there is a decrease in activity with further increase in temperature. All treatments made between 65° to 90° F may be equally effective (126). Above the optimum temperatures, excessive respirational losses of carbohydrates undoubtedly preclude translocation from the leaves (93). In cool weather, plant response is much slower, less intense, and may be greatly delayed (81, 126). Kelley (103) said, "When physiological processes are slowed down, as by low temperatures, the plants are less susceptible to 2, 4-D."

Soil Conditions

Plants are sensitive to 2, 4-D absorbed through roots (127, 82). After absorption, the chemical is translocated upward in the water-conducting tissues (94, 142). The action of 2, 4-D when used as a soil sterilant may therefore be a function of the transpiration rate. If entry into roots is not a limiting factor, upward movement of 2, 4-D should increase with the increase in transpiration.

Disappearance of 2, 4-D from soils is attributed to the decomposing activity of micro-organisms (157). Audus (10) reported the isolation of a bacterium (Bacterium globiforme group) that inactivates 2, 4-D in soil. DeRose and Newman (60) tested the persistence of 2, 4-D in untreated field soil and in soils freed of all micro-organisms by sterilization. They found that the chemical persisted in sterilized soil for 9 to 15 weeks, but disappeared from unsterilized soil in only 3 to 6 weeks. Other tests have shown that 2, 4-D may remain in soil under field conditions for as long as eleven weeks (59). Colmer (42) found that 2 or 4 pounds per acre of 2, 4-D did not decrease the population of Azotobacter, a nitrogen-fixing soil bacterium. Soil moisture conditions most favorable for biological activity favor most rapid disappearance of growth regulators.

Many investigators have noted a lowering of carbohydrate reserve following treatment of plants with 2, 4-D and other growth-regulating compounds (28, 194, 108, 145, 143). Rhodes (178) found that 2-methyl-4-chlorophenoxyacetic acid brought about depletion of starch when sprayed on tomato cuttings kept six days in darkness in a mineral nutrient solution containing sucrose. Other cuttings, not treated, still had an abundance of starch at the end of this time. Penfound and Minyard (170), using shade and full sunlight, corroborated these findings. Mitchell (144), working with naphthalene-acetic acid and naphthalene acetamide, found a similar lowering in carbohydrate content of treated bean plants. He said, "Carbohydrate metabolism and transport was so affected as finally to result in a deficiency in the amount of carbohydrate available in the portions of the plants where growth was stimulated for a period following treatment."

The lowering of carbohydrate reserves following treatment with 2, 4-D and other such substances is apparently due to the hydrolysis of starch and other complex storage forms into soluble sugars that can be translocated (143, 108). Hullinger (98), studying the effect of 2, 4-D on corn, reported a decrease in dry weight but an increase in reducing sugars and sucrose. Wort (232) found that sugar values fell continuously after treatment of plants with 2, 4-D. However, levels of all sugars are not necessarily lowered at the same rate. Weller et al. (223) treated kidney bean plants with 2, 4-D. There was no apparent loss of reducing sugars, but non-reducing sugars were depleted. Mitchell and Stuart (146) also found a decrease in sugar content. Mobilization of reserve carbohydrates, from an insoluble storage form to a soluble form, has been noted in nearly every plant part following treatment with 2, 4-D (194, 108, 98).

The effectiveness of growth regulators varies with the age of the plants. In young, fast-growing plants all or most available carbohydrates are used in synthesis of new tissues, and only a very small amount is translocated. Hence there is a relatively small translocation of growth regulators applied to young plant parts. Barrons (14) said, "Experience has shown that spraying before the leaves have fully developed will often result in inferior kills." Plants past maturity and approaching dormancy or senescence may also be hard to kill because of decreased translocation and the high content of carbohydrate reserves.

Opinions are divided as to whether growth regulators kill plants by depleting carbohydrates. Mitchell and Brown (141) treated morning glory plants (Ipomoea lacunosa L.) and said, "Readily available carbohydrates were essentially depleted within a period of three weeks in

plants that were growing vigorously...." They concluded, "Depletion of the carbohydrates was apparently a factor which resulted in death of the plants." Rasmussen (174) postulated that "...the action on dandelion of 2,4-D in herbicidial concentrations is principally the destruction of carbohydrate reserves, with most of the loss being accounted for by increased respiration." Rhodes (178) found that, "The phytocidal effect of 2-methyl-4-chlorophenoxyacetic acid may be due to the depletion of the available carbohydrates in the roots."

In opposition to this line of thought, a number of investigators believe that death occurs before reserves are depleted (229, 196). Eames (62) suggested that death of treated plants is due to disruption of the phloem. If reserves are not depleted before some other response to treatment kills the plants, i.e., disruption of the cortex or interruption of the phloem, exhaustion of reserves is likely to be the cause of death.

Effects of Growth Regulators on Respiration

Many workers have come to the conclusion that aerobically respiring plants, e.g., those using free oxygen, are more sensitive to treatment than those respiring anaerobically (31, 194, 195).[1] In practically all cases studied, growth regulators caused an increase in CO_2 evolution and a decrease in O_2 uptake, indicating an increase in anaerobic respiration.

West and Henderson (225), working with lupine seedling roots, found that 2,4-D renders oxygen unavailable and stimulates anaerobic respiration. Hsueh and Lou (96) found anaerobic respiration in rice to be stimulated by 2,4-D. Worth and McCabe (234), working with microorganisms, came to the same conclusion. They said, "...organisms which require free oxygen for respiration may be 'smothered' by 2,4-D," and that "organisms capable of anaerobic respiration only are not affected to any significant degree by 2,4-D." When Taylor (205) applied 2,4-D to plants in an oxygen-free atmosphere, treated plants evolved more CO_2 than untreated plants. Interference with respiratory enzymes (oxidases) may be the cause of this particular action of growth substances.

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[1] Apparent respiration may be measured by accounting for the oxygen uptake of tissue or plants, the carbon dioxide release, or both. When the ratio of oxygen uptake to carbon dioxide release approaches unity, aerobic respiration is usually dominant. However, when the proportion of carbon dioxide released is greater, anaerobic respiration is generally dominant.

Chemicals may stimulate respiration in reproductive plant parts as well as in vegetative parts (84).

Reserve carbohydrates mobilized by growth regulators are largely utilized in increased respiration (174, 194). Loomis (120) reported that respiration increases immediately after application of 2,4-D, and then declines. If plants are actively growing and are manufacturing all the food used in the increased respiration, there will be no lowering of reserves. However, if photosynthesis is not rapid enough to supply the foods used by increased respiration, death will ensue in a matter of days or weeks, depending upon the length of time needed to exhaust available reserves. Growth regulators may stimulate respiration proportionately more in starved than in unstarved tissue (105).

Meyer and Anderson (139) suggest several reasons why forced anaerobic respiration, sometimes called fermentation, may harm plants. The energy output is lower than in aerobic respiration and may not be enough to maintain cell processes. Also, substances like oxalic acid, citric acid, and lactic acid may accumulate to toxic levels under prolonged anaerobic conditions.

Translocation of Growth Regulators in Plants

Translocation of growth regulators is closely associated with movement of organic foods (73, 14). If foods are not present, or if they are not translocated, there will be no movement of the stimulus. Rohrbaugh and Rice (182) applied 2,4-D to "destarched" leaves in the dark, where food manufacture was nil. They found that the chemical was not translocated unless sugar was also applied to the leaves.

Under any circumstances, movement is not rapid. Only 3 percent of the chemical applied to velvet mesquite seedlings moved downward within 4 days (24). This makes the advice of Blair and Glendening (23) especially valuable. They recommend that when kill of dormant root-collar buds is desired, the chemical be applied as close to the base of a plant as possible.

Blair (22) suggested that failure of growth regulators to kill plants is due to insufficient absorption and translocation. If concentrations of the chemicals are excessively high, tissue may be killed at the point of application before the stimulus can be transmitted to other plant parts (118). Also, since movement is through the phloem, a living tissue, toxic amounts cannot be present at any instant (90).

Soluble carbohydrates tend to move toward regions of plants treated with growth substances (5, 200, 146). Since growth regulators move at the same time and in conjunction with carbohydrates, this may be one of the reasons for the low rate of translocation away from the point of application. This is consistent with the findings of Beevers and Gibbs (18) that the youngest tissues oxidize glucose more rapidly than older ones.

Difficulties in translocation may be the primary reason why growth regulators are comparatively ineffective on grasses. Fang and Butts (65) suggested that the intercalary meristems of grasses may serve as a series of blocks to movement of these compounds.

Hay and Thimann (89) found little or no translocation of growth regulators that had been applied as a basal spray. Death of tissues, at the point of spray application, resulted in death of the crown. The net effect was similar to that of a girdle. Sprouting from dormant root-collar buds seems probable unless the chemical is applied in such quantities that it flows down over these buds.

Seasonal Effects of Growth Regulators

The time for most efficient chemical control of plants coincides closely with the best time for burning or cutting. Arend (8) found that basal sprays of 2, 4-D and 2, 4, 5-T applied in late June, July, and August "following full leaf development" were more effective than those applied at any other season. Fisher et al. (67) stated that the best control with 2, 4, 5-T as an herbage spray "was obtained when treatments were made 45 to 90 days after mesquite first began to leaf out."

Other studies have generally shown growth regulators to be most effective during the same general time of the year. In tests of 2, 4, 5-T applied in frills on southern red oaks, spring applications gave by far the best crown kill.[2]/ Chaiken (38) observed that trees were killed more rapidly with 2, 4, 5-T frills and sprays just prior to leafing out. Campbell and Peevy (35, 36) found that "2, 4-D was most effective on trees in spring," particularly in April. Waldrip (213) noted that applications of 2, 4-D and 2, 4, 5-T to oaks and yaupon generally gave better kills in spring than in fall. The ammonium salt of 2, 4-D, used as a soil

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2/ Grano, C. X. 1953. Unpublished report on file at Southern Forest Experiment Station.

sterilant, controlled lawn weeds more effectively in May than in July (129). Late May and early June were the best times for applying growth regulators to Ribes (162). Kissinger and Hurd (107) found spring the best season to apply 2,4,5-T to sagebrush. Cornelius and Graham (46) found that late bloom is a better stage than early bloom for treating mountain buttercup with 2,4-D.

Although the basic mechanism of action is similar, all of the phenoxy compounds do not necessarily function most efficiently at the same phenological stages. In controlling big sagebrush it was found that low-volatile esters of 2,4-D and 2,4,5-T could be applied several weeks earlier than the high-volatile ones with equally good results (107).

When growth regulators are applied to dormant woody plants, they tend to accumulate in buds nearest the tip and are, in part, metabolized to other compounds before the start of spring growth (222). In any season, the chemical should be applied as close to the bud as possible, so as to obtain maximum accumulation of chemicals and kill (169).

Beatty (17) and McIlvain and Savage (136) point out that the best time to apply growth regulators is when the food supply is lowest. When reserves are low, depletion of carbohydrates and death are more likely to occur than when reserves are abundant. Rhodes (178) summarized the situation with this statement: "For perennial plants, conditions might be expected to be optimal for the application of MCPA [2-methyl-4-chlorophenoxyacetic acid] in late spring at a time when the first flush of growth is slowing down and before any appreciable new reserves of carbohydrate have been accumulated."

Adjuvants Used With Growth Regulators

Hitchcock and Zimmerman (94) stated that "...more effective general-purpose herbicides than those used to date are likely to contain more than one hormone, at least one toxicant [a contact poison such as pentachlorophenol], and additional adjuvants which are effective as wetting agents, solubilizers, penetrants, emulsifiers, and stickers." They used Benechlor, ammonium triocynate, ammonium sulfamate, diallyl maleate, and sodium bicarbonate in combination with 2,4-D: the combination gave a better kill than 2,4-D alone. Addition of a contact herbicide seemed to alter the permeability of the plant tissues and hastened the penetration of 2,4-D. Hance (83) used pentachlorophenol for this purpose. Zimmerman (235) demonstrated that penetration of growth regulators was aided by a flowing agent. Kelly and Avery (104) said, "In the presence of dinitrocresol, the stimulation of respiration

by 2, 4-D is additive." Other workers have also found that herbicides are more efficient in combination than singly (153, 125). Chemicals with potentialities for use in combinations should be freely tested. Only by bioassay on specific plants can the useful mixtures be determined.

There has been no general agreement as to the effectiveness of oil versus water carriers. In some cases oil emulsions have given the best results (156), while at other times water carriers have been equally effective (135). Oil seems always to be at least as good as water, and much of the time it is better.

Wolf et al. (229) found a strong interaction between the nitrogen level of the soil and the reaction of plants to 2, 4-D. They said, "The 2, 4-D treated plants receiving high-nitrogen solutions were dead 14 days after the 2, 4-D treatment was begun. At this time the medium-nitrogen plants showed severe chlorosis of leaves and stems, and splitting of the stems, whereas the low-nitrogen plants showed only mild chlorosis." The higher mortality of plants growing under high-nitrogen conditions may be due to the smaller amount of reserve carbohydrate to be depleted before hydrolysis of proteins and death take place. Frieberg and Clark (70) found a faster visible reaction in high-N plants than in low-N plants after treatment with 2, 4-D. Urea, used as a nitrogen source in foliage applications, was 50 percent absorbed within a few hours of application (29). Urea and 2, 4-D mix well in solution (128). This suggests the advisability of testing 2, 4-D and the other phen-oxyacetic compounds with some form of soluble nitrogen as an adjuvant. If death from 2, 4-D application occurs because of reserve depletion, the addition of immediately available nitrogen could shorten and intensify the period of carbohydrate mobilization.

Carbohydrates mobilized by sub-lethal amounts of 2, 4-D may be used in protein synthesis (176). Sell et al. (189) found a great increase of protein and amino acids in the stem tissue of plants treated with 2, 4-D. Greater amounts of nucleic acid, a protein precursor, have also been found in 2, 4-D-treated plants (175). An increase in the protein content of wheat seeds was noted after treatment with moderate amounts of 2, 4-D (64). Smith (194) applied 2, 4-D to bean plants and reported a marked accumulation of nitrogen in the meristematic regions, where protein-forming activity is intense.

CONCLUSIONS

1. Each spring, carbohydrate root reserves of grasses, herbs, and some trees are utilized in the vegetative growth of tops. Some woody plants may have enough food stored in stems and branches so that root reserves are not used in top growth.

2. Depletion of reserves continues until the photosynthetic area of leaves is large enough to furnish all carbohydrates required for growth.

3. Accumulation of root reserves then resumes, with the strongest period of accumulation taking place after maturation of the leaves. The largest reserve is found immediately prior to the end of the growing season.

4. Root growth, which also makes use of root reserves, can take place before, during, or after the main period of stem growth, depending upon the species.

5. During the dormant season, respiration causes a small but consistent loss of carbohydrate reserves in roots.

6. The annual march of carbohydrate reserves in some evergreen plants is reversed from that of top- and leaf-deciduous plants. Just prior to winter "dormancy" the roots of these plants have the smallest reserve of the entire year.

7. When a plant is defoliated, its root reserves are used in new top growth. Repeated defoliation can exhaust these reserves and kill the plant.

8. Top removal at seasons when root reserves are lowest is usually most effective in killing or weakening plants.

9. Low-nitrogen plants are usually less subject to reserve depletion than high-nitrogen plants.

10. The conditions most favorable for effective growth-regulator action are also those most favorable for good plant growth. The phytocides are translocated in association with carbohydrates.

11. Growth-regulator phytocides usually bring about a lowering in the amount of carbohydrate reserves, in addition to other effects.

12. Depletion of reserves may or may not be a cause of death after treatment with growth regulators, depending upon the amount of reserves and the rapidity of other plant responses to treatment.

13. The time of year for most efficient use of growth-regulator phytocides corresponds closely with the time of year for best eradication by top removal.

14. Used in combination, phytocides may be more effective than when used singly.

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