GREAT BASIN NATURALIST MEMOIR
ber 4 Brigham Young University

Soil-Plant-Animal Relationships Bearing on Revegetation and Land Reclamation in Nevada Deserts

GREAT BASIN NATURALIST

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No. 4 Brigham Young University, Provo, Utah 1980

PREFACE

Arthur Wallace[1]

Disturbed lands in desert ecosystems may require decades or centuries for natural return to their original condition. The fragile nature of deserts due to hostile climate partially explains this reclamation problem that investigators and developers are now faced with because of new governmental regulations.

This series of 30 papers relates to efforts to develop information which can be used either to prevent needless destruction of desert systems or to help restore disturbed lands to their original condition.

The studies involved cover a period of several years. Included were those years during which the International Biological Program, through the National Science Foundation, participated in desert ecosystems studies. The goals of that program included those of preservation, use, and restoration of deserts. The Nevada Operations Office of the Department of Energy (formerly Atomic Energy Commission and Energy Research and Development Administration) for the past decade has been vitally concerned about problems related to cleanup of some soils contaminated with radionuclides. Any cleanup operation would drastically alter natural ecosystems, possibly resulting in problems more difficult to solve than the original ones. Ongoing environmental and ecological studies at the Nevada Test Site have been made by members of our group since 1960.

The present 30 papers resulting from those studies can be divided into six groupings. The first group consists of a single paper that describes the amazing amount of variability encountered from year to year in the phenological events of the perennial plant species at the Nevada Test Site. This variability is of concern to those who would attempt to plant or manipulate any native desert species.

The second group of 11 papers describes how the plant communities are put together and explains some of their attributes. An understanding of plant sociological relationships in any ecosystem is prerequisite to any subsequent management. These papers concern

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distribution, interactions, turnover, habitat preferences, longevity, and other topics.

The third group of five papers relates to the carbon cycle under desert conditions. More specifically, the papers are concerned with below-ground aspects of plant communities in the desert areas studied. The below-ground contributions to biomass under desert conditions are poorly understood, and these studies, made with the help of the ^{14}carbon isotope, provide some answers. Information of the type contained in these five papers is particularly useful in land-cleanup procedures where soil is only partially removed.

The fourth group, consisting of six papers, relates to soil-plant relationships of desert vegetation and mineral composition of plants. Knowledge of soil preferences for plants is of prime importance for any attempt at revegetation and land reclamation. Almost as important is knowledge concerning the reasons for soil preferences for plants. These six papers provide some needed information in these areas. The introductory paper discusses the subject of how plants modify desert soils and redistribute mineral nutrients in them. This, without question, points out one of the most important problems associated with restoration of vegetation on disturbed desert land, that is, the destruction of the fertile spots in the desert created by long-time plant activity.

The fifth group, with four papers, concerns photosynthesis and transpiration processes. The first paper touches on the subject of C_3 and C_4 plants in regard to mechanisms of photosynthesis and shows relationships with water-use efficiency, which itself concerns transpiration. Attempts of man to manipulate and regulate deserts to achieve restoration or revegetation must consider the important aspects of adaptive and survival characteristics imparted by photosynthetic mechanisms, which in turn can be influenced by soil moisture conditions. These phenomena induce competitive effects among plant species. These studies contribute to understanding of deserts and will lead to more efficient management of them.

The sixth and last group (three papers) relates to practical aspects of desert revegetation. The first two papers of this group discuss the all-important interaction of native animals with new vegetation obtained either by natural reinvasion or by transplanting specimens onto disturbed lands. The problems caused by native animals and the one associated with "fertile islands" discussed in the fourth grouping of papers constitute formidable obstacles to certain types of desert land restoration. The final paper of the group and of the series is a summary chapter of the challenges involved in being able to comply with governmental regulations involved with southwestern deserts. Some synthesis of the total project is attempted in the final chapter.

Some important omissions from this series of 30 papers relate to soil characteristics, the nitrogen cycle, and water relationships. These were not purposely overlooked, and some publications on these topics have been made elsewhere as follows:

Farnsworth, R. B., E. M. Romney, and A. Wallace. 1978. Nitrogen fixation by microfloral-higher plant associations in arid to semiarid environments. Chapter 2, pages 17–19 *in* Nitrogen in desert ecosystems. US/IBP Synthesis Series 9. Dowden, Hutchinson & Ross, Inc., Stroudsburg, Pennsylvania.

Romney, E. M., V. Q. Hale, A. Wallace, O. R. Lunt, J. D. Childress, H. Kaaz, G. V. Alexander, J. E. Kinnear, and T. L. Ackerman. 1973. Some characteristics of soil and perennial vegetation in Northern Mojave Desert areas of the Nevada Test Site. UCLA 12-916.

Romney, E. M., A. Wallace, and R. B. Hunter. 1978. Plant response to nitrogen fertilization in the Northern Mojave Desert and its relationship to water manipulation. Chapter 16, pages 232–243 *in* Nitrogen in desert ecosystems. US/IBP Synthesis Series 9. Dowden, Hutchinson & Ross, Inc., Stroudsburg, Pennsylvania.

Wallace, A., E. M. Romney, and R. B. Hunter. 1978. Nitrogen cycle in the Northern Mojave Desert: implications and predictions. Chapter 14, pages 207–218 *in* Nitrogen in desert ecosystems. US/IBP Synthesis Series 9. Dowden, Hutchinson & Ross, Inc., Stroudsburg, Pennsylvania.

Wallace, A., E. M. Romney, G. E. Kleinkopf, and S. M. Soufi. 1978. Uptake of mineral forms of nitrogen by desert plants. Chapter 9, pages 130–151 *in* Nitrogen in desert ecosystems. US/IBP Synthesis Series 9. Dowden, Hutchinson & Ross, Inc., Stroudsburg, Pennsylvania.

A recent suggestion that desert sands catalyze photochemical formation of ammonia (Chem. Eng. News, 13 Nov. 1978) at rates of from 2 to 25 kg/ha per year could provide new insight into the desert nitrogen cycle.

A more complete listing of environmental

studies conducted previously at the Nevada Test Site is given in the Nevada Applied Ecology Group Publications. 1978. ORNL/EIS-127 and in T. P. O'Farrell and L. A. Emery. Ecology of the Nevada Test Site: A narrative summary and annotated bibliography. NVO 167. U.S. Department of Energy, Las Vegas, Nevada.

PHENOLOGY OF DESERT SHRUBS IN SOUTHERN NYE COUNTY, NEVADA

T. L. Ackerman[1], E. M. Romney[1], A. Wallace[1], and J. E. Kinnear[1]

ABSTRACT.— This study was done to document the variability in time of phenological events at different locations on the Nevada Test Site. Phenological events for desert shrubs were recorded, and rainfall and temperature data were gathered for four to six years at eight sites that are located within the northern Mojave Desert, the southern Great Basin Desert, and the transitional zone between them. Results have been graphically displayed to show the variability in phenological activity encountered during the study period and also to show the general correlation between these events and the environmental regime that triggered a particular phenological stage among different species. For a given location a four-to-six-week range in beginning events from year to year was common. In addition to the usual spring activity that normally followed winter rain and snow, most shrub species resumed new growth, and six species were observed to flower and fruit following rare summer or early fall rains. In comparison to surrounding locations, the closed drainage basins within the study area have lower temperatures at night that result in a delay of phenological events in most shrubs.

Faithful participants in the annual pilgrimage to view desert wildflowers and shrubs are cognizant of the extreme variability in time of phenological events at different desert locations. Each person visits his favorite location hoping that it will be a "good year" of splendorous color. Often he is rewarded, but some years fall short of expectations.

Phenological events are triggered mainly by rainfall and suitable temperature, although photoperiod is probably important for some species. The environmental regime that triggers a particular phenological stage varies among species: annual plants will not germinate and develop unless moisture and temperature conditions are suitable. Shrubs can survive long periods of low moisture and high or low temperature by dormancy or inactivity.

Desert areas are characterized by infrequent, low rainfall and extremes in temperature. Desert plants are adapted to these conditions. They are capable of a rapid growth response when conditions are favorable, and they rapidly become dormant or inactive when soil moisture is low or temperatures are extreme. This study reports phenology of desert shrubs on the Nevada Test Site in southern Nevada for eight sites in five valleys for a four-to-six-year period. The eight sites lie across a gradient within the northern Mojave Desert, the southern Great Basin, and the transition zone between them.

Blaisdell (1958), Wein and West (1972), and West and Gasto (1978) related environmental data to phenology in the Great Basin desert. Tueller et al. (1973) reported phenology for the Great Basin desert, and Beatley (1975) related climate to vegetation patterns across the Mojave/Great Basin desert transition of southern Nevada. Beatley (1974a) described the effects of rainfall and temperature on the distribution of *Larrea tridentata* (Sesse & Moc. ex DC.) Cov. on the Nevada Test Site, where *L. tridentata* is at its northern limits. Beatley (1974b) also developed a generalized word model relating phenology of desert plants to environmental triggers (temperature and rainfall) in the Mojave and transition desert portions of the Nevada Test Site.

The purpose of this study was to determine the influence of environmental factors on the phenology of desert shrubs along the transition from the Mojave Desert to the Great Basin desert. This study was part of a project to determine the climatic factors that cause the vegetative composition to change across this area. Because of the wide year-to-year varia-

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bility in desert weather patterns, many more years of data probably will be required to derive a complete understanding of the climate-phenology relationships.

TABLE 1. Species for which phenology was recorded (common names in parentheses).

Acamptopappus shockleyi A. Gray (Goldenhead)
Ambrosia dumosa (A. Gray) Payne (Bur-Sage)
Artemisia spinescens D. C. Eat. (Bud-Sage)
Artemisia tridentata Nutt. (Big Sagebrush)
Atriplex canescens (Pursh) Nutt. (Four-Winged Saltbrush)
Atriplex confertifolia (Torr. & Frem.) S. Wats. (Shadscale)
Ceratoides lanata (Pursh) J. T. Howell (Wintertat)
Coleogyne ramosissima Torr. (Blackbrush)
Ephedra nevadensis S. Wats. (Mormon Tea)
Eriogonum kearneyi Tidestr.
Grayia spinosa (Hook.) Moq. (Spiny Hop-Sage)
Hymenoclea salsola Torr. & Gray (Cheesebush)
Krameria parvifolia Benth. (Range Ratany)
Larrea tridentata (Sesse & Moc. ex DC.) Cov. (Creosote Bush)
Lycium andersonii A. Gray (Desert-Thorn)
Lycium pallidum Miers var. oligospermum C. L. Hitchc. (Box-Thorn)
Oryzopsis hymenoides (Roem. & Schult.) Ricker (Indian Rice-Grass)
Sphaeralcea ambigua A. Gray (Desert mallow)
Yucca schidigera Roezl ex Ortgies (Mojave Yucca)

MATERIALS AND METHODS

The species for which phenology was recorded are given in Table 1. Characteristics of the eight study sites are given in Table 2.

Phenological and environmental measurements were made weekly in the spring and early summer when plants were most active, and every two to four weeks during other seasons of the year. For each species we recorded the date of "first" observed leaf bud, leaf stage, flower bud, flower, fruit, seed or fruit fall, leaf fall, and dormancy. Within the time of these events there was a great variation from shrub to shrub.

Environmental data collected at the time of each observation included rainfall, maximum and minimum temperatures 30 cm aboveground and soil temperature at 15, 30, and 45 cm depths (Fenwall KA31L4 thermistors). Soil moisture was measured gravimetrically on samples taken at monthly intervals from 7 to 15 cm and 30 to 38 cm depths from 1968 to 1970. Thermocouple psychrometers (Wescor) were used from 1971 to 1973 for soil moisture measurements.

RESULTS AND DISCUSSION

Phenology, rainfall, and temperature data for the years 1968–1970 for the Mercury Val-

TABLE 2. Characteristics of the eight phenology study sites.

Site location	Elev. (m)	Distance N from Mercury Valley site	Desert type	Vegetation type	Years studied	Mean annual rainfall during study, mm
Rock Valley	1020	19.2 km (west)	Mojave	*Larrea-Ambrosia-Lycium*	1968–1973	172.5
Mercury Valley	1100		Mojave	*Larrea-Ambrosia-Lycium*	1968–1973	157.6
W. Frenchman Flat	1000	11.3 km	Mojave	*Larrea-Lycium-Ambrosia*	1968–1973	149.9
N. Frenchman Flat	950	20.1 km	Mojave	*Larrea-Atriplex canescens*	1968–1973	136.1
Yucca Flat 1	1200	33.6	Transitional	*Atriplex confertifolia-Lycium*	1969–1973	187.3
Yucca Flat 2	1225	33.6	Transitional	*Atriplex confertifolia-Lycium*	1969–1973	199.0
Yucca Flat 3	1300	33.6 km	Transitional	*Coleogyne-Yucca*	1969–1973	185.7
Pahute Mesa	1720	52.6 km	Great Basin	*Artemisia tridentata*	1970–1973	149.7

ley, Rock Valley, and Frenchman Flat sites have been reported (Wallace and Romney 1972). A correction should be made on page 286 of that report in the rainfall reported for Rock Valley in August 1969. The graph should show 0.35 cm of rain instead of 3.5 cm. The environmental data for these same sites for the years 1968 to 1970 were reported by Romney et al. 1973. Results for 1968–1973 for Rock Valley were reported by Ackerman and Bamberg (1974). Data for 1971 to 1973 are given in the diagrams of Figures 1–8 of this report. Four-to-six-year summaries of ranges of beginning dates of phenophases, with means, are given in Figures 9–16.

General Response to Moisture and Temperature

In this area the gentle winter and early spring (October to March) rains are more important for growth in the spring than the infrequent intense rains of summer. Usually from late November through early January the night air temperatures are near or below freezing, so most of the moisture from rains during this period is stored in the soil until favorable conditions permit budding and leafing out of plants. Low moisture or low temperatures may result in a delayed start of the growth season, i.e., phenology of each species is determined by the right moisture and temperature range. A case in point follows. Compared to 1971, the spring growth season for the early species was delayed one to three weeks by low temperatures in 1972, and that of 1973 was delayed two to four weeks by cool, cloudy, rainy weather from January through March.

For a given species, leafing out and flowering started earlier at Mercury Valley than at the Frenchman Flat sites (which are more than 11 km farther north). The timing varied from one week to more than a month in different years. Phenologies at the Frenchman Flat sites were usually the same as at Yucca Flat Station 3, which is 100 m higher in elevation and more than 13.5 km farther north, but sometimes plants were slower in leafing out and flowering. The Frenchman Flat sites had lower minimum spring air temperatures (means ranged from 2–5 C lower for all years) and higher maximum spring air temperatures (means ranged from 3–4 C higher for all years). The lower minimums are probably due to temperature inversion. The Yucca Flat Station 1, near Yucca Playa, generally was a week or more behind Station 3 in phenology. The latter site is 100 m higher in elevation upon the Bajada and 1.9 km SW of Station 1. Station 1 had lower minimum air temperatures (means ranged from 2.4 to 5.6 C for all years) probably again due to an inversion of cooler air. Beatley (1975) mentions that Frenchman Flat and Yucca Flat are both closed drainage basins with low temperature inversion layers. Flowers and flower buds of *Atriplex canescens* (Pursh) Nutt. at the north Frenchman Flat station appeared from 10 days to a month earlier than at the Pahute Mesa station, which is 770 m higher in elevation and 22.5 km farther north.

Effects of Summer Rains

Summer rains are local, infrequent, and of such intensity that much water runs off and little penetrates the soil to become available for plant growth, except in drainage channels. The effect of these rains varies depending on the amount and penetration in the soil. The Mojave Desert sites appeared to need rains greater than 2 cm in the summer for any effect on the shrubs. Shrubs responded after such rains in August 1972 at Mercury Valley, Rock Valley, Frenchman Flat, and Yucca Flat. Summer rains, however, can vary in the amounts of moisture deposited in different valleys. In 1970 north French Flat had 61 mm of rain in August; shrubs responded with new growth or breaking of dormancy, and some flowered. Other sites in west Frenchman Flat and sites in Rock Valley and Mercury Valley received less than 20 mm rain from the same storm system, and no shrubs responded. In 1971, only shrubs at Rock Valley (50 mm of rain) and Yucca Flat Station 1 (24 mm of rain) responded to summer rains. Active growth of shrubs after summer rains usually occurs over a two-to-three-week period. Plants usually then become inactive and deciduous species soon start dropping their leaves, probably because of the high summer air temperatures (above 35 C), which cause high evaporation and trans-

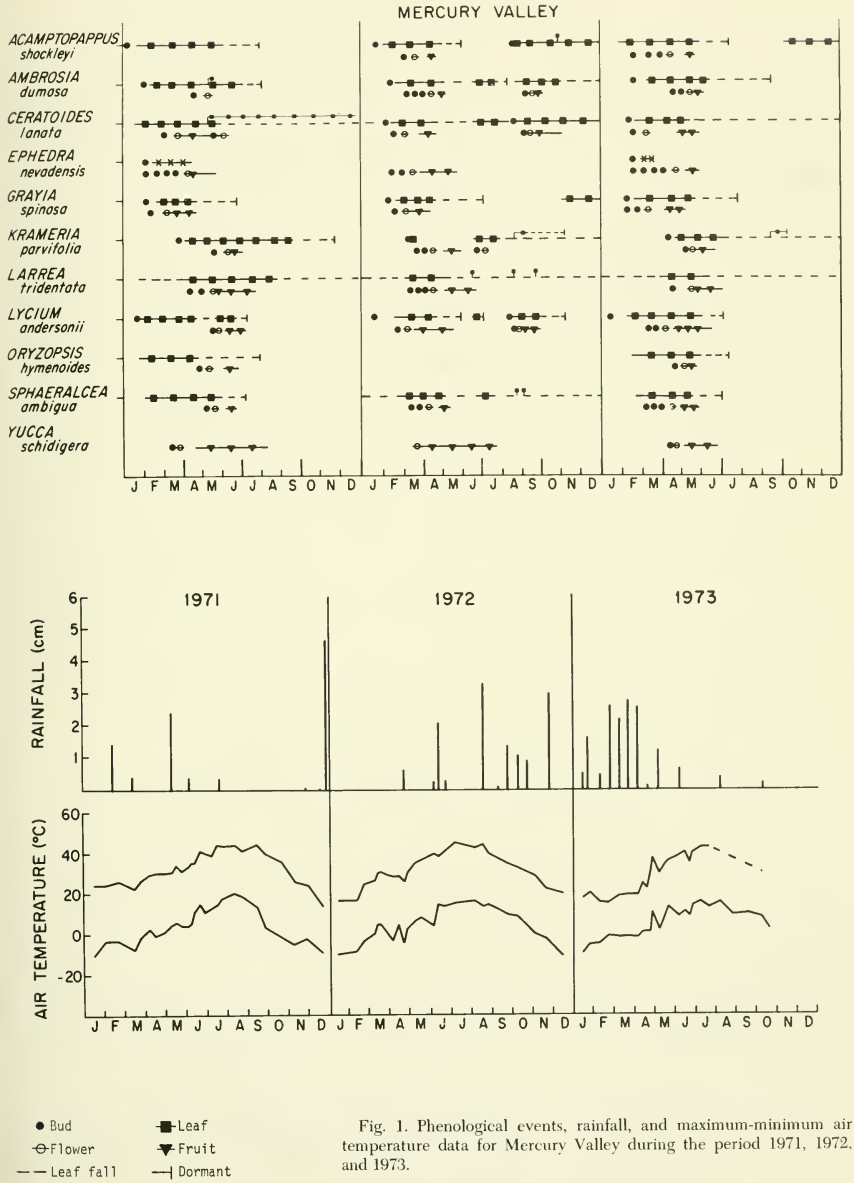
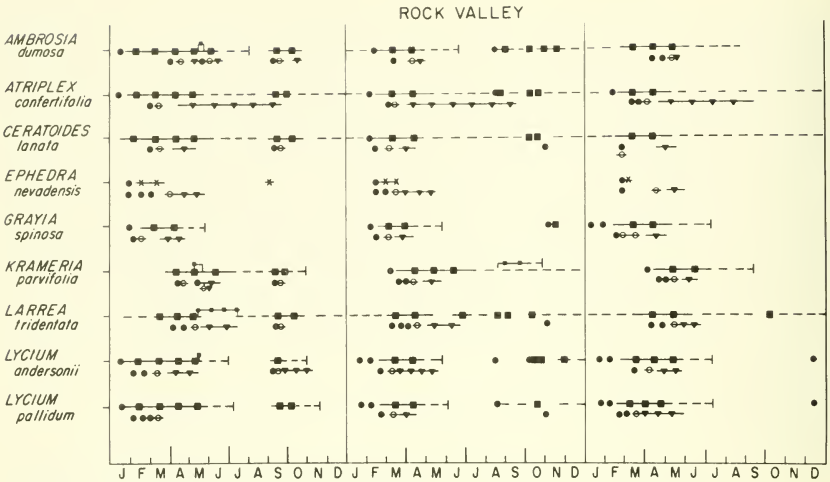
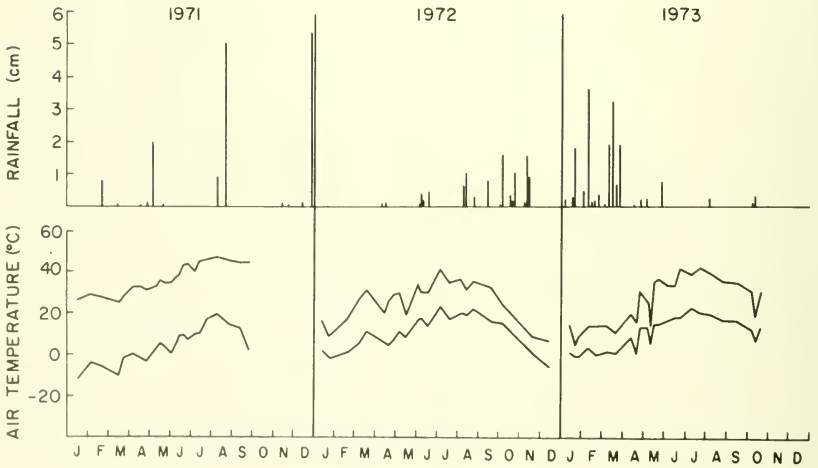


Fig. 1. Phenological events, rainfall, and maximum-minimum air temperature data for Mercury Valley during the period 1971, 1972, and 1973.





● Bud ■ Leaf
○ Flower ▼ Fruit
— — Leaf fall —| Dormant

Fig. 2. Phenological events, rainfall, and maximum-minimum air temperature data for Rock Valley during the period 1971, 1972, and 1973.

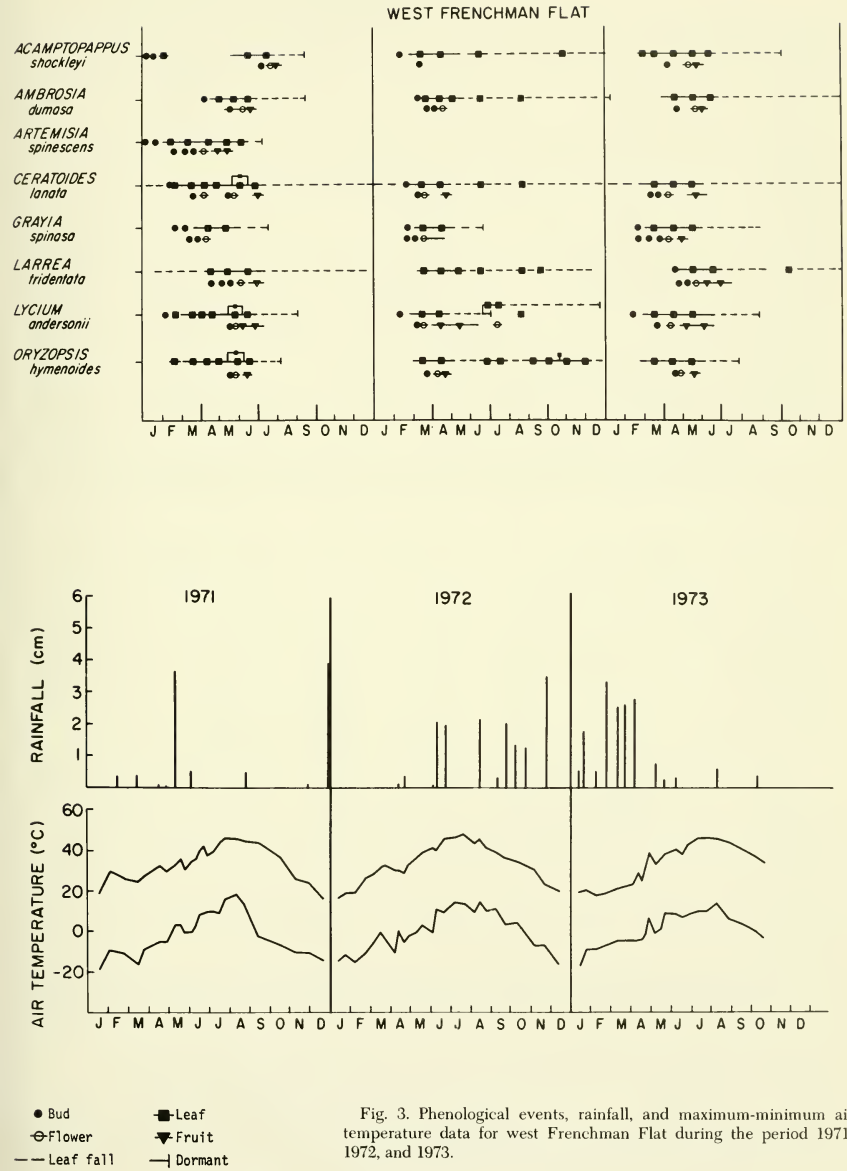
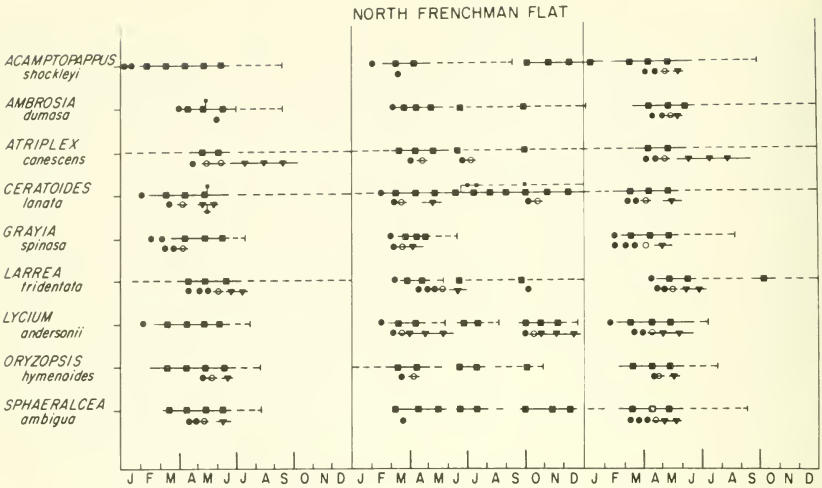
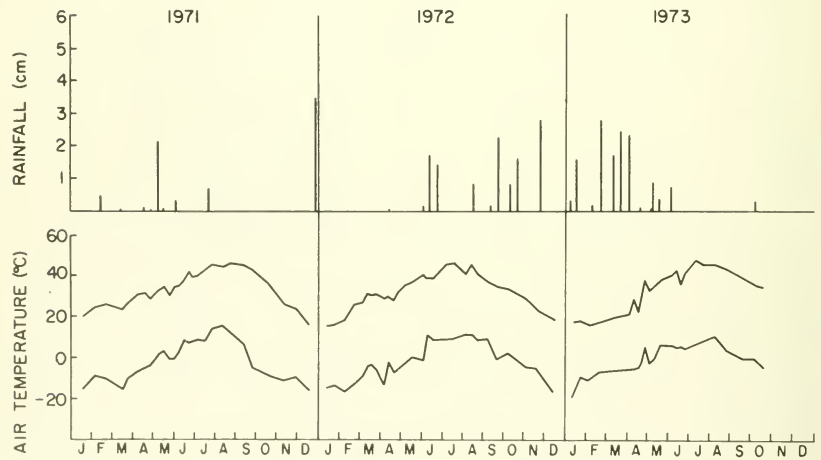


Fig. 3. Phenological events, rainfall, and maximum-minimum air temperature data for west Frenchman Flat during the period 1971, 1972, and 1973.





● Bud ■ Leaf
⊖ Flower ▼ Fruit
— — Leaf fall —| Dormant

Fig. 4. Phenological events, rainfall, and maximum-minimum air temperature data for north Frenchman Flat during the period 1971, 1972, and 1973.

piration rates. *Grayia spinosa* (Hook.) Moq. and *Artemisia spinescens* D. C. Eat. shrubs have not been observed to break dormancy after summer rains; they do, however, break dormancy after fall rains.

Different Species Response

Each species has a temperature range in which it will grow if adequate soil moisture is present. The two *Lycium* species were the

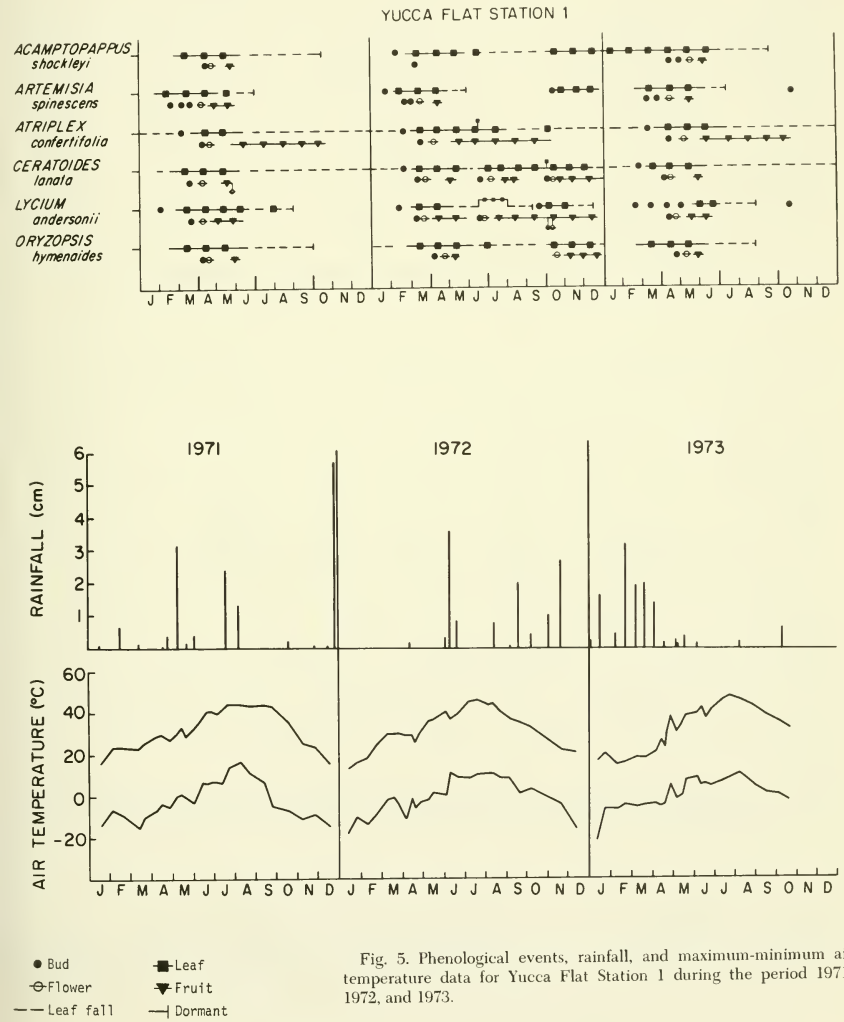
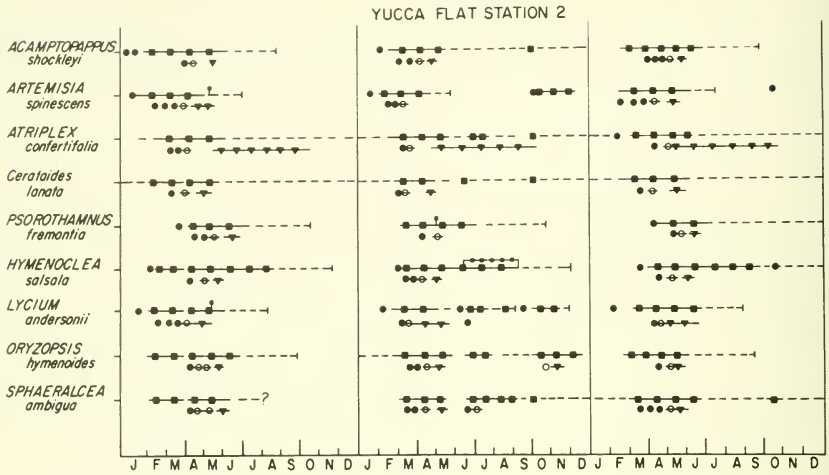
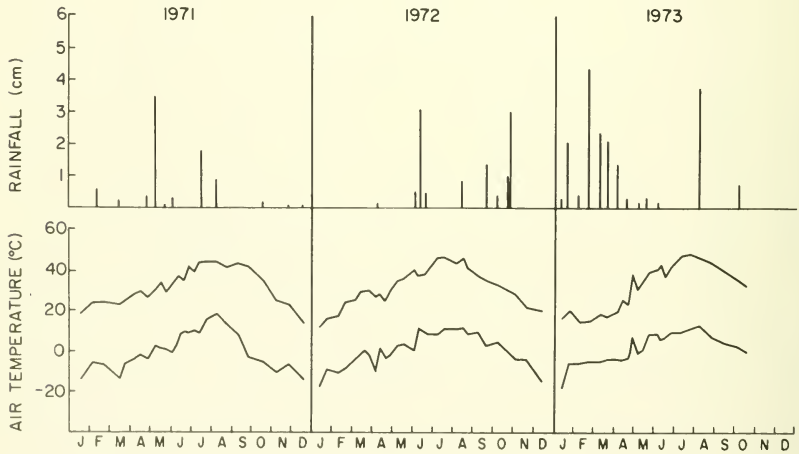


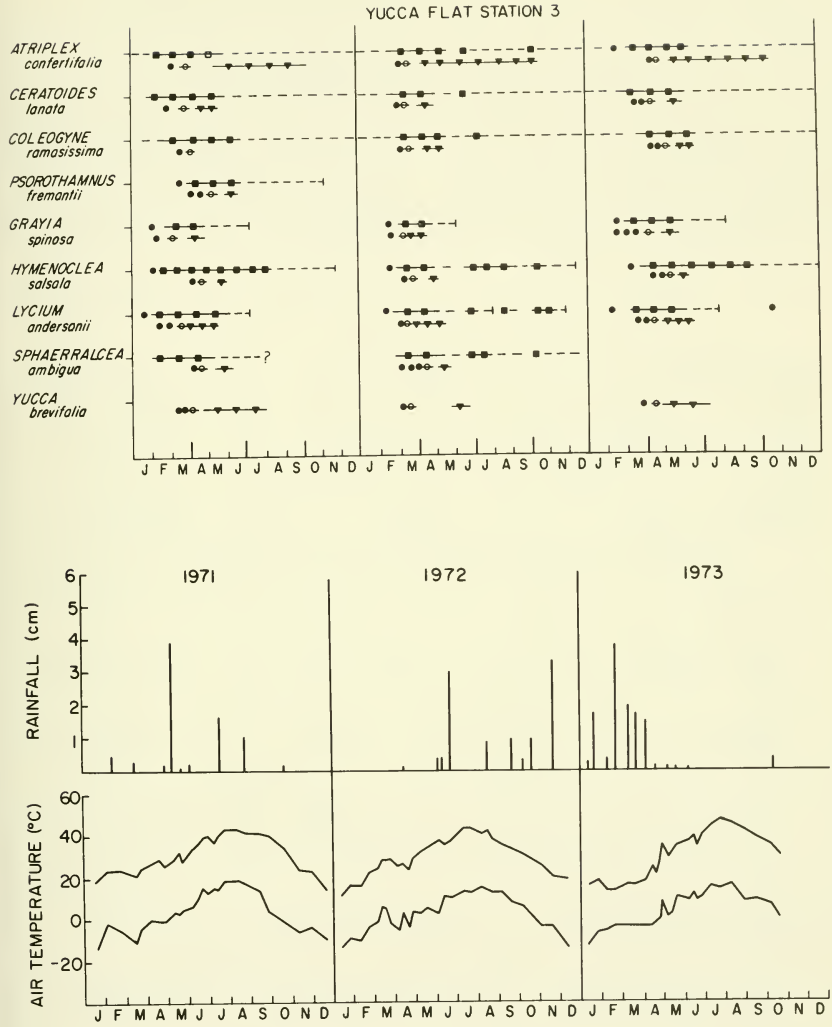
Fig. 5. Phenological events, rainfall, and maximum-minimum air temperature data for Yucca Flat Station 1 during the period 1971, 1972, and 1973.





● Bud ■ Leaf
⊖ Flower ▼ Fruit
— — Leaf fall —| Dormant

Fig. 6. Phenological events, rainfall, and maximum-minimum air temperature data for Yucca Flat Station 2 during the period 1971, 1972, and 1973.



● Bud ■ Leaf
⊖ Flower ▼ Fruit
— — Leaf fall ⊣ Dormant

Fig. 7. Phenological events, rainfall, and maximum-minimum air temperature data for Yucca Flat Station 3 during the period 1971, 1972, and 1973.

first to break dormancy, and this occurred when night air temperatures were around freezing and maximum air temperatures averaged 15 C (Ackerman and Bamberg 1974). *Krameria parvifolia* Benth. was the last species to break dormancy in the spring in the Mojave Desert, and this occurred when maximum air temperatures were over 27 C and minimum air temperatures over 6 C (Ackerman and Bamberg 1974). *Krameria parvifolia* was never dormant in the summer, no matter how dry the soil. *Larrea tridentata* was the last species to flower (usually in May) in the Mojave Desert. Next to the last was *A. canescens*. Bamberg et al. (1975) found that *L. tridentata* and *K. parvifolia* in Rock Valley had net photosynthesis during the summer when their plant tissue water potentials were -65 bars and -72 bars, respectively. *Larrea tridentata* put out new leaves 4 October 1973, after maximum air temperatures of 25–34 C and minimum air temperatures of 10–15 C. There had been only one slight summer rain on 4 August of 2.3 mm.

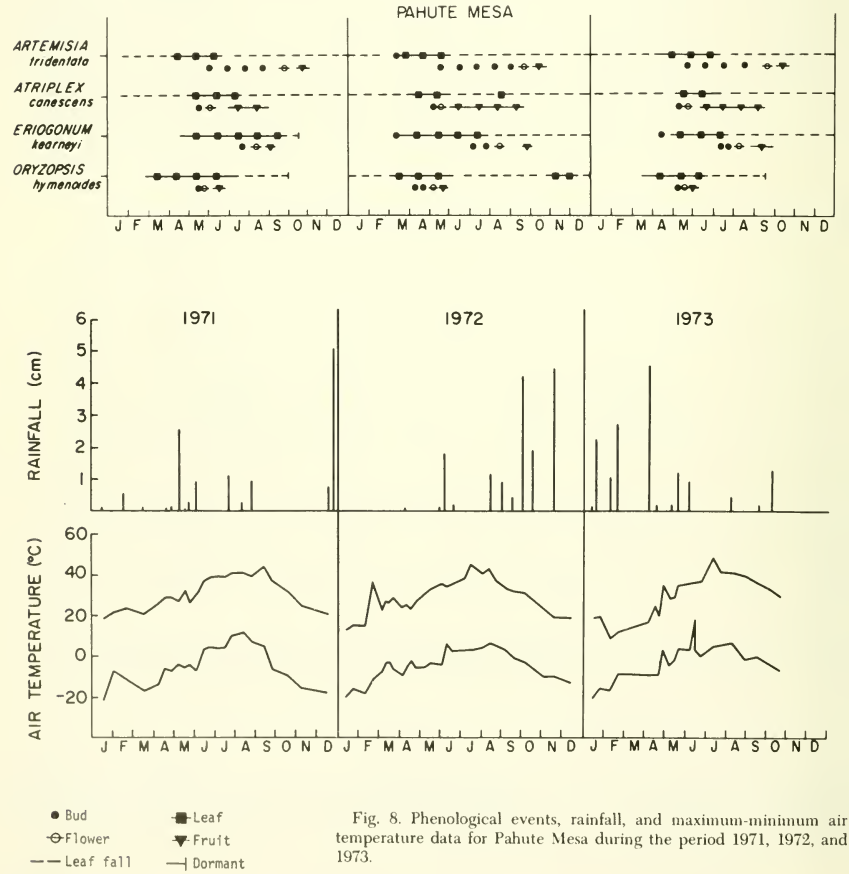


Fig. 8. Phenological events, rainfall, and maximum-minimum air temperature data for Pahute Mesa during the period 1971, 1972, and 1973.

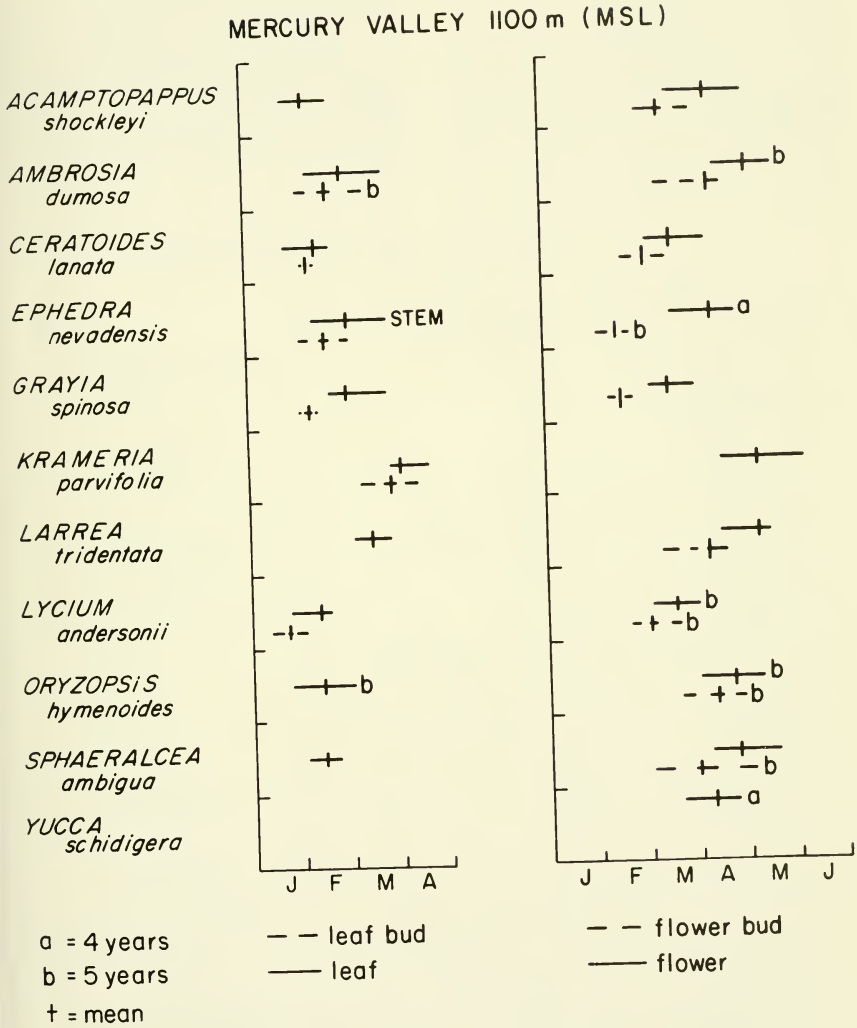


Fig. 9. Summaries of the average date and ranges of beginning dates of phenophases, at Mercury Valley during six years, except where otherwise noted.

Flowering

Shrub species which flowered only in the spring (probably determined by photoperiodism) are: *Ephedra nevadensis* S. Wats., *Atriplex confertifolia* (Torr. & Frem.) S. Wats., *Coleogyne ramosissima* Torr., *G. spinosa*, *Hymenoclea salsola* Torr. & Gray., *Psorothamnus fremontii* (Torr.) Barneby, and *Yucca schidigera* Roezl ex Ortgies. *Artemisia tridentata* Nutt. flowered only in the fall. Species that flowered anytime during the spring, summer, and fall, if they received enough rain, were: *Larrea tridentata*, *Ceratoides lanata* (Pursh) J. T. Howell, *Lycium andersonii* A. Gray, and *Ambrosia dumosa* (A. Gray) Payne. *Lycium pallidum* Miers var. oligospermum C. L. Hitchc. produced flower buds after the fall rains of 1972. *Oryzopsis hymenoides* (Roem. & Schult.) Ricker pro-

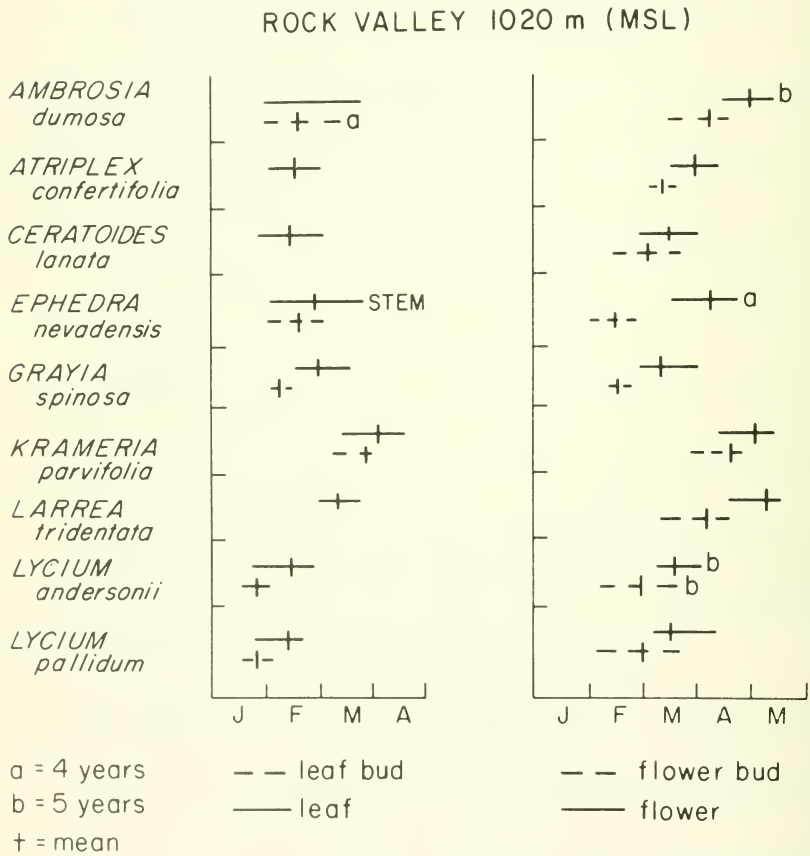


Fig. 10. Summaries of the average date and ranges of beginning dates of phenophases, at Rock Valley during six years, except where otherwise noted.

duced flowers after rains in the fall of 1972 at Yucca Flat Station 1, as well as in the spring, but not after summer rains, which probably indicates it needs lower temperatures to flower than are present in the summer.

The amount of moisture in the soil at the start of the spring growth period seemed to determine initial flowering response. Lack of moisture at this time resulted in a species producing few or no flowers. For example, at north Frenchman Flat in 1971, where the lowest rainfall was recorded in the spring for all areas and all years, *Lycium andersonii*, *Ambrosia dumosa*, and *Acamptopappus shockleyi* A. Gray produced no flowers. Moisture later in the spring growing season may result in either renewed growth or late flowering or reflowering. In 1971 at west Frenchman Flat, *L. andersonii* and *O. hymenoides*, which usually produce flower buds in February or March, did not produce any until after a May rain of 37 mm. *Lycium andersonii* in Mercury Valley also had the same delayed flowering. This May rain caused *Ceratoides lanata* to reflower at both places. In Rock Valley it caused reflowering in *A. dumosa* and *Krameria parvifolia*.

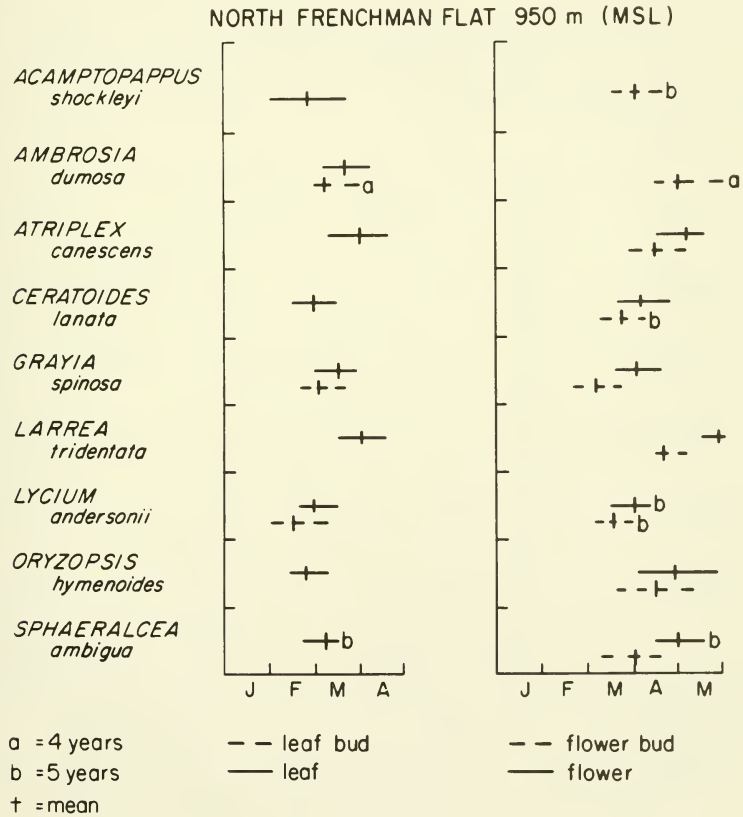


Fig. 11. Summaries of the average date and ranges of beginning dates of phenophases, at north Frenchman Flat during six years, except where otherwise noted.

Dormancy

Dormancy in desert shrubs is a complex phenomenon involving physiological changes, drought, and temperature responses. As the growing season progresses to early summer, soil moisture is depleted by rapid evaporation and transpiration as daily air and soil temperatures rise. During this time deciduous shrubs start to shed their leaves and soon became dormant. An interaction of high temperatures and low soil moisture probably results in summer dormancy for some species. *Artemisia spinescens* and *Grayia spinosa* always became dormant when daytime air temperatures were over 40 C, and they did not break dormancy even after summer rains. Wallace and Romney (1972) found that *G. spinosa* would break dormancy only after a low temperature period (5 C or less) or after an application of gibberellin. Dormancy in *G. spinosa* is probably induced by an internal physiological mechanism triggered by either heat or photoperiod. In 1972, *G. spinosa*

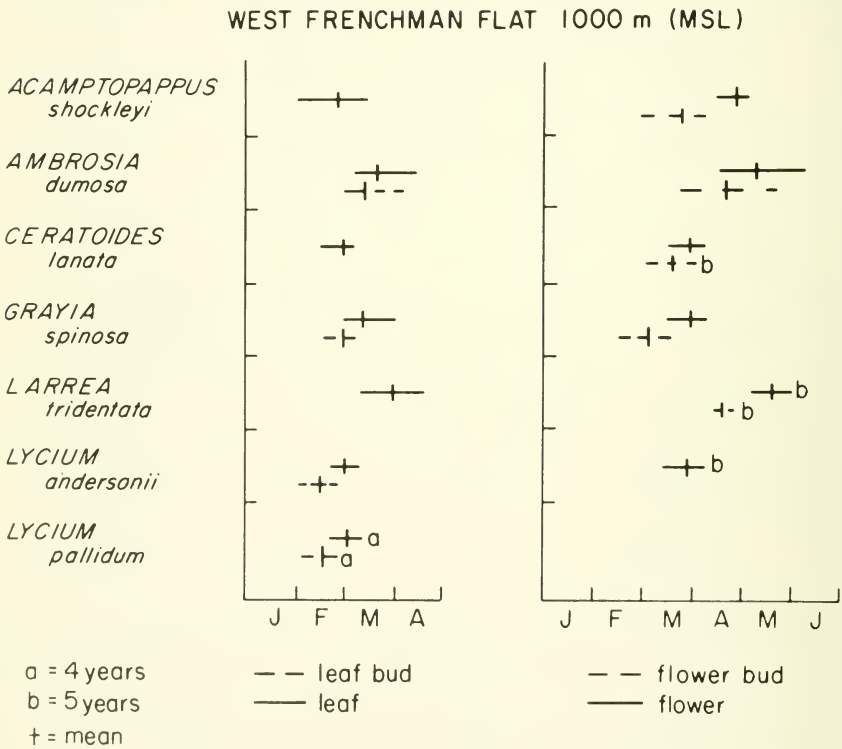


Fig. 12. Summaries of the average date and ranges of beginning dates of phenophases, at west Frenchman Flat during six years, except where otherwise noted.

broke dormancy on 10 November after fall rains when night air temperatures were below 0 C. *Artemisia spinescens* always broke dormancy after fall rains. *Krameria parvifolia* started going dormant in the fall only when air temperatures fell below 4 C at night. In addition to having a heat dormancy period in the summer, some species can have an induced dormancy during the winter because freezing night temperatures kill their leaves. This happened to *Ambrosia dumosa* during the winter of 1968 in Rock Valley and Mercury Valley, in 1970 and 1972 at north Frenchman Flat, and in 1972 at west Frenchman Flat, when all of its leaves froze. This species escaped the freeze during the winter of 1972 in Mercury Valley and Rock Valley. Leaves of *Lycium andersonii* were killed on 14 December 1972, at Yucca Flat Station 3, but not in Rock Valley. *Ephedra nevadensis* has only small scalelike leaves, so it is difficult to determine when it is physiologically active. This shrub, however, grows new stems after summer and fall rains and has a stem color change from green to brown during periods of apparent inactivity.

Shrub species that never drop all leaves (therefore, are considered evergreens) and which put out new growth after spring, summer, and fall rains are *Larrea tridentata*, *Coleogyne ramosissima*, *Atriplex canescens*, *A. confertifolia*, *Ceratoides lanata*, and *Artemisia tridentata*. During the dry summer with high air temperatures, these shrubs may lose most of their leaves but they retain enough to justify their classification as evergreen. In extreme conditions during dry years, either stem ends or complete stems died in some specimens of these species.

A partial summary of some of the phenolo-

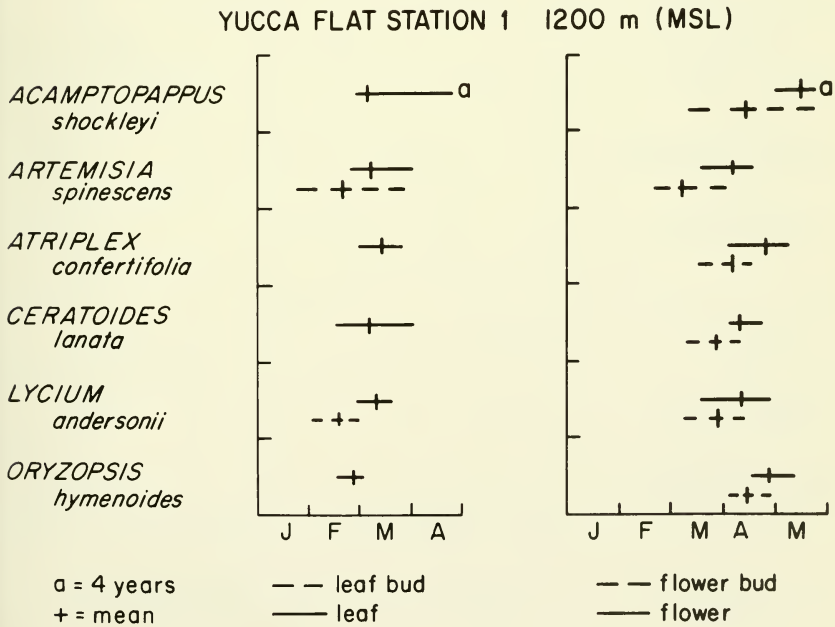


Fig. 13. Summaries of the average date and ranges of beginning dates of phenophases, at Yucca Flat Station 1 during six years, except where otherwise noted.

gical events for six plant species at three locations is shown in Figure 17. The three locations were chosen from the eight studied to show a north-south gradient of 33.6 km in which considerable variation in climate occurs. There is also an elevation gradient of 1100 to 1200 m going from south to north for the three locations.

Phenological events occurred progressively later for *Acamptopappus shockleyi* in the three sites going from south to north. The range in appearance was a month or more. *Lycium andersonii* was the only other of the six species chosen that appeared in all three locations, and its behavior was similar to that of *A. shockleyi* except that this species had a somewhat narrower range in appearance of leaf buds, leaves, flower buds, and flowers. *Lycium andersonii* seems to be under less precise control than *A. shockleyi* because of its narrow range for appearance of new leaves, etc. This species will also leaf out

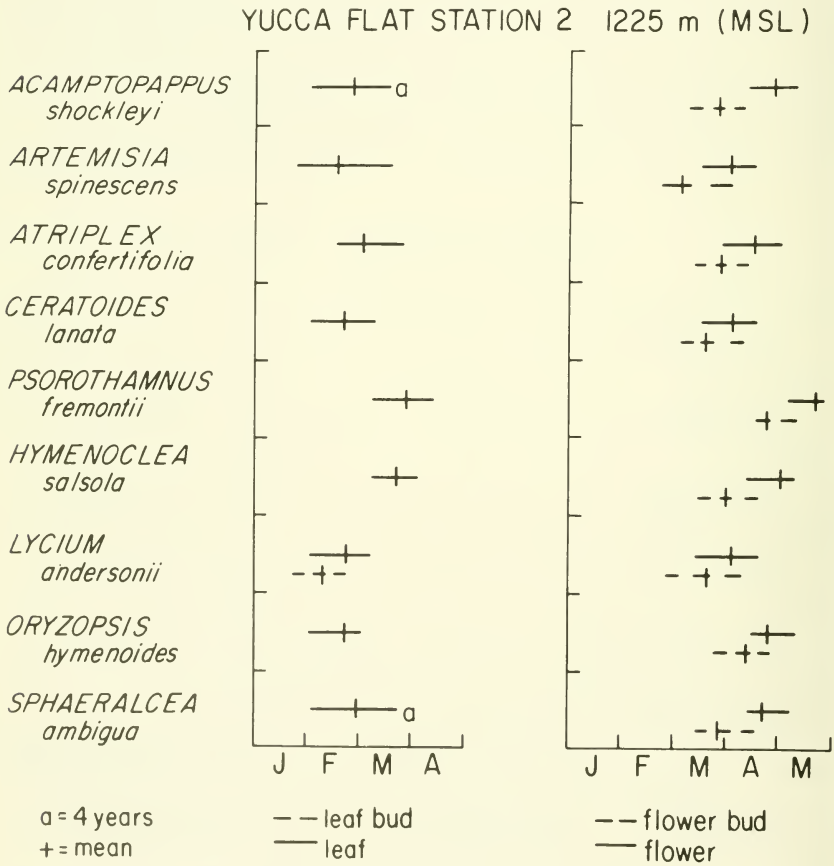


Fig. 14. Summaries of the average date and ranges of beginning dates of phenophases, at Yucca Flat Station 2 during six years, except where otherwise noted.

late in the summer when rains occur after plants have entered dormancy.

Three of the six species shown in Figure 17 occur in only two of the three stations. They are absent at Yucca Flat Station 1, the northernmost of the three stations. Two of the three species are considered as Mojave Desert species (*Ambrosia dumosa* and *Larrea tridentata*). The third, *Grayia spinosa*, grows in both southern Great Basin and northern Mojave deserts. Leaves and flowers appeared later on *L. tridentata* than on *A. dumosa*. The range of events was more narrow for *L. tridentata* than for *A. dumosa*. *Grayia spinosa* leaves also appeared earlier than *L. tridentata*, and its flowers appeared earlier than both *L. tridentata* and *A. dumosa*.

Krameria parvifolia occurred only at the southernmost of the three stations. Its phenological events occurred late in comparison with other species at that site. It is of interest that species with late-phenological events

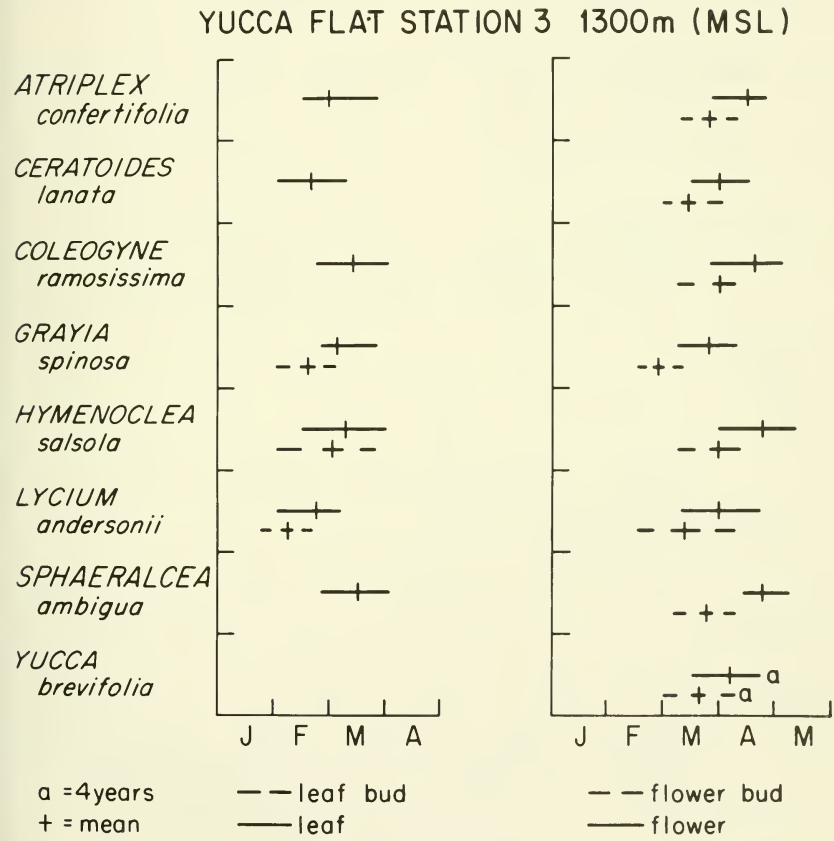


Fig. 15. Summaries of the average date and ranges of beginning dates of phenophases, at Yucca Flat Station 3 during six years, except where otherwise noted.

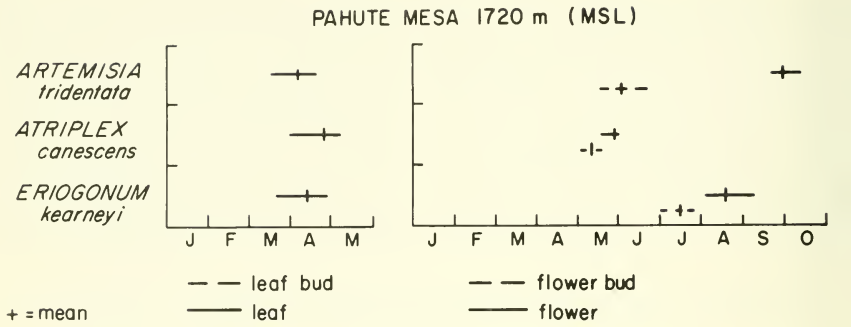


Fig. 16. Summaries of the average date and ranges of beginning dates of phenophases, at Pahute Mesa during six years.

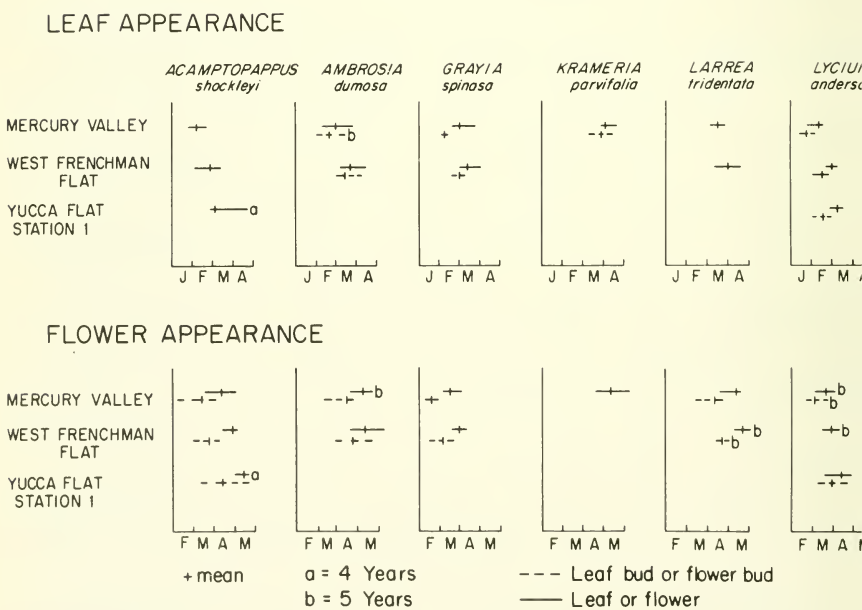


Fig. 17. Summary of phenological data for leaf and flower appearance for six of the plant species at three of the locations (Mercury Valley, west Frenchman Flat 13.3 km north of Mercury Valley, and Yucca Flat Station 1 33.6 km north of Mercury Valley). Six years of data are involved unless otherwise stated.

were absent from one or two of the sites. A wide amplitude is possibly characteristic of plants that leaf and flower under cool conditions.

ACKNOWLEDGMENT

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RESIDUAL EFFECTS OF SUPPLEMENTAL MOISTURE ON THE PLANT POPULATIONS OF PLOTS IN THE NORTHERN MOJAVE DESERT

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ABSTRACT.— Residual effects of sprinkle irrigation from 1968–1970 on populations of Mojave Desert shrub communities were observed in late 1974. The sprinkle-irrigated plots showed a residual increase in density of four species, but other species either failed to reproduce in significant numbers or lost all gains made during the years following treatment. The seven-year change for the irrigated plots was equivalent to a gain of 1178 perennial plants per ha, but the nonirrigated plots lost an average of 1050 plants per ha equivalent during the same period. The biomass gain after seven years was equivalent to 1000 kg/ha for irrigated plots and 310 for nonirrigated plots.

This study was made on plots which were established in early 1968 (Wallace and Romney 1972b). The objective of the work reported herein was to measure changes in biomass and density of plant species during a seven-year period that included three years of sprinkle irrigation followed by four years of natural rainfall.

MATERIALS AND METHODS

The site of the study area is Mercury, Nevada, near the waste water ponds from the local sewage processing system. Close proximity to a source of irrigation water was one prerequisite for the overall research program. The soil at this site is underlain by virtually impervious hardpan at depths varying from 15 to 75 cm. The thickness of the hardpan layer is usually greater than 10 cm. Perennial plants grow both singly and in clumps, separated by bare areas of desert soil. The size and spacing of the clumps are irregular. As many as 10 different species may grow together in a single clump.

A census was made in early spring of 1968 of all perennial plants (including shrubs, grasses, herbs, and their seedlings) in 25 circular experimental plots, each plot being 30.5 m in diameter. Each plant was categorized by species position and dimension analysis. This census effort involved more than 19,000 individual plants representing 28 different species.

A special method was devised for the purpose of locating and cataloging each plant in each plot. A permanent standpipe for mounting a surveyor's transit was installed at the center of each plot, with a marker located on magnetic north at a distance of 15.25 m. Orientation for each vegetational unit (clump) was the measured distance from the plot center to the vegetational unit center. The azimuth to each unit was measured from magnetic north (0°) to the center of the vegetational unit. The unit's greatest and smallest width and its species content were recorded. Each species within a unit was measured in like manner, and it was further identified by height. These data were recorded and transferred to punch cards for computer processing.

For both sprinkler-irrigated and control plots, the height and two widths of each shrub were recorded. From this information shrub volume and biomass were calculated using a dimension measurement regression line (Wallace and Romney 1972a). In November 1974, the census in several plots was repeated and dimensional measurements were also made. Abiotic data obtained from Rock Valley located about 20 km west of the study plots are given in Table 1.

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RESULTS AND DISCUSSION

Changes induced by supplemental sprinkle irrigation were still apparent four years after the last application of water. In particular, there remained a net gain in population on the watered plots and a net loss on the dry plots after seven years (Table 2).

Population changes depended significantly on species. *Ceratoides lanata* (Pursh) had a much more rapid turnover during the course of the study than did most other species, losing 12 to 36 percent of its population on dry plots while its population increased on irrigated plots. *Sphaeralcea ambigua* A. Gray lost an even higher proportion, 55 to 93 percent on the dry plots, and nearly as much, 47 to 79 percent, on watered plots. Grazing rabbits are especially hard on *S. ambigua*, a preferred food source; therefore, survival data may have little relationship to earlier plot treatment.

The population of *Acamptopappus shockleyi* A. Gray increased on all plots, watered or not. Gains on dry plots ranged from 6 to 55 percent and on watered plots from 8 to 105 percent.

Numbers of *Ambrosia dumosa* (A. Gray) Payne increased slightly on watered plots and decreased slightly on dry plots. This species, especially, showed visible increases in new biomass in response to supplemental moisture.

Other species generally showed negligible changes in populations. For several species this low turnover rate is considered to be significant. *Krameria parvifolia* Benth., *Ephedra funerea* Cov. & Mort., *Ephedra nevadensis* S. Wats., *Yucca schidigera* Roezl ex Ortgies, and *Salazaria mexicana* Torr. must have unusually long life spans if our data are representative. Similarly, their invasion of disturbed sites must be very slow.

The biomass changes by species on these plots are reported in Table 3. In the seven-year period of this study, biomass increased more than 25 percent for 6 species and decreased more than 25 percent for 2 species

TABLE 1. Abiotic factors in the general environs of study plots. Data are from the USWB station located in Rock Valley about 20 km west of Mercury.

	1963–1964	1964–1965	1965–1966	1966–1967	1967–1968	1968–1969	1969–1970	1970–1971	1971–1972	1972–1973	1973–1974	1974–1975	1975–1976
						Rainfall, mm (USWB)							
July	–	20.0	9.1	6.8	7.1	51.0	3.0	10.2	0.5	0.0	0.0	25.6	0.0
August	19.5	8.1	4.8	3.8	50.2	4.3	1.0	22.6	33.3	21.3	3.5	1.6	1.8
September	34.2	0.0	0.0	1.0	10.1	0.0	0.2	0.0	0.0	9.0	0.0	0.0	5.3
October	3.3	4.0	0.7	0.2	0.0	11.6	7.0	0.0	0.0	34.2	3.6	25.9	0.5
November	18.5	3.3	49.2	2.5	28.1	2.5	17.0	19.6	0.8	32.8	15.0	2.5	4.8
December	0.7	0.0	62.4	10.6	10.1	4.3	0.0	17.8	40.6	0.0	12.4	32.8	0.0
January	1.7	10.6	8.8	32.7	1.5	68.0	0.3	0.0	0.0	26.0	34.0	1.0	0.0
February	0.7	0.0	16.2	0.0	30.7	103.0	44.5	8.1	0.0	49.3	1.0	4.1	39.0
March	0.6	12.4	1.2	0.0	7.3	19.0	14.0	1.3	0.0	73.3	6.4	26.9	1.0
April	10.6	60.1	0.7	26.6	5.5	3.0	1.8	0.0	2.0	14.9	0.0	9.9	6.0
May	0.5	2.2	8.6	5.3	0.0	1.0	0.0	19.3	0.0	10.7	0.2	8.1	3.0
June	5.0	0.5	1.7	11.4	3.0	12.0	0.8	0.0	14.5	4.2	0.0	0.0	0.0
						Mean air temperatures (C) USWB							
July	27.2	28.6	26.6	29.1	29.7	28.6	31.1	29.2	30.1	34.1	31.5	30.1	30.6
August	25.8	27.2	25.2	29.4	31.4	23.6	29.7	30.3	28.3	28.3	29.5	28.7	28.8
September	23.9	23.3	21.1	23.6	23.9	23.0	24.9	22.2	22.1	23.9	24.5	27.5	26.8
October	20.5	20.5	19.4	16.9	18.6	17.5	17.2	14.7	16.7	14.2	18.0	17.5	20.3
November	12.7	9.2	12.5	11.1	13.3	12.8	8.4	9.5	6.1	7.9	9.0	10.2	9.0
December	8.3	8.4	8.6	6.1	2.0	3.3	8.4	2.6	4.6	3.8	6.5	3.8	8.1
January	5.3	8.4	0.6	6.7	7.3	7.8	6.4	8.8	6.5	3.1	2.7	4.3	7.8
February	5.0	8.3	5.9	9.5	12.2	2.8	10.3	6.1	11.7	6.9	7.4	5.7	8.9
March	11.7	11.4	13.1	10.8	13.1	13.6	13.1	9.0	19.3	7.0	12.3	7.6	9.9
April	13.6	15.0	16.1	10.0	13.6	16.7	11.1	12.0	16.1	14.4	14.4	9.4	13.1
May	16.4	17.2	20.8	19.4	20.3	22.7	19.2	14.9	20.8	22.5	22.6	19.5	22.8
June	23.0	21.4	25.0	20.3	25.8	23.6	23.9	24.3	27.1	28.0	29.5	26.6	–

on nonirrigated plots. The number of species showing gains in the seven years for the nonirrigated plots was 9; 2 showed neither gain nor loss and 5 species showed losses. In the seven-year study period, biomass increased more than 25 percent for 14 species and decreased more than 25 percent in one species

on the irrigated plots. The number of speci showing gains in seven years for the irrigate plants was 16, and one showing a loss. It very clear that irrigation in 1968, 1969, ar 1970 resulted in a larger biomass persisti through 1974 ($P < 0.01$ by significance test

TABLE 2. Population changes (averages and standard errors of the means for three plots) in sprinkle-irrigated pl and control plots over a seven-year period (1968–1974). Water was applied to plots in 1968, 1969, and 1970. Area each plot is 730 m^2.

	Start		New		Died		Seven-year change		
Species	Number	SEM	Number	SEM	Number	SEM	Number	SEM	Perce
			Irrigated plots						
A. shockleyi	198	57.7	88.7	19.0	35.0	16.2	+53.7	19.3	+26
A. dumosa	178	3.7	16.3	4.4	4.3	1.2	+12.0	5.5	+6
A. confertifolia	15.3	7.9	1.7	1.7	9.3	4.8	−7.7	4.6	−50
Cactus spp.	3.3	1.5	2.0	1.5	0.0	0.0	+2.0	1.5	+60
C. lanata	129.3	34.9	54.3	23.3	24.7	11.6	+29.7	14.5	+23
C. ramosissima	1.0	1.0	0.0	0.0	0.7	0.7	−0.7	0.7	−70
E. funerea	21.0	7.9	2.0	2.0	0.3	0.3	+1.7	1.7	+8
E. nevadensis	26.3	7.2	3.0	0.6	1.0	0.0	+2.0	0.6	+7
G. spinosa	21.0	7.6	13.3	8.5	2.0	0.6	+11.3	8.1	+53
K. parvifolia	80.3	3.0	2.0	1.0	3.3	1.5	−1.3	2.4	−1
L. tridentata	45.7	8.9	0.7	0.3	1.7	0.3	−1.0	0.6	−2
L. fremontii	4.0	4.0	27.0	13.3	0.7	0.7	+26.3	13.3	+657
L. andersonii	60.3	6.4	1.0	0.6	0.7	0.6	+0.3	0.7	+0
M. tortifolia	9.3	6.4	10.0	2.7	1.3	1.3	+8.7	3.8	+93
M. spinescens	3.0	2.0	5.0	5.0	0.0	0.0	0.0	0.0	0
O. hymenoides	12.3	4.3	2.0	1.5	8.0	2.1	−6.0	1.2	−48
S. mexicana	5.7	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0
S. ambigua	72.3	14.7	22.7	16.3	71.0	28.2	−48.3	14.8	−66
S. pauciflora	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0
S. speciosa	0.7	0.7	3.0	0.6	0.3	0.3	+2.7	0.7	+385
Y. schidigera	6.7	0.9	0.7	0.3	0.0	0.0	+0.7	0.3	+10
			Nonirrigated plots						
A. shockleyi	61.0	17.2	21.0	2.3	11.3	5.2	+9.7	2.9	+15
A. dumosa	83.7	10.4	3.3	1.9	4.7	1.8	−1.3	0.9	−1
A. confertifolia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0
Cactus spp.	1.3	0.7	1.0	1.0	0.7	0.3	+0.3	0.9	+23
C. lanata	273.3	44.2	36.3	12.4	100.3	13.5	−64.0	25.5	−23
C. ramosissima	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0
E. funerea	3.7	1.9	1.3	0.3	0.0	0.0	+1.3	0.3	+35
E. nevadensis	4.0	3.1	2.3	0.9	0.0	0.0	+2.3	0.9	+57
G. spinosa	26.3	3.5	9.3	4.1	2.0	1.2	+7.3	2.9	+27
K. parvifolia	22.0	4.6	0.3	0.3	0.3	0.3	0.0	0.6	0
L. tridentata	50.0	10.7	1.0	1.0	1.3	0.9	−0.3	1.8	−0
L. fremontii	0.7	0.7	1.0	0.6	0.0	0.0	+1.0	0.6	142
L. andersonii	36.0	5.1	0.3	0.3	1.0	0.6	−0.7	0.9	−1
M. tortifolia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0
M. spinescens	0.7	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0
O. hymenoides	6.7	4.0	2.0	0.6	3.0	2.1	−1.0	1.5	−14
S. mexicana	9.0	3.7	0.0	0.0	0.7	0.7	−0.7	0.7	−7
S. ambigua	44.0	7.4	2.0	1.0	30.7	1.5	−28.7	0.7	−65
S. pauciflora	0.7	0.7	0.3	0.3	0.3	0.3	0.0	0.6	0
S. speciosa	20.7	8.1	4.3	1.4	5.7	2.3	−1.3	1.9	6
Y. schidigera	4.0	1.0	0.7	0.7	1.3	0.3	−0.7	0.3	−17

TABLE 3. Biomass and changes in kg/ha (averages and standard errors of the means for three plots) in sprinkle-rrigated and control plots over a seven-year period (1968–1974).

	1968		1974		Seven-year change		
Species	Mean	SEM	Mean	SEM	Mean	SEM	Percent
			Irrigated (n = 3)				
A. shockleyi	104.9	29.6	146.6	33.8	+ 41.7	11.7	+ 39.8
A. dumosa	328.1	66.1	560.9	64.3	+ 237.8	42.5	+ 72.5
A. confertifolia	38.5	22.8	74.4	59.6	+ 36.0	36.8	+ 93.7
C. lanata	152.0	56.0	310.8	111.0	158.8	57.0	+ 104.5
E. funerea	312.1	134.6	372.9	167.8	61.8	48.0	+ 19.8
E. nevadensis	41.1	11.4	68.2	13.4	+ 27.1	5.18	+ 66.0
G. spinosa	40.6	23.2	241.1	149.8	+ 200.5	126.6	+ 494.2
H. salsola	0.13	0.13	2.9	2.9	+ 2.8	2.8	+ 213.9
K. parvifolia	91.8	18.3	117.4	15.4	+ 25.8	4.2	+ 28.1
L. tridentata	211.8	86.5	289.2	133.0	+ 77.4	48.7	+ 36.6
L. fremontii	0.00		11.6	4.9	+ 11.6	4.9	+ ∞
L. andersonii	383.2	53.8	493.9	57.2	110.4	8.0	+ 28.8
M. spinescens	9.7	8.5	16.3	13.3	+ 6.5	4.9	+ 66.7
O. hymenoides	0.24	0.16	0.003	0.003	–0.24	0.16	–100
S. ambigua	2.2	0.44	2.52	1.47	0.28	1.7	+ 12.5
S. speciosa	0	0	0.07	0.07	+ 0.07	0.07	+ ∞
			Nonirrigated (n = 3)				
A. shockleyi	42.0	14.4	53.5	19.2	+ 11.4	4.8	27.2
A. dumosa	201.5	33.0	160.1	53.2	58.7	22.1	29.1
A. confertifolia	0	0	0		0		0.0
C. lanata	557.5	30.2	516.4	66.9	–41.1	37.6	–7.9
E. funerea	25.9	13.4	44.4	23.0	+ 18.5	9.7	+ 71.2
E. nevadensis	33.5	32.2	62.2	59.7	+ 27.8	27.5	+ 83.0
G. spinosa	59.2	18.7	108.8	42.9	+ 70.0	17.8	+ 118.0
H. salsola	0		0		0		0.0
K. parvifolia	44.3	14.4	51.5	15.9	+ 7.3	2.50	+ 16.4
L. tridentata	550.4	56.5	571.7	161.9	+ 120.3	32.6	+ 21.9
L. fremontii	0.03	0.03	0.45	0.27	+ 0.42	0.24	+ 1400
L. andersonii	334.3	30.1	372.9	27.6	+ 38.6	15.7	+ 11.5
M. spinescens	1.12	0.72	0.93	0.67	–0.19	1.0	–17.0
O. hymenoides	0.04	0.02	0		–0.04	0.02	–100
S. ambigua	1.81	0.27	0.31	0.04	–1.50	0.31	–82.9
S. speciosa	0.09	0.05	0.07	0.04	–0.02	0.03	–22.2

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THE PULSE HYPOTHESIS IN THE ESTABLISHMENT OF *ARTEMISIA* SEEDLINGS AT PAHUTE MESA, NEVADA

E. M. Romney[1], A. Wallace[1], and R. B. Hunter[1]

ABSTRACT.— New *Artemisia* seedlings are not established each year. Many that are established fail to survive be cause of unfavorable rainfall in succeeding years. A total of 184 young plants was examined for the number of annua growth rings to ascertain the year of establishment after all vegetation had been killed near the time of a nuclear tes event in 1965. The three most important recent years for establishment and survival of new seedlings (as of 1976 an based on a sample of 184 plants) were 1966 (9 percent), 1969 (29 percent), and 1973 (36 percent). A total of 2 percent was established in the other years from 1965 to 1976. These three years were also the years with high rainfal input during preceding winter and spring months. If old plants are killed, seeds germinate with much lower input of precipitation. Many seedlings germinated in 1968 at a site where old ones had been burned off even though th rainfall was not favorable. Plants of a given age varied greatly in size according to their competition. Seedlings ge minating in old stands grew little in comparison with those germinating in areas where old plants had been killec One exception was an area where intense competition occurred due to large numbers of new plants, resulting i growth restriction on all plants.

It is generally considered that favorable rainfall years are necessary for the establishment of perennial plants under desert conditions (Beatley 1975, Wallace and Romney 1972). There is some question about the need for more than one favorable year in succession for establishment of new plants, at least under some circumstances (Wallace and Romney 1972). Studies made of ages or size of desert perennial plants most often indicate a rather uniform distribution of the input of new perennial plants (El-Ghonemy et al. 1979, this volume). Such studies, however, are obscured by the fact that differences in shrub size tend to disappear after a few years. The present study was undertaken because data for precipitation for recent years are available for Pahute Mesa, and because *Artemisia* can be dated by counting annual growth rings (Ferguson 1960).

MATERIALS AND METHODS

The Pahute Mesa area of the Nevada Test Site is located at an elevation of about 2000 m. The predominant vegetation in many areas of it is *Artemisia tridentata* Nutt. an *Artemisia nova* A. Nels. (Beatley 1975, 1976) Revegetation studies following nuclear test ing have been conducted there previously and the age of many of the plants in stud plots is determined by knowledge of whe they germinated (Wallace and Romne 1972). The past 12 years of the history of th area is fairly well known. By 1976 some o the known seedlings had attained the size o many other plants in the population, eve though they were much younger. This infor mation was useful in determining the plant which should be sampled. On 15 July 1976, total of 184 plants was measured by dimen sion analysis using methods reported (Wal lace and Romney 1972), and then cut and ex amined for ring count (Ferguson 1960) Sampling was done at five different sites es tablished to track vegetation recovery fro the Palanquin and Cabriolet plowshare test (Rhoads et al. 1969). Dates of these nuclea tests were April 1965 and January 1968 Plant weight by dimension analysis was ca culated from the regression of weight = 3479V + 0.081. V is volume in m^3; weight i in g dry weight.

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RESULTS AND DISCUSSION

Seedlings that initially germinated in areas where vegetation was killed by the 1965 Palanquin test were essentially all destroyed in the drought of 1968. It was determined at that time that rabbits had eaten the plants in a desperate attempt for their own survival (Wallace and Romney 1972).

Results obtained from the 1976 sampling are presented in Table 1. The first year of most pronounced establishment of seedlings after disturbance was in 1969, except at Cabriolet where germination occurred one year earlier (1968). The Cabriolet event was in January 1968 and by spring and summer months the pressure of old plants using the available soil moisture was absent in the newly killed area. Fallout radiation destroyed nearby standing vegetation, but not the seed supply in soil. As a result, the old seeds were available for germination in the spring of 1968, when soil moisture became more plentiful due to death of the old plants.

The year 1969 was one of high rainfall in February, resulting in extensive germination

TABLE 1. Number, size, and age of 184 young *Artemisia* plants from Pahute Mesa according to dimensional measurements and annual ring counts.

	No. of plants	No. of rings	1976 mean above-ground dry wt per plant g dry weight	Coefficient of variation weight Percent	Year of germination
		Normal vegetation (control)			
	1	15	59.9	–	1961
	12	10	14.76	17.64	1966
	13	7	12.28	18.76	1969
	5	6	5.57	1.42	1970
	5	3	0.37	0.16	1973
	11	2	0.16	0.10	1974
Total	47	–	–	–	–
		Adjacent to roadside in control area			
	2	10	154.4	67.6	1966
	20	7	49.9	57.9	1969
	2	3	0.24	0.02	1973
	1	1	0.08		1975
Total	25	–	–	–	–
		Palanquin partially killed area (1965)			
	13	7	244.6	244.8	1969
	3	5	64.4	34.3	1971
	37	3	8.2	9.7	1973
	1	2	0.17	–	1974
Total	54	–	–	–	–
		Palanquin totally killed area (1965)			
	5	10	567.3	218.3	1966
	3	7	185.4	58.7	1969
	1	2	0.42	–	1974
	19	3	4.55	7.09	1973
	1	4	188.1	–	1972
Total	29	–	–	–	–
		Cabriolet totally killed area (1968)			
	22	8	7.82	2.18	1968
	4	7	7.88	2.27	1969
	3	3	8.10	2.15	1973
Total	29	–	–	–	–

of new seedlings that survived in large numbers. The years 1966, 1969, and 1973–74 were also good years for establishment of seedlings in both control and disturbed areas. Area 12 Mesa station recorded 24.7 cm of rainfall in the 1968–1969 season and 18 cm in the 1972–1973 season. The November and December rainfall for 1965 was about 9 cm, and the relatively cool spring months made 1966 a favorable year. Tueller and Clark (1976) reported similar precipitation data for the Pahute Mesa area.

Most seedlings established on a scraped roadside installed in 1965 were related to the high rainfall year of 1969.

The percentages of the total new plants for all areas for the three most important years were 9 (1966), 29 (1969), and 36 (1973). Results confirm the idea that new seedlings in this ecosystem truly come in pulses related either to rainfall or to disturbance that kills old plants and makes more favorable soil moisture for the seedlings.

The sizes of the plants in Table 1 are of considerable interest. They differ considerably for given ages, a fact related to natural competition in the environment. Even after 7 and 10 years, plants in old, nondisturbed areas were still small and had survived with difficulty. They were usually close to old plants even though in disturbed areas most germination was between old plants (Wallace and Romney 1972). These new plants may remain small until old ones die naturally. In disturbed areas plants of the same age were much larger, except in the Cabriolet area, where so many seedlings germinated that competition kept them small. Seedlings also remained small in the control area, where a normal stand of vegetation was present.

There seems to be a niche among old, established plants where new ones become established and await the chance to replace the older plants.

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THE ROLE OF PIONEER SPECIES IN REVEGETATION OF DISTURBED DESERT AREAS

A. Wallace[1] and E. M. Romney[1]

ABSTRACT.— The northern Mojave Desert, as are many deserts, is characterized in part by small "fertile islands" in which exist individual shrub clumps each containing two or more plants. These fertile sites promote characteristic organization of both plant and animal activity in the desert. Destruction of these fertile sites makes revegetation extremely difficult because most seedlings germinate in these sites. Some pioneer species do, however, germinate and survive in the bare areas between the fertile sites. Four such species in the northern Mojave Desert are *Acamptopappus shockleyi* Gray, *Lepidium fremontii* Wats., *Sphaeralcea ambigua* Gray, and *Atriplex confertifolia* (Torr. & Frem.) Wats. These four species may have a role in starting new fertile islands.

MOJAVE DESERT CHARACTERISTICS

Revegetation procedures have been studied for some years by our group as a means of land reclamation of disturbed desert areas (Romney et al. 1971, Wallace and Romney 1975, 1976, Wallace and Romney, 1972a, 1972b, Wallace et al. 1977). The revegetation process is ordinarily slow, partly because the low rainfall in many years just will not support the establishment of new seedlings. A more important reason, however, is that the soil surface becomes organized as a result of prior plant activity, which results in microwatersheds. When this basic structure is destroyed, revegetation is extremely difficult to achieve either naturally or by manipulation.

Rainfall in the Mojave Desert is enough to support only a small amount of vegetation. An interesting feature of this desert is that just part of the soil surface (10 to 20 percent) is generally occupied by clumps of growing plants, and the other 80 percent to 90 percent serves mainly as watershed for the 10 to 20 percent of area supporting vegetation (Charley 1972, Romney et al. 1977, Garcia-Moya and McKell 1970). The land surface structure has been in place for decades, or centuries (Wallace and Romney 1972b), and has resulted in the soil beneath shrub clumps becoming very fertile areas that compare favorably with agricultural soils or those of grassland or forest ecosystems. The fertile areas are high in soil organic materials and available nutrients. Roots of plants in the fertile shrub clumps extend outward into the bare areas so that the soil moisture of the total land area potentially becomes available to the clumps. This system is much more efficient in sustaining plants than would a system in which the soil organic matter and readily available nutrients are uniformly distributed throughout the whole soil area but at a much lower level. That condition would result in much nitrogen deficiency.

ROLE OF PIONEER SHRUB SPECIES

The bare desert soil between shrub clumps generally is low in organic materials, and it characteristically has an unfavorable soil structure (less aeration) that tends to inhibit the establishment of new seedlings as well as the growth of other plants. Plant species that are capable of invading bare areas, especially when sufficient soil moisture is available, must be adapted to conditions related to poor soil structure and low organic matter.

When land disturbance destroys these fertile islands, it is well known that the natural revegetation problem is formidable (Wallace and Romney 1975, Wallace et al. 1977). There are some common perennial species in the northern Mojave Desert, however, which

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are able to pioneer by growing in the less fertile bare areas. Somehow they obtain sufficient N, but likely not through fixation of atmospheric N_2 (Hunter et al. 1977). They also obtain sufficient other nutrients, and they must be adapted to growth in soil of poor structure. Four such species are *Acamptopappus shockleyi* Gray, *Lepidium fremontii* Wats., *Sphaeralcea ambigua* Gray, and *Atriplex confertifolia* (Torr. & Frem.) Wats. The latter is ubiquitous in the western deserts. The encouragement of these species to grow on disturbed sites and studies to help make this possible are of urgent priority if revegetation required by land restoration legislation is to be achieved successfully in the northern Mojave Desert. It is of considerable importance to learn the nutrient status, water and oxygen requirements, and other ecological behavior characteristics of these four pioneer species that can help solve land reclamation problems.

A CASE HISTORY

In 1967, at Mercury, Nevada, a site 18 m in diameter was cleared of vegetation. The main crown roots of the plants were removed, but the fertile islands were not destroyed. The original purpose was to change the soil moisture status. After nine years, on 28 May 1976, the following numbers of invading perennial plants were counted in the plot: 14 *Ceratoides lanata* (Pursh) J. T. Howell, 4 *Lycium andersonii* A. Gray, 33 *A. shockleyi*, 26 *L. fremontii*, 4 *Ambrosia dumosa* (A. Gray) Payne, 3 *Machaeranthera tortifolia* (A. Gray) Cronq & Deck, 6 *Oryzopsis hymenoides* (Roem. & Schlt.) Ricker, 18 *S. ambigua*, 2 *Sitanion jubatum* J. G. Sm., and 2 *Krameria parvifolia* Benth. No *L. fremontii* were involved in the adjacent nondisturbed area, but plants for seed stock were located in a nearby wash. Seventy-three percent of the invading perennial plants in this plot were of the species defined above as pioneer species, and they were the only ones that were found in the original bare areas between the fertile islands. Most of the other new plants had invaded the old fertile island sites. Very few annuals were present in the nondisturbed areas, but some were found in the cleared area.

Atriplex confertifolia was not found at or near this particular test plot area, but we have observed its pioneering capabilities at a number of disturbed sites located elsewhere around the Nevada Test Site.

Acamptopappus shockleyi can survive for a number of years. On a particular site where 29 seedlings were observed eight years earlier, 21 of them were still surviving in 1976. The mortality after the eight years was 28 percent.

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FREQUENCY DISTRIBUTION OF NUMBERS OF PERENNIAL SHRUBS IN THE NORTHERN MOJAVE DESERT

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ABSTRACT.— Frequency distribution according to plant size as measured by dimensional analysis on different mathematical bases were determined for 10 common perennial plant species from Rock Valley in the northern Mojave Desert in Nevada. A total of 4282 individual plants was measured. The data provide information concerning the stability and prosperity of the natural vegetation as judged by the relative proportions of individuals in the size-class spectrum, as well as show graphically the relative abundance of the different species in the study area.

On the species level, the populations were close to normally distributed on the $\log_e$ basis, but with remarkably negative skewness due to better segregation of the small-sized individuals into many segmental units. On the arithmetic basis, three categories of frequency pattern were recognized, but all with marked positive skewness due to better segregation of large-sized individuals into many segmental units.

The feature common to all species studied is the preponderance of young individuals, which in many cases could have an abundance many times that of large individuals. The natural vegetation in Rock Valley, therefore, represents a reasonably active stage.

Assembling and comparing observations on the size classes of the component species of the natural vegetation are of primary concern for understanding the stability and prosperity of the vegetational cover. The size-class spectrum may also reveal valuable information in relation to climatic features occurring in the past during the early life of the existing vegetation, as well as the possible segregation of the individual species into two or more ecotypes.

The purpose of this study is to demonstrate through two different mathematical approaches the size-class frequency distribution for 10 common perennial species in the Rock Valley area of the northern Mojave Desert. The site involved and the original data obtained are part of the US/IBP Desert Biome studies.

MATERIAL AND METHODS

A system random-number-generating function (Wallace and Romney 1972) was used to select the random number pairs whose intersection identify sample location within the study area. A total of 4282 randomly selected individuals from 190 sampling plots (50 × 2 m) have been considered. The sampling technique was designed so that sampling points could be randomly distributed over the entire area. Each individual was identified by species and measured for height and width (mean of dimension) in 1971 at the Rock Valley IBP validation site. Calculations using these dimensional measurements were made to estimate shrub biomass, using previously calculated regression equations of dry weight on volume indices for the different species investigated (Wallace and Romney 1972).

Frequency for size-class distributions were made for shoot weights on arithmetic and $\log_e$ bases. A computer program was developed in which the class interval on the X axis and the scale of abundance on the Y axis were kept constant for all species, when data were illustrated on the $\log_e$ basis. In the arithmetically illustrated data, the scale on both Y and X axes varies from one species to the other.

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RESULTS AND DISCUSSION

The results of the size-class distribution on the $\log_e$ basis are illustrated graphically in Figure 1. The frequency distribution for all species is close to normal, with some negative skewness, the degree of which differs from

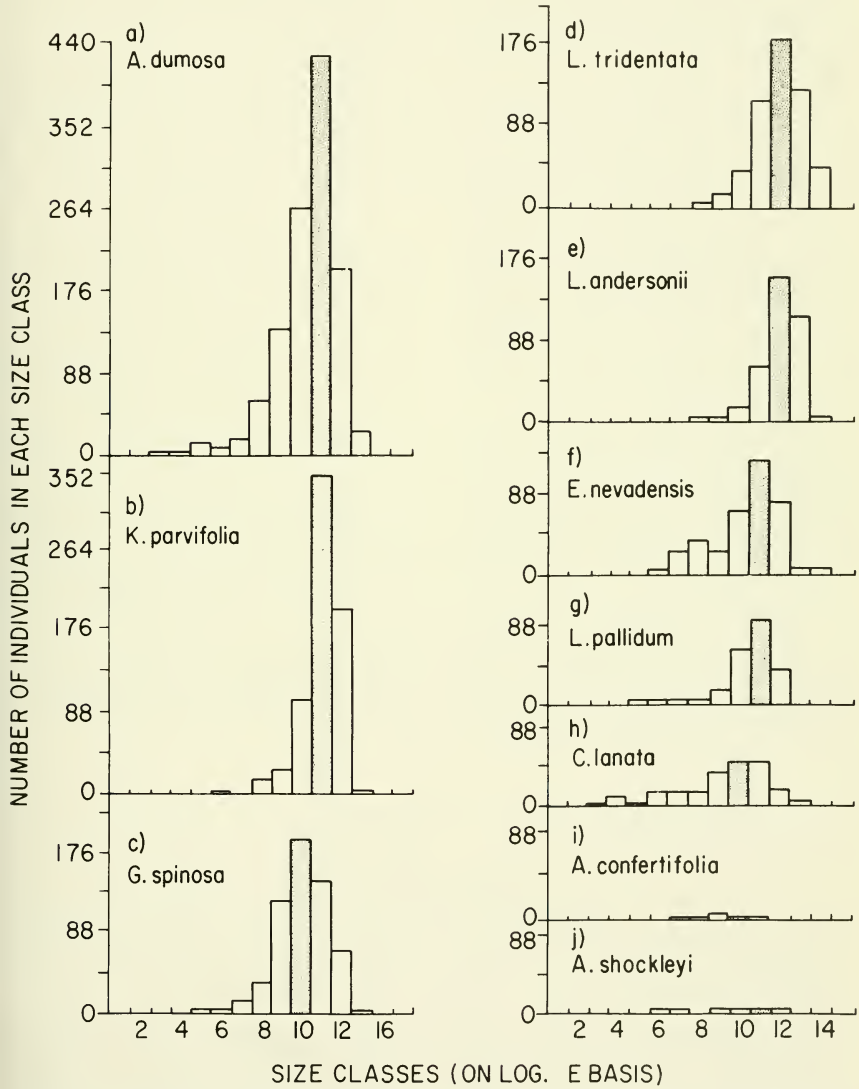

Fig. 1. Size distribution of 10 shrubs based on stem dry weights. Size-class interval is constant for all species (975 g). Shaded bars represent size classes with individuals that are close to the average weight for the species.

one species to the other. This negative skewness is attributed to the fact that the transformation of data into natural log values has resulted in a better segregation of small-sized individuals into many classes. This can be readily observed when examining the number of size classes on both sides of that class representing those individuals with an average weight.

The abundance of the different species, as reflected by their absolute frequencies (which represent one aspect of the species importance), is given in Table 1 and can also be easily detected from Figure 1. *Ambrosia dumosa* (A. Gray) Payne is the most frequent species in the study area. It has been randomly recorded 1183 times out of 4282 records for all species. The species poorly represented are those of *Atriplex confertifolia* (Torr. & Frem.) Wats. and *Acamptopappus shockleyi* Gray, represented by 37 and 23 individuals, respectively.

Another point of interest is the fact that all species exhibit large standard deviation (Table 1) relative to the means. This is particularly remarkable for *A. dumosa*, *Larrea tridentata* (Sesse & Moc. ex DC.) Cov., *Lycium pallidum* Miers, and *A. shockleyi*. The standard deviation for these species exceeds the mean weights.

The relation between size classes and the total number of individuals, irrespective of their taxonomic position, is given in Table 2. Examination of these data shows that size class 11 with $\log_e$ ranging from 4.169 to 5.144 (arithmetic range from 64.63 to 171.4 g/plant) embraces the higher number of individuals (1,361 out of 4,282). In this class, *A. dumosa*, *Krameria parvifolia* Benth., *Ephedra nevadensis* Wats., and *A. confertifolia* attain their maximum abundance. On either side of this class the number of individuals progressively decreases.

The preponderance of younger individuals, as reflected in Figure 1, is an indication of vitality and prosperity of the species; it is mostly due to successful germination of seeds and survival of seedlings. Rainfall in the year 1969 was above normal and may be the source of the seedlings observed.

The size-class frequency distribution on the arithmetic basis shows another interesting picture. Figure 2 shows the frequency distribution for three representative shrubs, each with its specific pattern. Three shapes of frequency distribution have been recognized; the j-shape, asymmetric, unimodal, positively skewed shape, and the asymmetric, polymodal shape. Categorizations of the 10 species studied according to the shape of their frequency distribution are given in Table 3. It is obvious that seven species belong to category (a), i.e., with a J-shape distribution. These species are *L. tridentata*, *A. dumosa*, *Grayia spinosa*, *E. nevadensis*, *Ceratoides lanata* (Pursh) J. T. Howell, *L. pallidum*, and *A. confertifolia*. A similar pattern of size-class distribution for *L. tridentata* has been previously demonstrated by Chew and Chew (1965). In category (b) the representative species are *K. parvifolia* and *L. andersonii*. Category (c) is represented by *A. shockleyi*.

TABLE 1. Some statistical attributes reflecting abundance and distribution of total stem weights (g) of ten Rock Valley shrubs (of 4282 randomly selected plants).

Species	No. of individuals	Mean weight of stem g/plant	Standard dev. g/plant	Maximum g/plant	Minimum g/plant	Range g/plant
Ambrosia dumosa	1183	108.7	111.0	952.6	0.1	952.5
Krameria parvifolia	732	136.4	96.9	682.6	1.0	681.6
Grayia spinosa	591	74.3	85.8	716.0	0.3	715.7
Larrea tridentata	517	437.9	454.1	3164.0	<0.1	3164.0
Ephedra nevadensis	387	119.1	202.9	2878.0	0.7	2877.0
Lycium andersonii	351	371.4	266.3	1470.0	8.2	1462.0
Ceratoides lanata	234	62.7	96.9	640.9	<0.1	640.9
Lycium pallidum	227	264.4	216.4	1041.0	1.2	1040.0
Atriplex confertifolia	37	33.7	32.8	107.2	2.1	105.2
Acamptopappus shockleyi	23	68.3	82.8	371.8	0.9	370.9

It should be mentioned, however, that the lack of unified scale (in all species) either on the X or Y axes for this type of mathematical representation of frequency distribution makes it impossible to draw quick comparison between species, particularly with regard to their abundance. However, it is clear from Figure 2 that, in contrast to Figure 1, the skewness is positive, which is an indication of better segregation of the large-sized individuals into more segmental units. Accordingly, the two approaches applied for the frequency distribution are rather useful and complementary.

The discontinuity represented in Figure 2 for *A. shockleyi* might indicate that the input of new seedlings of *A. shockleyi* in the ecosystem is not a steady process, but rather is affected by the prevailing environmental variables, particularly rainfall. However, the fact that this species is represented in this survey by relatively few individuals makes it difficult to explain precisely the causal factors behind its asymmetric polymodal frequency distribution.

A point of interest is that in these types of grouped frequency distributions the degree of skewness and even its sign are rather artifacts and are controlled by the scale of class interval. Accordingly, these two parameters cannot be considered as 100 percent reliable tools for reflecting the rate of new seedlings input (in a given ecosystem) versus the rate of loss of old individuals. More reliable information might be gained through comparing the actual number of individuals in the different size classes on either side of the average class and the rate of their input and loss. The fact that grouped frequency distributions, in contrast to regular frequency distributions, sacrifice some information for convenience by combining several score values in a single class interval has been reported by Welkowitz et al. (1971).

Another interesting point is the fact that a bimodal distribution often indicates that two major kinds of cases are concealed within the one distribution. In the present study the possibility of the presence of two or more ecotypes of a given specific population might be one of the causal factors for the presence of polymodal frequency distribution. Whether or not *A. shockleyi* consists of different ecotypes needs further detailed investigation, however. The possibility of the presence of two distinct ecotypes of *L. tridentata* in Rock Valley that differ on the basis of size and leaf characteristics has been previously reported by Wallace and Romney (1972). In the present set of data, the segregation of *L. triden-*

TABLE 2. Pooled distribution of individuals of 10 species in 15 size-classes (g per plant). The size classes that contain the most individuals of each species is identified.

Size	$\log_e$ range	Arithmetic range	Total no. of individuals	Maximum abundance size classes for the species
1	< -4.606	< 0.01	–	
2	-4.606 to -3.507	0.01 to 0.03	1	
3	-3.507 to -2.659	0.03 to 0.07	7	
4	-2.655 to -1.561	0.07 to 0.21	14	
5	-1.561 to -0.713	0.21 to 0.49	22	
6	-0.713 to 0.270	0.49 to 1.31	43	
7	0.270 to 1.244	1.31 to 3.47	91	
8	1.244 to 2.219	3.47 to 9.2	182	
9	2.219 to 3.194	9.2 to 24.39	399	
10	2.194 to 4.169	24.39 to 64.65	794	*Grayia spinosa*
11	4.169 to 5.144	64.65 to 171.4	1361	*Ambrosia dumosa, Krameria parvifolia, Ceratoides lanata, Ephedra nevadensis, Atriplex confertifolia*
12	5.144 to 6.119	171.4 to 456.5	999	*Larrea tridentata, Lycium andersonii*
13	6.119 to 7.094	456.5 to 1204.7	326	
14	7.094 to 8.069	1204.7 to 3193.9	43	
15	> 8.069	> 3193.9	–	

tata individuals into different ecotypes has not been demonstrated. The different ecotypes of *L. tridentata* might differ physiologically and consequently might be spatially separated. These two distinct life forms of *L. tridentata* are comparable in many respects to what is known in the Australian semiarid regions as Whip-stick and Bull Mallee, two distinctly different forms of *Eucalyptus oleoca* (Beadle 1948, El-Ghonemy 1967).

It can be concluded from the above study that the perennial species in the Rock Valley area are in a reasonably active state. The current rate of entrance of new plants into the ecosystem generally exceeds the rate of loss, with a consequent preponderance of younger individuals.

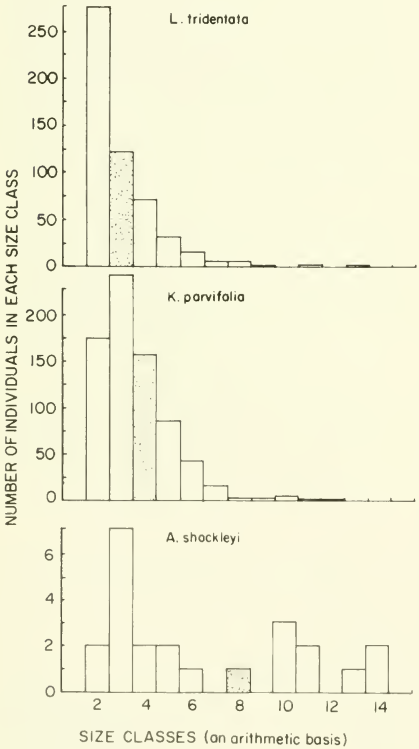

Fig. 2. Size distribution of three representative shrubs based on stem dry weight. Size-class intervals are 316 g for *Larrea tridentata*, 64.8 g for *Krameria parvifolia*, and 11.2 g for *Acamptopappus shockleyi*. Shaded bars represent size-classes that contain individuals that are close to the average weight for the species.

TABLE 3. Frequency distribution of individuals of different plant species in relation to the number included in the size class that includes individuals of the average weight for the species.

Species	Number of individuals in relation to their weight		
	<average	average	>average
(a) Species with J-shaped distribution curve			
Larrea tridentata	280	117	120
Ambrosia dumosa	632	314	237
Grayia spinosa	386	104	101
Ephedra nevadensis	232	58	97
Ceratoides lanata	163	7	64
Lycium pallidum	127	41	59
Atriplex confertifolia	20	4	13
(b) Species with unimodal, positively skewed distribution curve			
Krameria parvifolia	412	159	161
Lycium andersonii	165	87	99
(c) Species with asymmetric, polymodal distribution curve			
Acamptopappus shockleyi	14	1	8

ACKNOWLEDGMENTS

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FURTHER ATTRIBUTES OF THE PERENNIAL VEGETATION IN THE ROCK VALLEY AREA OF THE NORTHERN MOJAVE DESERT

S. A. Bamberg[1], A. Wallace[1], E. M. Romney[1], and R. E. Hunter[1]

ABSTRACT.— Above-ground and below-ground biomass, percent dead shrubs by species, and percent of dead stems of living species were determined for a site in the northern Mojave Desert.

The Rock Valley area of the northern Mojave Desert was used as an International Biological Program (IBP) Desert Biome validation site (Turner, 1973, 1975, 1976, Turner and McBrayer, 1974). Some characteristics of the vegetation of that site are described elsewhere in this volume (El-Ghonemy et al. 1980, Wallace et al. 1980). This report summarizes some other aspects of the vegetation on this site.

MATERIALS AND METHODS

The techniques used are described in El-Ghonemy et al. (1980). Briefly, a total of 4282 randomly selected individuals over the large plot was used in the study. Each individual was identified and subjected to various measurements. Live and dead plants were also determined.

Abiotic data for the area have been recorded in the validation site reports (Turner, 1973, 1975, 1976, Turner and McBrayer 1974). The zone numbers (20 to 25) are defined in these reports.

RESULTS AND DISCUSSION

The dry weight estimates of the stem portions of the plants are in Table 1. These values obtained by dimension analysis (Wallace and Romney 1972) were used to calculate the aboveground stem biomass per unit area (Table 2). The ratios of root/stem obtained in one study (Wallace et al. 1974) and corrected in another (Wallace et al. this volume 1980) were used to calculate below-ground standing biomass for this area (Table 2). The proportion of below-ground biomass is greater than that obtained with our ^{14}C techniques, but does seem to be a bit lower than that obtained for the Great Basin desert (Caldwell and Camp 1974).

Carcasses of many dead shrubs were on the site, and numbers were determined for each of the major perennial species as percent of dead to live plus dead numbers (Table 3). On the average, from 10 to 15 percent of the individuals for each species were dead. The correlation coefficients between the number of plants per hectare and percent dead were not significant (Table 3).

It can be expected that there is some relationship between the percent of dead plants and longevity. Species with the largest span of life most likely would show the smallest percentage of dead plants at any one time. This hypothesis, of course, would be in error if any species took several times as long as another to decompose and disappear from the system. This does not seem to be the case, however. *Ephedra nevadensis* S. Wats. and *Atriplex confertifolia* (Torr. & Frem.) S. Wats. then would have the shortest life span of the shrubs represented. *Krameria parvifolia* Benth. and *Lycium andersonii* A. Gray would have the longest.

Each plant had a portion of dead wood, and an estimate of it for each species is also given in Table 3. It is noted that half or more of the stems of *Ambrosia dumosa*, *Atriplex*

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confertifolia, Ceratoides lanata, and *Larrea tridentata* were dead. No species had more than 26 percent of its stems dead on the average.

Results from this investigation indicate that vast areas of the northern Mojave Desert support stands of vegetation in which as much as one-fourth of the standing crop may be dead wood. This represents a large reservoir of organic material that eventually must undergo breakdown, decomposition, and mineralization. The fact that so much of this dead wood remains standing above ground for decades after death suggests that either the woody material has little value as food for existing insect populations, it is resistant to breakdown by insects or microbes, or species are not present to serve the role in stem tissue breakdown that exists in less arid ecosystems.

ACKNOWLEDGMENTS

This study was supported in part by Contract EY-76-C-03-0012 between the U.S. Department of Energy and the University of California and by the US/IBP Desert Biome, Utah State University, Logan.

TABLE 1. Mean dry stem weight (g) and its standard deviation per plant determined by random quadrat counts and dimensional analysis in Rock Valley validation site.

		Zone				
Species	20	21	22	23	24	25
1. *Acamptopappus shockleyi*	48.8	–	–	–	–	60.9
Standard deviation	59.2	–	–	–	–	45.1
Number	10					9
2. *Atriplex confertifolia*	–	–	–	–	48.5	16.4
Standard deviation	–	–	–	–	33.9	21.6
Number					20	17
3. *Ephedra nevadensis*	109.5	46.7	138.9	126.7	150.9	162.5
Standard deviation	225.5	67.9	132.1	88.0	345.2	204.5
Number	182	41	41	33	20	70
7. *Ceratoides lanata*	59.7	51.1	54.9	46.9	80.0	80.0
Standard deviation	91.2	53.6	64.8	103.2	109.4	111.3
Number	33	46	4	50	32	69
8. *Ambrosia dumosa*	108.8	73.0	133.8	100.4	124.2	107.1
Standard deviation	98.0	78.3	160.4	102.2	127.8	104.7
Number	390	120	107	89	182	295
9. *Grayia spinosa*	108.8	89.3	162.3	82.1	70.8	65.7
Standard deviation	123.3	106.5	234.7	112.6	73.7	66.6
Number	44	34	9	42	160	302
11. *Krameria parvifolia*	134.5	129.1	126.8	170.2	156.0	133.6
Standard deviation	87.8	97.1	97.8	128.5	117.9	106.5
Number	419	46	75	32	56	104
12. *Larrea tridentata*	455.9	433.2	386.5	386.3	511.7	372.8
Standard deviation	481.2	424.1	393.6	348.0	517.5	385.8
Number	240	44	43	24	73	93
14. *Lycium andersonii*	386.0	393.2	362.4	224.4	362.8	320.5
Standard deviation	250.3	253.8	212.1	220.9	245.0	218.7
Number	243	22	35	17	6	28
15. *Lycium pallidum*	275.4	322.8	395.7	191.5	325.0	202.3
Standard deviation	166.1	227.4	253.3	157.6	250.6	182.9
Number	19	34	8	16	59	91

TABLE 2. Stem and root dry weight per hectare (kg/ha) in the Rock Valley validation site.

	Zone											
	20		21		22		23		24		25	
Species	Stem	Root	Stem	Root	Stem	Root	Stem	Root	Stem	Root	Stem	Root
Acamptopappus shockleyi	2.2	2.1	–	–	1.0	0.8	4.6	4.2	0.9	0.9	6.2	5.8
Atriplex confertifolia	–	–	–	–	–	–	–	–	13.4	10.0	3.1	2.3
Ephedra nevadensis	93.0	138.1	39.5	57.9	163.5	239.6	182.2	266.9	41.5	60.9	127.6	186.9
Ceratoides lanata	9.3	14.7	48.6	76.7	6.7	10.5	102.2	161.5	35.4	56.0	61.8	97.6
Ambrosia dumosa	200.6	406.6	180.6	366.1	401.1	813.1	389.3	789.0	311.0	630.4	364.4	738.7
Grayia spinosa	22.1	27.7	62.7	78.6	40.9	51.4	150.2	188.5	155.9	195.7	222.6	279.4
Krameria parvifolia	263.2	364.5	122.8	215.5	266.7	369.3	237.3	328.5	120.6	167.1	155.8	215.7
Larrea tridentata	511.5	1113.2	392.9	689.5	465.6	1013.2	404.1	879.4	513.7	1117.0	388.8	846.1
Lycium andersonii	438.5	642.5	177.7	260.4	355.5	520.9	160.0	234.5	30.1	44.1	100.6	147.4
Lycium pallidum	24.2	69.8	227.9	658.3	88.6	255.5	133.5	385.6	264.9	765.0	206.3	596.0
Total	1564.6	2779.2	1252.7	2403.0	1789.6	3273.5	1763.4	3238.1	1487.4	3047.1	1637.2	3115.9
Total root + stem	4343.8		3655.7		5063.1		5001.5		4534.5		4753.1	

TABLE 3. Standing dead plant material on the Rock Valley validation site in 1971 separated into the percentage of dead shrubs out of the total shrubs calculated from random quadrat counts (given in columns 1–7) and into the percentage of dead wood as a portion of living shrubs derived from destructive whole shrub sampling given in Column 8.

	Zone								
Species	20	21	22	23	24	25	Total site*	Dead wood as percent of standing live and dead stem	Correlation coefficient (percent dead × no. of shrubs per ha) r
	Dead shrubs, percent								
Ambrosia dumosa	6.8	14.4	7.8	17.1	13.2	13.4	11.2 ± 4.0	66.5	+0.70
Atriplex confertifolia	–	–	–	–	29.3	21.0	25.4 ± 5.9	54.9	–
Ephedra nevadensis	26.1	20.8	29.9	6.8	12.8	19.4	22.5 ± 8.5	29.4	–0.10
Ceratoides lanata	1.4	3.7	6.9	7.9	8.6	9.1	6.5 ± 3.1	66.3	+0.31
Grayia spinosa	7.6	16.2	21.4	7.0	13.7	12.6	11.4 ± 5.4	47.9	–0.24
Krameria parvifolia	0.9	1.7	1.9	3.1	0.6	1.4	1.2 ± 0.9	32.8	+0.19
Larrea tridentata	7.2	6.0	4.4	11.7	4.8	9.3	7.1 ± 2.8	68.6	–0.13
Lycium andersonii	1.3	5.0	10.0	2.2	0.0	4.9	2.7 ± 3.6	29.2	+0.32
Lycium pallidum	1.4	5.6	21.3	2.0	5.7	6.0	5.7 ± 7.3	26.1	–0.29

*± is standard deviation.

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MULTIVARIATE ANALYSIS OF THE VEGETATION IN A TWO-DESERT INTERFACE

A. A. El-Ghonemy[1], A. Wallace[2], and E. M. Romney[2]

ABSTRACT.— This report further describes the distribution and ecological characteristics of the natural vegetation at the Mojave Desert-Great Basin Desert interface. The region studied is one of extraordinary biological interest because of its geographic location straddling the boundaries of two large deserts of the western United States, and because of the kind and manner of its past land use (atmospheric and underground testing of nuclear devices). The present analysis determines the magnitude of variations in the phytosociological structure in this region and evaluates some relationships between its vegetation and environment. Vegetation and soils were sampled in 66 stands representing many possible physiographic variations. Relative density and relative coverage were determined for each perennial species and summed to provide an estimate of its importance value (I.V.). Importance values were used to ordinate stands to provide a synthesis of the phytosociological data and to portray the compositional relationships of species. The results of this study indicate that the area is dominated by several interrelated vegetational groupings. Correlations between the vegetational groups and the different environmental variables indicate that the distributional pattern of the vegetation is controlled largely by soil physical properties, salinity, and fertility levels.

The landscape of the Nevada Test Site is one of the most intensively studied and best understood deserts in the United States. Its potential is unique for studies critical to better understanding of arid lands. Previous phytosociological studies in this area are largely descriptive (Wallace and Romney 1972, Romney et al. 1973, Beatley 1976).

The objective of this study was to use some multivariate methods to analyze sociological relations among plant communities of the natural vegetation on the Nevada Test Site. This study is closely related to that previously carried out by the authors (El-Ghonemy et al. 1980), in which an account is given on the location, physiography, climate, vegetational groupings, and community diversity.

MATERIALS AND METHODS

Procedural details involving selection of stands and sampling techniques for soil and plants at 66 sites (Table 1) have been reported by Wallace and Romney (1972) and Romney et al. (1973). For treatment of data, one classification and two ordination techniques were used to analyze a data matrix consisting of the importance values for each of the perennial species encountered in each of the stands.

The classification technique involves the unweighted pair-group agglomerative clustering, using arithmetic averages to compute the similarity between a cluster and a stand which is a candidate for entry into a cluster (Sneath and Sokal 1973). The Euclidean distances (Ed) were used as the measure of similarity between stands.

The first ordination technique is that of Wisconsin (Gray and Curtis 1957) as modified by Beals (1969). The raw data were normalized by row and column, and interstand similarities were calculated using the formula $2w \div (a + b)$, where w represents the sum of the smaller values for common species; a and b represent the sum of all species in stands A and B, respectively. The maximum dissimilarity value was set equal to the maximum similarity value found in the similarity matrix. Ten percent of the i'th axis was searched to locate the second end stand for the (i + 1)'th axis.

The second ordination technique involves principal component analysis of the matrix of interstand correlation coefficients (Sneath and Sokal 1973). Eigenvectors (normalized to the eigenvalues) were not rotated.

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RESULTS

1. Classification of the Vegetation Data

(a) *The clustering units.*— The program cluster was used and Ed was selected as a measure of similarity. It should be mentioned that with this method of classification the stands are clustered into cells regardless of whether they form discrete groups in nature or whether they are merely parts of a continuum. The dendrogram shown in Figure 1 is derived from this cluster analysis. Because the paired and grouped stand clusters in the dendrogram result in linkages at various levels of similarity, an ecologically meaningful classification is not automatically indicated. Classification can be obtained, however, by setting more or less arbitrary threshold values. Threshold values used were set at 10, 15, 20, and 29 Ed. These are indicated by horizontal dash lines on the dendrogram.

At Threshold Line 4 there are three main clusters. Cluster 1 links together 58 stands (1 through 62) at Ed distance of about 28. Cluster II links together 5 stands (21 through 24) at Ed of 20. Cluster III links together stands 33, 39, and 35 at Ed of about 16.

At Threshold Line 3 clusters II and III remained unaltered, but cluster I became distinguishable as three subclusters: subcluster IA that links together 50 stands (1 through 65), subcluster IB that links together stands 54 and 62. At this level of similarity stands 19, 31, and 11 became so dissimilar to other stands that they remain rather isolated.

At Threshold Line 2 the subcluster IA became distinguishable as five vegetational groupings. The first grouping, IAa, links together 11 stands (3 through 34). The second grouping, IAb, links together 12 stands (6 through 51) at Ed of 12. The third grouping, IAc, links 8 stands (4 through 15) at Ed of about 14. The fourth grouping, IAd, links 6 stands (12 through 48) at Ed of about 14.5. The fifth grouping, IAe, links together stands 50, 64, 66, and 65 at Ed of about 16. At this level of similarity many individual stands or

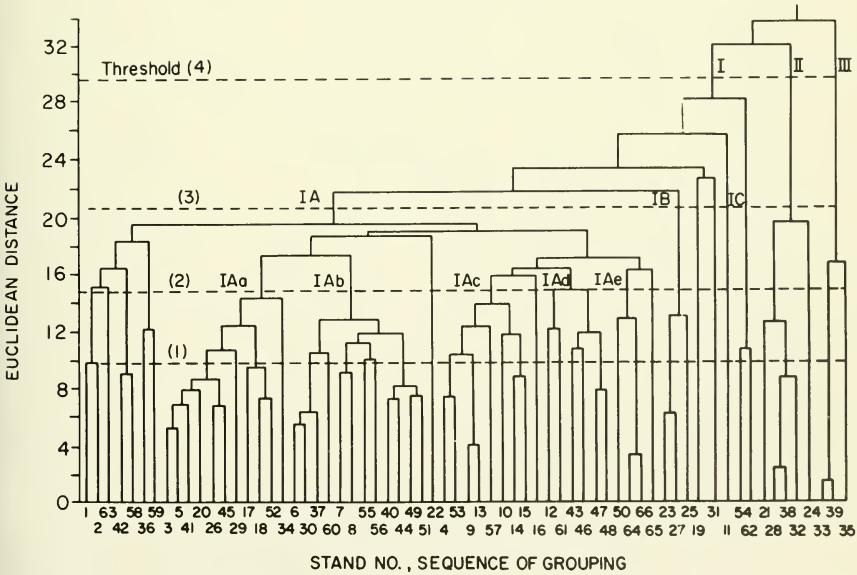


Fig. 1. Dendrogram resulting from the application of the agglomerative clustering analysis. The dotted lines denote the levels at which the dendrogram yields different vegetational groupings.

TABLE 1. Relative dominance of major species in each of the 66 stands (those 2 percent or more for a given stand). (See Table 2 for plant abbreviations.)

Stand no.	As	Aco	Ef	Lt	Ys	La	Ms	Ad	Gs	Kp	Cl	Plr	Plant species En	Lp
														Mercury Valley
1	2.3	14.4	25.4	31.1	25.4									
2			7.1	37.6		10.3	13.8							
3			6.3	46.0	14.9	15.4		8.8	3.6	3.6				
4	14.4		2.3	21.9	6.7	19.4		11.1	13.0		8.9			
5				42.0	13.7	15.3		12.9	2.2	5.9		3.4	4.5	
6	2.5			46.7		2.3		34.6		10.1			2.4	
7				9.2		2.5		71.9		16.3				
8			10.8	26.7				38.2		7.4			15.0	
9	23.1			22.5		14.9			31.6					
10	6.8			36.8				3.4	40.0					
11						10.9								
12						9.8			6.0	2.6		22.6	16.1	
13	31.6			13.3		15.8			23.1		5.3		5.0	
														Frenchman Flat
14	6.3			20.3		8.5		3.4	16.8		8.6			30.8
15	3.2			33.8		20.9		4.8	25.3		11.8			
16	3.7							15.1	4.9		24.2			11.7
17	2.3			84.3					4.9		6.4			
18				81.1		8.1		2.3	4.4					
19														
20				62.3		7.0		3.5	7.8					17.5
21						4.1								33.6
22				20.4		3.0		7.4		22.3		43.4		
23	5.2	4.4		37.9										
24		8.4												
25		13.8	4.5	4.4			5.8	9.7		6.3		2.9		
26				53.9		25.0		5.1		15.3				
27	2.5	7.4		53.6										
28														
29		4.6		50.7				2.1		9.1		5.3	5.7	
30	2.8			71.7				15.5		6.9	2.5			
31		39.4		54.0							5.4			
32		31.5												
33		100.0												
34				91.3										
35		65.2						2.0			5.7			
36		12.3		6.7				8.9		24.5			47.2	
37		3.7		64.6				13.4	3.3		14.0			
38														
39		97.6									2.4			
40				28.6				22.8	34.1				10.9	
41				57.4		14.9		5.9	8.3				11.8	
42		2.2		50.3		4.6	29.6	2.3		3.4	2.9			
														Rock Valley
43				6.3		7.5		11.7	20.3	28.6	2.8		6.2	16.4
44		7.6		11.3		5.8		31.3	20.0	7.0			3.3	11.8
45				46.3		27.7		13.6		8.5			2.1	
46				15.6		30.0		12.4		23.3			16.8	
47				21.1		39.0		12.0	14.4	4.2	2.2			6.6
48				34.5		31.5		6.6	5.4	4.2			7.8	9.7
49				24.0		15.4	2.4	22.2	10.8				11.9	7.8
50				8.6		2.1		12.5	59.4				5.6	11.7
														Jackass Flats
51				26.0		21.0		35.9	8.8			2.6	3.3	
52				84.1		4.0		11.6						
53	14.6			29.6		5.6		13.6	5.7		11.9			14.1
54				39.5										
55	3.6			19.4		1.5	3.9	26.5	2.2	6.0	7.3			
56	2.2			3.3			5.4	39.9		12.8			27.9	
57	28.7			42.9			2.6		16.2				8.0	
58				27.5			26.5			7.0			16.6	
59				19.0			19.0		14.5		3.8		43.7	
60	16.4			31.3			11.3	37.3			3.2			
														Yucca Flat
61		5.2				12.3							13.0	
62						11.7							6.1	
63	11.5	41.4					16.9				6.8			
64						17.8			57.0				8.8	
65				18.5		10.8			16.5				17.2	
66						23.0			38.9				14.8	

Table 1 continued.

Hs	Lf	Sp	Mt	Mp	Ta	Ssp	Aca	Asp	Pp	Ls	Cr	Yb	Hc
5.9													
	36.1	52.7											
22.7	3.4	5.6	6.5	3.3									
2.0					2.0								
						4.3							
12.9					3.8		18.6	2.3					
									2.0				
				24.1			60.9						
							61.5						
										52.0			
	32.3						57.4						
										36.9	11.9		
										36.3			
							98.4						
3.3												17.6	
4.6													
							68.5						
							7.0						
4.1							22.7						
							4.4						
							99.7						
													4.5
											60.2		
											29.4		
											8.2		
											22.0		
3.3											34.9	26.7	
12.1					5.0						62.1		
				3.8								14.0	
				3.3							4.9		7.2
											35.7		
11.5											9.5		

couples of stands become mostly dissimilar to the well-defined clusters so that they remain isolated (Fig. 1).

Classification at Threshold Line 1 resulted in many fragmentary units of limited generalizable value.

Sociological significance of the vegetation groupings.— For purposes of discussion each of the clusters identified, irrespective of its hierarchal level on the dendrogram, was called a vegetational grouping and named after the most abundant species, that is, the species with the highest average importance value.

Table 2 includes the average importance values for the different species in the various vegetational groupings. Inspection of this table gives the following explanation of the results of the cluster analysis.

Vegetational Grouping *IAa—Larrea tridentata* (Sesse & Moc. ex DC) Cov.: This grouping is represented by stands from Frenchman Flat (7 stands), Mercury Valley (2), Jackass Flats (1), and Rock Valley (1). The clustering seems to be based on the presence of *L. tridentata* as a leading dominant in all the stands in the cluster. The average importance value of *L. tridentata* (Table 2) is 93.4 (out of 200). The associated species are generally of minor importance, except *Ambrosia dumosa* (A. Gray) Payne (I.V. = 23.8). Stand 36 (Fig. 1), although dominated by *L. tridentata* (I.V. = 112), is the last to join the cluster. This is primarily due to the presence of *Atriplex canescens* (Pursh) Nutt. in substantial amounts (I.V. = 55).

Vegetational Grouping *IAb—A. dumosa*: This cluster does not appear to be a very natural unit, and on the basis of the subleading dominant species there would be grounds for the recognition of three smaller clusters (Fig. 1). The most influential species responsible for the segregation of this vegetational grouping into smaller clusters are *L. tridentata* (in stands 6, 30, 37), *Krameria parvifolia* Benth and *Coleogyne ramosissima* Torr. (in stands 7, 8, 55, 56), *Grayia spinosa* (Hook.) Moq. (in stands 40, 44, 49, 51), and *Oryzopsis hymenoides* (Roem. & Schult.) Ricker (in stand 60). The average importance value for *A. dumosa* in this grouping is 77. Associated species of pronounced significance are *L. tridentata* (I.V. = 37) and *K. parvifolia* (I.V. = 29.4).

Vegetational Grouping IAd—Transitional: Stands of this grouping also show little resemblance and mostly fuse in pairs above an Ed of about 10. Dominance is shared by many species, among them *Lycium andersonii* A. Gray (I.V. = 22.2), *Ephedra nevadensis* S. Wats. (I.V. = 22.1), *O. hymenoides* (I.V. = 17), and *C. ramosissima* (I.V. = 15).

Vegetational Grouping *IAe—G. spinosa*: The relatively high similarity between stands 64 and 68 (Fig. 1) is not only due to the dominance of *G. spinosa*, but also due to the preponderance of *L. tridentata*, *E. nevadensis*, and *C. ramosissima*. The average importance value of *G. spinosa* in this grouping is 71, followed by 23 for *L. andersonii* and 22.5 for *C. ramosissima*.

Vegetational Grouping IB—*Lycium shockleyi* A. Gray (*L.* rickardii) C. H. Mull.: All stands of this cluster are also dominated by *L. shockleyi*, with an average importance value of 88. Other important species are *L. tridentata* (I.V. = 35) and *Atriplex confertifolia* (Torr. & Frem.) S. Wats. (I.V. = 27).

Vegetational Grouping IC—*C. ramosissima*: All of the five stands representative of this cluster are dominated by *A. canescens*. Stands 28 and 38, which fuse at very high similarity levels, are overwhelmingly dominated by *A. canescens* (I.V. = 188 and 185, respectively). The average importance value for *A. canescens* in this cluster is 150. Species of some importance are *Stanleya pinnata* (Pursh) Britt. (I.V. = 18) and *Lycium pallidum* Miers (I.V. = 8.4).

Vegetational Grouping III—*A. confertifolia*: This is the last cluster to join the dendrogram, and it enters at a very low level of similarity (Ed = about 33). All stands are dominated by *A. confertifolia*. Stand 33 (I.V. = 200) fuses with 39 (I.V. = 193) at the highest recorded level of similarity (Ed = 0.8). Stand 35, which is also dominated by *A. canescens*, has a high (45.6) importance value for *A. canescens* as well as for *Ceratoides lanata* (Pursh) J. T. Howell (I.V. = 22). This results in its fusion with stands 33 and 39 at a relatively low similarity level (Fig. 1). Other species in this grouping are of little significance.

2. Ordination of the Vegetation Data

(a) *Ordination of Stands*: According to the Bray and Curtis (1957) technique, the two-dimensional ordination of stands (Fig. 2) has resulted in three distinct hyperspheres which correspond to the vegetation groupings identified at Threshold Line 4 on the dendrogram derived from the cluster analysis and superimposed on the ordination plane. Smaller vegetational groupings identified at higher similarity levels (Threshold 2) are mostly interconnected on the ordination plane (see dashed lines), but are still distinguishable in the form of successive groups of stands segregated along the primary X axis.

In the application of principal component analysis (PCA), five components or axes were extracted that account for 65.3 percent of the total variation (Table 3). Plotting of stand scores (Figs. 3 and 4) on the two axes that showed a greater number of significant corre-

TABLE 2. Average importance values for 35 perennial species in the different vegetational groupings (see Fig. 1).

	Lt (IAa)	Ad (IAb)	As (IAc)	Trans* (IAd)	Gs (IAe)	Ls (IB)	Cr (IC)	Aca (II)	Aco (III)
Larrea tridentata (Lt)**	93.4	39.2	30.3	41.8	13.5	38	24.0	—	—
Ambrosia dumosa (Ad)	23.8	77.4	15.8	14.5	14.0	2	0.3	0.5	1.3
Oryzopsis hymenoides (Oh)	7.0	7.2	10.1	1.0	3.3	3	—	3.1	2.2
Ceratoides lanata (Cl)	5.0	3.6	23.7	4.0	2.9	—	0.6	1.0	9.3
Sphaeralcea ambigua (Sa)	2.6	1.2	2.0	1.2	—	2	3.3	2.2	—
Lycium andersonii (La)	16.0	5.3	17.4	38.0	23.0	—	11.0	2.4	—
Mirabilis pudica (Mp)	0.1	—	—	2.6	—	1	—	3.0	—
Hymenoclea salsola (Hs)	0.8	—	2.5	11.2	5.1	1	8.1	—	2.7
Acamptopappus shockleyi (As)	6.8	7.4	44.9	—	—	21	—	—	—
Ephedra funerea (Ef)	2.0	1.1	2.3	—	—	4	—	—	—
Psorothamnus fremontii (Pfr)	5.6	0.7	0.1	9.2	—	—	—	—	—
Krameria parvifolia (Kp)	5.2	29.4	3.9	22.2	—	5	—	—	—
Yucca schidigera (Ys)	3.3	—	0.8	—	—	—	—	—	—
Yucca brevifolia (Yb)	1.8	—	—	5.0	—	2	—	—	—
Lycium pallidum (Lp)	3.1	3.1	9.0	10.3	—	—	—	8.4	—
Lepidium fremontii (Lf)	0.3	0.4	0.5	1.9	—	—	—	—	—
Ephedra nevadensis (En)	5.5	6.8	3.9	22.1	20.0	—	6.3	—	—
Menodora spinescens (Ms)	—	1.3	0.5	0.5	—	4	0.8	—	—
Grayia spinosa (Gs)	11.1	10.3	37.4	17.0	71.5	—	—	0.9	0.6
Coleogyne ramosissima (Cr)	—	4.5	—	15.0	22.5	6	137.0	—	—
Machaeranthera tortifolia (Mt)	—	1.0	0.6	5.1	—	—	2.4	—	—
Cactus spp. (Ca)	1.0	—	—	—	0.2	—	0.4	—	—
Stipa speciosa (Ssp)	—	—	0.9	—	22.0	—	0.8	—	—
Tetradymia axillaris (Ta)	—	—	1.0	0.3	0.4	—	3.3	—	—
Atriplex confertifolia (Aco)	—	1.0	—	—	—	23	0.4	12.8	188.0
Atriplex canescens (Aca)	5.0	1.0	—	—	—	—	—	150.0	15.0
Stanleya pinnata (Sp)	—	—	—	0.3	—	—	—	18.0	—
Hilaria rigida (Hr)	—	0.1	0.3	—	—	—	—	—	—
Lycium shockleyi (Ls)	—	—	—	—	—	88	—	—	—
Artemisia spinescens (Asp)	—	—	0.6	—	—	—	—	—	—
Prunus fasciculata (Pf)	—	—	—	—	—	—	—	—	—
Salazaria mexicana (Sm)	—	—	—	—	—	1	—	—	—
Thamnosma montana (Tm)	0.2	—	—	—	—	—	—	—	—
Haplopappus cooperi (Hc)	—	—	0.6	—	—	—	—	—	—
Psorothamnus polyadenius (Pp)	1.0	—	—	—	—	—	—	—	—

*Transitional

**Letters in parentheses indicate abbreviations for species' names. Table headings correspond to these abbreviations.

lations with environmental variables, viz., Axes I and III, show that the application of PCA technique has resulted in much better segregation of stands into groups comparable with those derived from the clustering technique at Threshold Line 2 on the dendrogram.

The two vegetation groupings of *A. canescens* and *A. confertifolia* are separated at the negative side of the first axis. Separation of the two groupings from one another is affected by the third axis. Stand 35, which joins the *A. confertifolia* grouping at a relatively low level of similarity (Fig. 1), appears on the ordination plane to be more associated with the *A. canescens* grouping. The groupings of *L. tridentata* and *A. dumosa*, which have more or less overlapping scores on the first axis, are

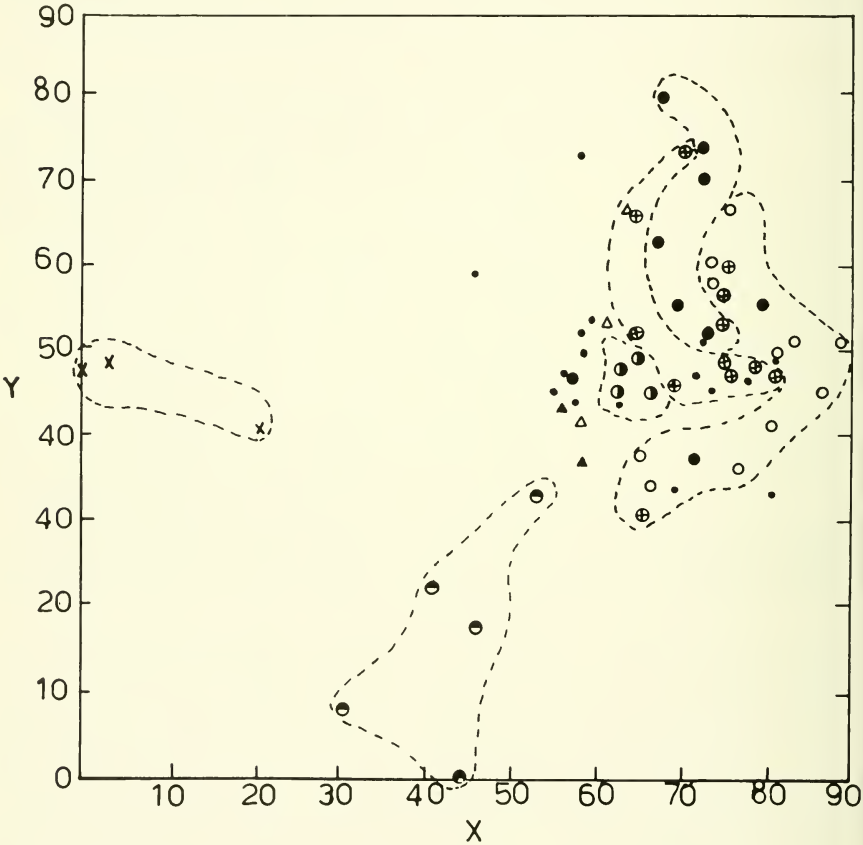


Fig. 2. Ordination of the stands on the first axes derived from the Wisconsin ordination (Bray & Curtis) technique. The classification of stands according to the cluster analysis has been superimposed on the ordination diagram. Dashed lines connect some of the vegetational groupings. Empty circles are stands of *L. tridentata* (IAa), crossed circles are stands of *A. dumosa* (IAb), vertically half-blocked circles are stands of *C. spinosa* (IAc), horizontally half-blocked circles are stands of *A. canescens* (II), large blocked circles are stands of *A. shockleyi* IAc), blocked triangles are stands of *C. ramosissima* (IC), empty triangles are stands of *L. shockleyi* (IB), crosses are stands of *A. confertifolia* (III), and small blocked circles are transitional stands (OAd).

clearly separated on the third axis. Along this axis *A. dumosa* scores positive values, but those of *L. tridentata* are negative. Along the first axis the groupings of *L. tridentata*, *A. shockleyi*, *L. shockleyi*, and *C. ramosissima* are also separated from one another. The grouping of *G. spinosa* is primarily separated from other groupings along the third axis. It is also apparent (Fig. 4) that the groupings of *L. shockleyi* and *C. ramosissima* occupy a more or less central position between other groupings.

(b) *Behavior of species along the environmental gradients*: The behavioral pattern of eight common species as expressed by their importance value is represented separately on the ordination derived from the first and third axes of the PCA (Fig. 5:A–H). *Larrea tridentata* and *A. dumosa* attain their high importance values at the high and medium positions of the positive side of the axis. Along the third axis the two species behave rather differently: the high values of *A. dumosa* are on the positive side and the high values of *L. tridentata* are on the negative side. *Grayia spinosa* and *L. andersonii* also exhibit definite patterns, with their high importance values at the medium position on

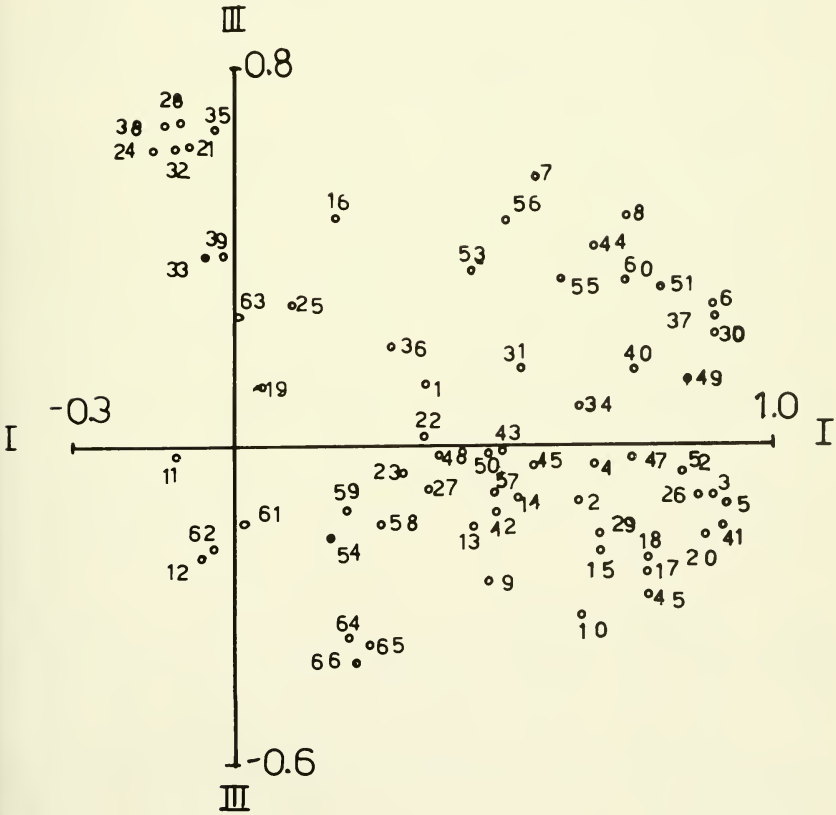


Fig. 3. Plotting of stands on axes I and III from the principal component analysis (PCA).

the first axis. *Acamptopappus shockleyi* shows its high values at medium to lower positions on the positive side of the first axis. On the third axis most of the high values are on the negative side. More definite patterns are those of *A. canescens* and *C. ramosissima*. They have attained their high importance values at the extreme positive and the extreme negative end of the third axis, respectively. *Atriplex confertifolia* attained its high importance values at the central positions of the first axis and at medium positions with regard to the positive side of the third axis.

(c) *Ecological significance of phytosociological gradients*: Simple correlation coefficients between the phytosociological gradients represented by the five axes extracted from the PCA and the various environmental variables are given in Table 3. Most of the correlations are extremely low. The lowest negative correlation (–0.39) is that between the first axis and field capacity for water relations in soil. This axis is also significantly correlated with both sodium (negative) and iron (positive). Axis 2 shows no significant correlations with any of the variables studied. Axis 3 shows significant correlations and most of the variables correlated significantly with the first axis, but with opposite trends. This axis also shows significant correlations with both potassium (positive) and nitrogen (negative). Axis 4 shows significant positive correlations with electrical conductivity and potassium, and axis 5 shows significant positive correlations with soil moisture retention capacity, electrical conductivity, calcium, magnesium, copper, and nitrogen.

It is apparent from these correlation studies that the segregation of the vegetation cover into distinct groupings on the ordination plane is largely attributed to variations in soil properties. The vegetational grouping of *A. canescens* and *A. confertifolia* occupy sites poor in phosphorus, organic matter, and nitrogen, but rich in sodium, potassium, copper, and percent of clay. The grouping of *A. dumosa* reflects sites rich in phosphorus, iron, and to some extent in sodium, but poor in nitrogen. The *Grayia spinosa* grouping occupies sites decidedly poor in sodium, potassium, and fine particles, but rich in nitrogen and iron. The groupings of *L. shockleyi* and *C. ramosissima* occupy sites with more or less intermediate soil characteristics.

(d) *Correlation among species and species ordination*: The spatial pattern of one species may be modified by another. This leads to the question of interspecific correlation. The causes of these correlations are, however, varied. The most common cause is, no doubt, the mutual response to varying environments. There also are interactions between species that do not involve independent environmental factors (allelopathic effect, competition, or amelioration or degradation of environmental conditions). It is, however, difficult to reach firm conclusions as to the cause of cor-

TABLE 3. Simple linear correlation coefficients (r) between five principal components and the various environmental parameters*

Parameter PCA axes	Proportion of total variance Percent	Accumulated variance Percent	F. Cap.	pH	EC	Lime Percent
1	31.1	31.1	–0.39***	–0.13	0.04	–0.20
2	11.1	42.2	0.05	0.21	0.08	0.21
3	8.1	50.3	0.10	0.07	0.09	–0.06
4	7.9	58.2	0.22	–0.03	0.27*	–0.07
5	7.1	65.3	0.38***	0.07	0.31**	0.08

*A single asterisk denotes a significant correlation at 5 percent probability level. Double and triple asterisks denote a significant correlation at 1 percent and 0.1 percent probability levels.
F. Cap. is water retention at field capacity.
EC is electrical conductivity.
Cations are exchangeable.
Fe, Zn, and Cu are from 0.005 *M* DTPA extract.
N is total soil nitrogen.

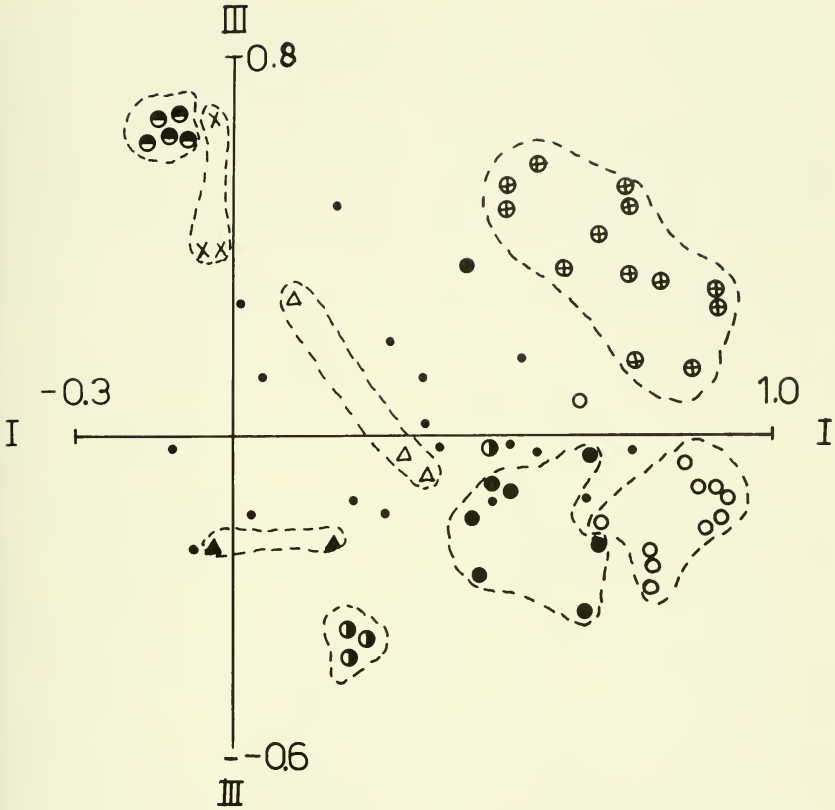


Fig. 4. Ordination of stands on axes I and III from the principal component analysis. The classification of stands according to the agglomerative clustering analysis has been superimposed on the ordination diagram. For identification of groupings see Fig. 2.

Table 3 continued.

Na	K	Ca plus Mg	Na	P	Fe	Zn	Cu	N	
me/100 g			%	μg/g	μg/g DTPA ext.			%	Elevation
-0.34***	-0.19	-0.17	-0.30**	-0.32***	0.31**	-0.06	-0.28*	0.10	0.18
0.12	0.08	-0.10	0.15	-0.17	-0.21	0.05	-0.22	-0.13	0.03
0.35**	0.28*	-0.14	0.34***	-0.16	-0.37***	-0.21	-0.15	-0.31**	-0.10
0.23	0.34***	0.17	0.17	0.05	0.07	0.14	-0.21	-0.10	-0.1
-0.12	0.21	0.25*	-0.20	0.18	0.11	0.13	0.31**	0.27*	0.03

relations by simply observing the spatial distribution of the two species in nature; however, if neither species separately shows any patterning but the two random distributions are coincidental (or countercoincidental), a direct relationship between the species seems the most likely explanation (Goodall 1970).

In Table 4 a partial simple linear correlation matrix is given for 35 common species showing the positive and negative relationships present. The species constellation based on correlation values is illustrated in the form of a three-dimensional diagram in Figure 6. The components involved in the construction of this diagram were extracted using the principal component analysis of the matrix of interspecific coefficients (Sneath and Sokal 1973). Five groupings of species are apparent—a central group and four peripherals. The arrangement of species in this diagram

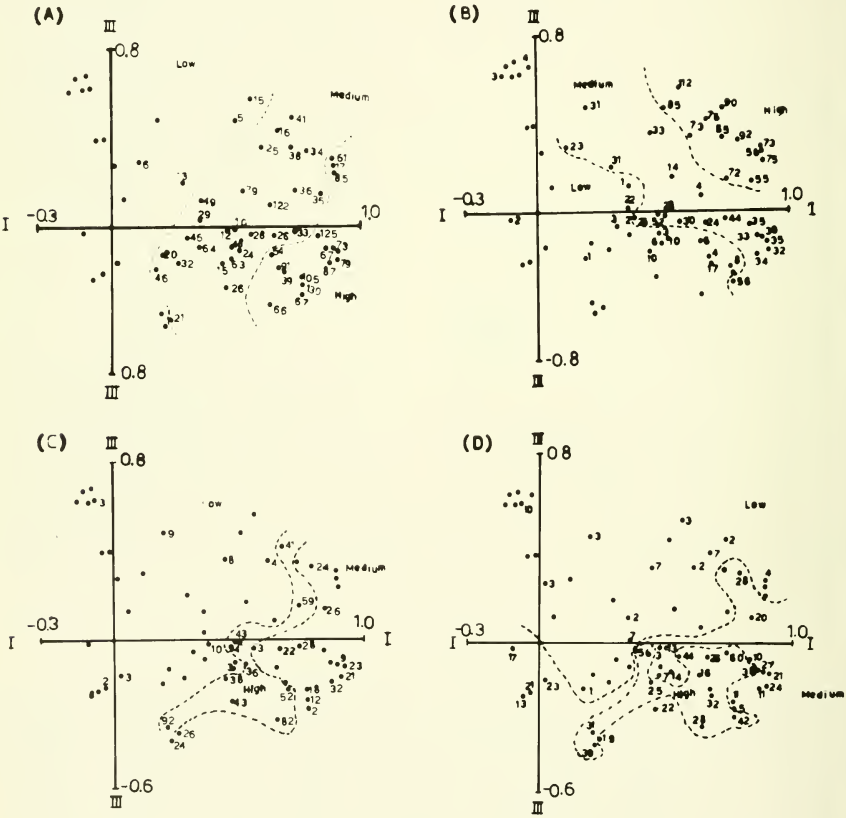


Fig. 5. (A–H). The behavior of eight species as expressed by their importance values along the phytosociological gradients expressed by the first and third axes of the principal component analysis. The importance value for each are superimposed upon a common ordination plane. High, medium, and low values are indicated where appropriate. A is *L. tridentata*, B is *A. dumosa*, C is *G. spinosa*, D is *L. andersonii*, E is *A. shockleyi*, F is *A. canescens*, G is *C. ramosissima*, and H is *A. confertifolia*.

reflects positive correlations in the main, the general position of each grouping of species being related to the negative correlations also present. The following are the five groups identified:

Group 1 (upper left-hand side of the diagram): *Grayia spinosa, L. andersonii, L. pallidum, Stipa speciosa.*

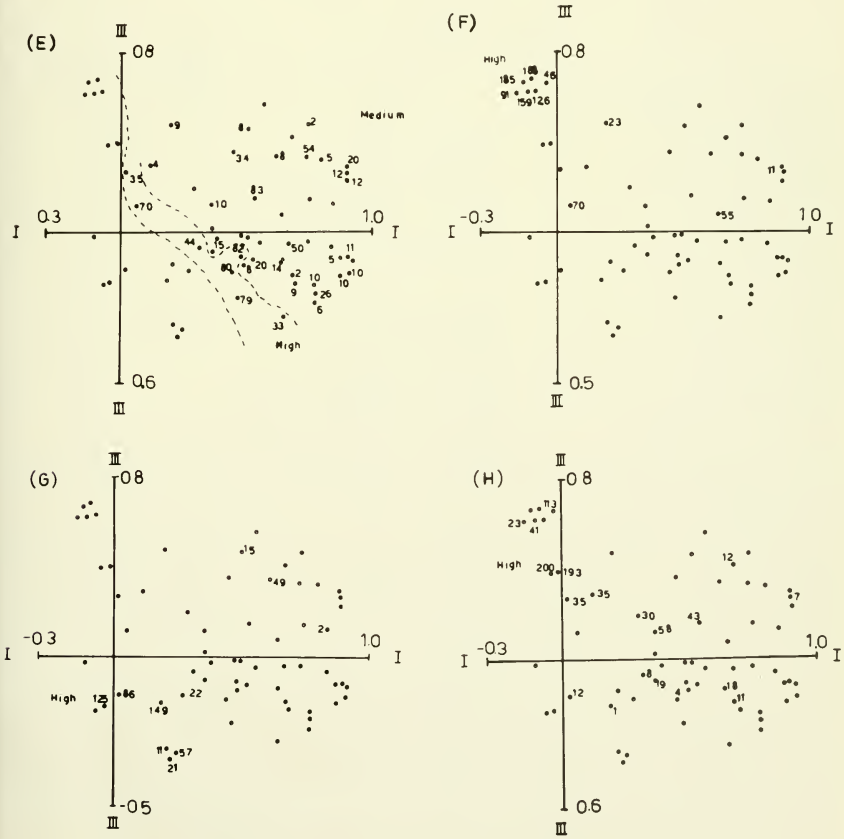
Group 2 (lower left-hand side): *Ambrosia dumosa, Hilaria rigida* (Thurb.) Benth. ex Scribn., *Yucca schidigera* Roezl ex Ortgies, *Ephedra funerea* Cov. & Mort., *Salazaria mexicana* Torr., *E. nevadensis, K. parvifolia.*

Group 3 (upper right-hand side): *Hymenoclea salsola* Torr. & Gray, *Tetradymia axillaris* A. Nels., *A. shockleyi, Machaeranthera tortifolia* A. Gray, *Sphaeralcea ambigua* A. Gray.

Group 4 (lower right-hand side): *Yucca brevifolia* Engelm. in Wats., *Thamnosma montana* Torr. & Frem., *Psorothamnus fremontii* (Torr.) Barneby, *Prunus fasciculata* (Torr.) A. Gray, Cactus species.

Group 5 (central): *Psorothamnus polyadenius* (Torr.) Rydb., *A. canescens, A. confertifolia, Mirabilis pudica* Barneby, *O. hyme-*

Fig. 5 continued.



noides, Mendora spinescens A. Gray, *L. tridentata, S. pinnata, P. fremontii, Haplopappus cooperi* (A. Gray) Hall, *L. shockleyi, C. lanata, Artemisia spinescens* D. C. Eat., *C. ramosissima.*

It is equally clear that none of these five groups is an isolated entity; each is linked to the adjacent group by correlations of different magnitude between member species of the representative groups or through intermediate species.

The deduction that these correlated groups of species represent significant communities in nature may not necessarily hold. The very obvious group on the lower right-hand side of the diagram (Group 4) includes species of minor significance in vegetation structure (very low importance values), and consequently such a group is not detectable in nature. On the other hand, group 1, dominated by *G. spinosa, L. andersonii, S. speciosa,* and *C. ramosissima,* is well defined in nature and floristically structurally comparable with the *G. spinosa* grouping previously defined by stand classification and ordination techniques.

DISCUSSION

The data obtained by measuring the amount of a species in each of n stands can be represented by a scatter diagram of n

TABLE 4. Part of simple linear correlation matrix for 35 perennial specimens for the northern Mojave Desert showing positive and negative species' relationships.

Acamptopappus shockleyi (As)	+ 0.34***Oh, + 0.29*Mp
Atriplex confertifolia (Aco)	-0.28*La
Ephedra funerea (Ef)	+ 0.75 Ys, + 0.29*Hr
Ceratoides lanata (Cl)	+ 0.27*Lp, + 0.35***Ta, + 0.63***Asp
Ambrosia dumosa (Ad)	+ 0.26 + Kp, + 0.28*Hr
Krameria parvifolia (Kp)	+ 0.50***En, + 0.27*Pfr, + 0.25*Ca, + 0.29*Pf, + 0.26*Ad
Larrea tridentata (Lt)	-0.27*Ta, -0.25*Aca, + 0.36***Pp
Lycium andersonii (La)	+ 0.38***Gs, + 0.25*Oh, -0.60***Pp, -0.28*Aco
Menodora spinescens (Ms)	
Yucca schidigera (Ys)	+ 0.75***Ef
Sphaeralcea ambigua (Sa)	+ 0.33***Mt, + 0.25*Hs
Ephedra nevadensis (En)	+ 0.50***Gs
Grayia spinosa (Gs)	+ 0.33***Ssp, + 0.38***La
Lepidium fremontii (Lf)	+ 0.68***Sp
Oryzopsis hymenoides (Oh)	+ 0.25*La, + 0.62***Mp, + 0.34***As
Machaeranthera tortifolia (Mt)	+ 0.33***Sa, + 0.41***Pfr, + 0.75***Hs
Psorothamnus fremontii (Pfr)	+ 0.27 Kp, + 0.41***Mt, + 0.33 Hs, + 0.63***Ca, + 0.82***Pf, + 0.27*Tm
Coleogyne ramosissima (Cr)	+ 0.32***Ta, + 0.25*Ssp
Lycium pallidum (Lp)	+ 0.27*Cl
Hilaria rigida (Hr)	+ 0.29*Ef, + 0.28*Ad
Hymenoclea salsola (Hs)	+ 0.25*Sa, + 0.75***Mt, + 0.33 Pfr, + 0.48***Ta, + 0.33***Ta
Stanleya pinnata (Sp)	+ 0.68***Lt
Stipa speciosa (Ssp)	+ 0.33***Gs, + 0.25*Cr
Tetradymia axillaris (Ta)	+ 0.35***Cl, -0.27*Lt, + 0.32 Cr, + 0.48***Hs, + 0.61***Asp
Mirabilis pudica (Mp)	+ 0.29*As, + 0.62***Oh
Atriplex canescens (Aca)	-0.25*Lt
Artemisia spinescens (Asp)	+ 0.63***Cl, + 0.33***Hs, + 0.61***Ta
Psorothamnus polyadenius (Pp)	+ 0.36***Lt
Cactus sp. (Ca)	+ 0.25*Kp, + 0.63***Pfr, + 0.53***Pf, + 0.45***Yb, + 0.72**Tm
Prunus fasciculata (Pf)	+ 0.29*Kp, + 0.82***Pf, + 0.53***Ca
Lycium shockleyi (Ls)	+ 0.35***Sm
Yucca brevifolia (Yb)	+ 0.45***Ca, + 0.51***Tm
Salazaria mexicana (Sm)	+ 0.35***Ls, + 0.51***Tm
Thamnosma montana (Tm)	+ 0.27*Pfr, + 0.72***Ca, + 0.51***Yb
Haplopappus cooperi (Hc)	

*Denotes a correlation at 5 percent probability level, ** at 1 percent probability, and *** at 0.1 percent probability.

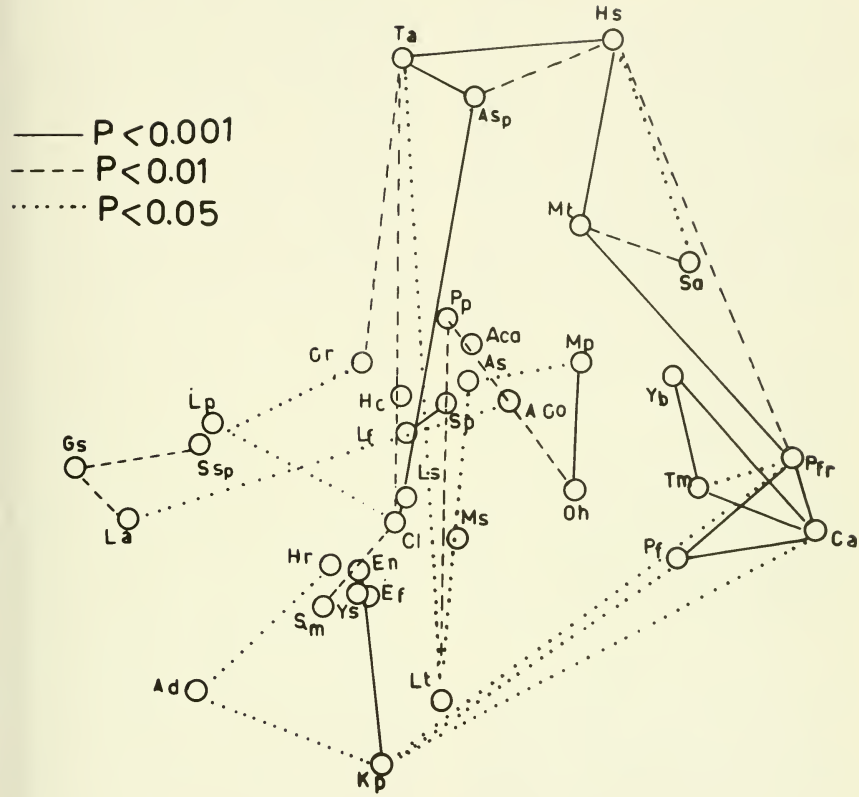


Fig. 6. Special ordination on the first three axes derived from the principal component analysis. Species showing positive correlations are interconnected. Letters beside each circle indicate abbreviations for species' names.

1. As = *Acamptopappus shockleyi*
2. Aco = *Atriplex confertifolia*
3. Ef = *Ephedra funerea*
4. Cl = *Ceratoides lanata*
5. Ad = *Ambrosia dumosa*
6. Kp = *Krameria parvifolia*
7. Lt = *Larrea tridentata*
8. La = *Lycium andersonii*
9. Ys = *Yucca schidigera*
10. Ms = *Mendora spinescens*
11. Sa = *Sphaeralcea ambigua*
12. En = *Ephedra nevadensis*
13. Gs = *Grayia spinosa*
14. Lf = *Lepidium fremontii*
15. Oh = *Oryzopsis hymenoides*
16. Mt = *Machaeranthera tortifolia*
17. Pfr = *Psorothamnus fremontii*
18. Cr = *Coleogyne ramosissima*
19. Lp = *Lycium pallidum*
20. Hs = *Hymenoclea salsola*
21. Hr = *Hilaria rigida*
22. Sp = *Stanleya pinnata*
23. Mp = *Mirabilis pudica*
24. Ta = *Tetradymia axillaris*
25. Ssp = *Stipa speciosa*
26. Aca = *Atriplex canescens*
27. Asp = *Artemisia spinescens*
28. Pp = *Psorothamnus polydenius*
29. Ca = *Cactus* sp.
30. Pf = *Prunus fasciculata*
31. Ls = *Lycium shockleyi*
32. Sm = *Salazaria mexicana*
33. Yb = *Yucca brevifolia*
34. Hc = *Haplopappus cooperi*

points in an s-dimensional coordinate frame. Classification consists of subdividing the swarm of points into a number of disjointed sets. If the points chance to fall into several compact, widely separated groups, no difficulty arises and formal rules for effecting a classification are scarcely needed. According to Pielou (1969) this ideal result is rarely obtained when vegetation is randomly sampled. More often than not, the points representing the stands are diffusely scattered and any classification procedure is largely arbitrary.

A way out of this difficulty is to ordinate the stands rather than to classify them. The purpose as in classification is still to simplify and condense the mass of raw data yielded by vegetation sampling in the hope that relationships among the plant species, and between them and the environmental variables, will be manifested.

Ordination consists of plotting n stands in a space of fewer than s dimensions in such a way that none of the important features of the original s-dimensional pattern is lost. Ordination has two great advantages over classification. It obviates the necessity for setting up arbitrary criteria for defining the classes, and there is no need to assume that distinct classes, if there are any, are hierarchically related. However, the compatability of the two approaches, viz., the classification and the ordination techniques, was pointed out by Anderson (1965) and Goodall (1970), and in recent years it has become more common for classification and ordination to be used on the same data (Gray and Bunce 1972, Williams and Walker 1974, Ayyad and El-Ghonemy 1976).

The importance of the study area from the phytogeographical point of view may be due to its position straddling the boundaries of the Great Basin to the north and the Mojave Desert to the south. The behavior of the biotic communities of the Mojave Desert in general, or in some of its sectors, has attracted the attention of many biologists. Shreve and Wiggins (1964) have described the Mojave Desert as showing its most distinctive development between 600 and 1200 m elevation (2000–4000 ft.). When it is followed thence toward the northeast or southeast, it loses some of its characteristic vegetational features and much of its distinctive flora. The basic structure of the vegetation throughout the Mojave Desert is open stands of *L. tridentata* and *A. dumosa*. On the western edge the plants are joined and to some extent replaced by *A. tridentata*, *G. spinosa*, *T. axillaris*, and other perennials; and at high elevations on the north, *C. ramosissima*, *G. spinosa* are dominant.

In the northern sector of the Mojave Desert, particularly in the Nevada Test Site and its surroundings, phytosociological studies have been carried out by many authors. Among these are Beatley (1963, 1969, 1974, 1975, 1976), Allred et al. (1963), Rickard and Beatley (1965), Brown and Mason (1968), Wallace and Romney (1972), Romney et al. (1973), Tueller et al. (1974), and El-Ghonemy et al. (this volume). In these studies some of the vegetational units have been identified and named by various terms as communities, associations, types, subtypes, and vegetational groupings. In the most recent work by El-Ghonemy et al. (1980) the correlation between the various vegetational groupings identified and the environmental variables have been demonstrated, as well as the vegetation diversity and the successional trends among the different groupings.

In the present study the application of the agglomerative clustering technique has proved useful in classifying stands into several vegetational groupings. However, most of these groupings are not distinct. The members of each pair of groupings are, in most cases, linked together by having one or more of the dominant species in common. This, as Goodall (1954) mentioned, does not preclude the possibility of the classification for particular ends, but it is generally more appropriate to ordinate stands.

In the present study the application of both Wisconsin and PCA ordination techniques emphasizes this idea and indicates that the vegetational groupings yielded by the clustering technique are generally interconnected. However, the PCA technique has proved more efficient in segregating stands in a manner more or less similar to that achieved by the clustering approach. The better segregation of stands along the PCA ordination plan makes the description and correlation of the vegetational grouping more efficient.

The vegetational groupings identified in the study area are more or less similar to those previously identified by El-Ghonemy et al. (this volume) with stands clustered into groupings according to their leading dominant species (i.e., species with highest importance values). Because in the multivariate analysis the similarity between stands involves the use of similarity functions that take into account the whole number of species involved in community structure, the stand's characteristics for a given vegetation unit may not have the same leading dominant species. Consequently, the detailed structure of comparable vegetation groupings derived from the two approaches may not be the same.

The spatial arrangement of stands along the different vegetational gradients provides evidence that variations in vegetation composition are expressed by more than one axis of the ordination components. This implies that the distribution of vegetation in the study area is controlled by complexes of interrelated factors. These fall into three main groups. The first group relates to soil fertility, as reflected by the concentrations of phosphorus, nitrogen, potassium, and other nutrient elements. The second complex expresses soil salinity, and the third complex relates to soil texture and water-retention capacity. The role of soil fertility as a factor in the delimitation of the natural plant communities has been stressed by several authors (Beadle 1954, 1962, El-Ghonemy 1966, Ayyad and El-Ghonemy 1976).

In the present study the association of certain vegetational groupings, for example, that of *A. dumosa*, with phosphorus-rich soil, has been demonstrated. The role of total soil salinity or of particular salt has been critically reviewed by Chapman (1960), Gates et al. (1956), Ayyad and El-Ghareeb (1972), and Beatley (1976). The *Atriplex* communities at the Nevada Test Site have been described by Beatley (1976) as occupying sites at the high end of the soil salt content and fine particle gradients. These results are in full agreement with the results obtained in the present study.

CONCLUSIONS

(1) The application of the multivariate analysis resulted in the segregation of the vegetational cover into more or less distinct groupings.

(2) The application of the principal component analysis for the ordination of the vegetation data resulted in the segregation of stands into more or less distinct sets, comparable in structure to the vegetation groupings derived from the cluster analysis.

(3) The physical and chemical properties of the soil play a definite role in the delineation of the vegetational groupings.

(4) The ordination of species scores may result in groupings of correlated species that could be floristically different from those obtained if ordination is based on stand scores.

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A PHYTOSOCIOLOGICAL STUDY OF A SMALL DESERT AREA IN ROCK VALLEY, NEVADA

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ABSTRACT.— The aim of this study was to gain more understanding of the compositional structure of vegetation in the US/IBP Desert Biome validation site located in Rock Valley, Nevada. The vegetation data collected from 85 stands, randomly distributed to cover all physiographic variations in the study site, permitted categorization of the vegetation units either by coordinates or by class membership. The vegetational groupings so identified were then used for constructing a more reliable vegetation map for the Rock Valley validation site.

Multivariate statistical methods have been increasingly used in an attempt to reduce the complexity of plant ecological data and provide a clearer understanding of the underlying pattern. This in turn can form the base of a second, more rewarding phase of phytosociology, i.e., the causal nature of this pattern.

Two basic approaches have been used to simplify the complex ecological data:

1. CLASSIFICATION: In this approach the stands or the sampling units are arranged in groups, the members of which have certain common properties.

2. ORDINATION: Such a technique attempts to find the major axes of variation. Each sample unit can then be related to one or more of these axes so as to convey maximum information about its composition and relationships with other sample units. As Goodall (1970) points out, any particular piece of vegetation can be categorized either by coordinates or by class membership, the latter being less precise but more convenient.

The initial inventory of Rock Valley began in 1971. The US/IBP Desert Biome Program, in seeking to understand the functioning of the arid land ecosystem, has established research areas in each of four major arid land types in western North America. One of them was in Rock Valley, Nevada.

The Desert Biome research program design embraced two types of endeavors. One involved the investigation of specific abiotic and population processes and the development of models of these processes and of the function of large systems. The other involved the testing of these models by comparing their prediction with actual measurements of changes in the states of the desert ecosystem. The validation of a system model required, then, an exhaustive initial inventory of the system followed by periodic evaluations of extensive arrays of state variables and the external influences impinging upon them.

During the spring of 1971, the IBP validation site in Rock Valley was delimited. The site is about 0.46 km^2 in extent. In July 1970 the site was being photographed at two scales, 1:2400 and 1:600. These photographs are being kept as a permanent record and could be used to evaluate changes brought about by continued use of the area. Other descriptions of the site are reported by Turner (1973, 1975, 1976) and Turner and McBrayer (1974). The plant taxonomy of the area is given by Beatley (1976).

The objective of this work was twofold: (1) conduct initial inventory of the microvariations in vegetational structure, and (2) present such variations in the form of a vegetation map delimiting the boundaries of the identified vegetational units. Such information is prerequisite for future assessments in vegetational changes.

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This study is closely related to those previously carried out by El-Ghonemy et al. (1980a, 1980b, this volume) in the northern Mojave Desert, in which full account is given on the location, physiography, climate, vegetational groupings, successional trends, and community diversity.

METHODS

SELECTION OF STANDS AND SAMPLING TECHNIQUE: Sampling of perennial vegetation was carried out in 190 stands in quadrats of 50 × 2 m size. The coordinates of these quadrats were generated by a computer program designed to insure random dispersion (Wallace and Romney 1972). Density measurements of each species at each site were determined. Shrubs with canopies overlapping the quadrat boundaries were counted inside only when their root crowns were inside the boundary line.

Detailed characterization of soil was develped from four soil profiles excavated at each of the four corners of the validation site. These profiles were dug to the respective hard pan layer underlying the area. The soil profiles were described and characterized according to the USDA 1960 soil classification and seventh approximation system. Soil chemical analysis was according to the U.S. Salinity Laboratory Staff (1954) procedures.

MULTIVARIATE ANALYSIS OF THE VEGETATION DATA: One classification and one ordination technique were applied. The classification technique is the unweighted pair-group method of the agglomerative clustering technique, using the arithmetic averages to compute the similarity between a cluster and a stand which is a candidate for entry into a cluster (Sneath and Sokal 1973). The Euclidean distance (ED) was used as a measure of similarity among stands.

The ordination technique is that of the principal component analysis of the matrix of interstand correlation coefficients (Sneath and Sokal 1973). Eigenvectors (normalized to eigenvalues) were not rotated. To facilitate data processing, the number of stands (190) was reduced through random selection to 85 stands.

RESULTS AND DISCUSSION

CLASSIFICATION OF THE VEGETATION DATA: Figure 1 shows cluster analysis dendrograms with the dotted horizontal lines denoting the levels at which clusters were distinguished

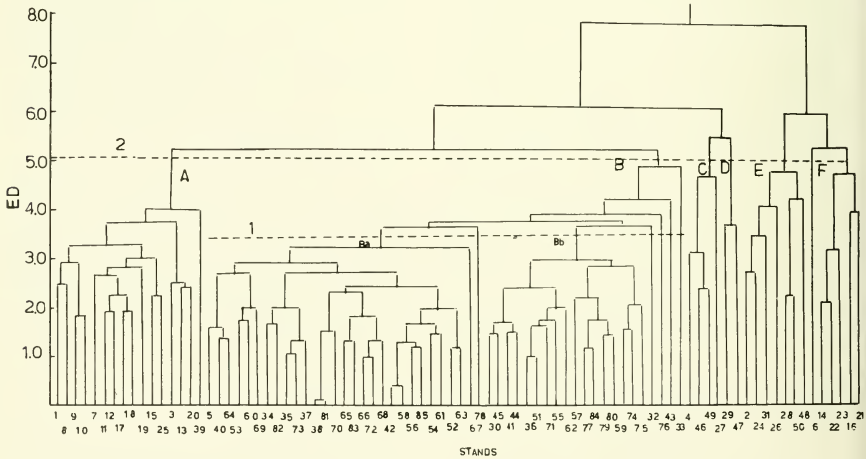


Fig. 1. Dendrogram resulting from the application of the agglomerative clustering analysis. The pecked lines denote the levels at which the dendrogram yields meaningful vegetational groupings.

TABLE 1. Estimated densities (number of individuals/ha) of the perennial species in seven vegetational groupings on the Rock Valley validation site, with relative density as percentage given in parentheses.

Species	Vegetational groupings*						
	A	Ba	Bb	C	D	E	F
*Ambrosia dumosa***	2635 (29.5)	1098 (18.6)	2635 (36.5)	4026 (36.0)	2050 (15.9)	4758 (32.6)	3806 (24.6)
Grayia spinosa	2342 (26.2)	132 (2.2)	176 (2.4)	630 (5.6)	2196 (17.0)	3118 (21.3)	4978 (32.2)
Lycium pallidum	878 (10.0)	220 (3.7)	410 (5.7)	659 (5.8)	1244 (9.6)	878 (6.0)	1025 (6.6)
Krameria parvifolia	878 (10.0)	1479 (25.0)	1318 (18.2)	878 (7.8)	1771 (13.7)	1098 (7.5)	1756 (11.3)
Larrea tridentata	732 (8.2)	1186 (20.0)	849 (11.7)	732 (6.5)	805 (6.0)	732 (5.0)	1610 (10.4)
Ephedra nevadensis	439 (4.9)	659 (11.0)	805 (11.1)	1464 (13.1)	658 (5.0)	1171 (8.0)	644 (4.2)
Ceratoides lanata	439 (4.9)	15 (0.2)	88 (1.2)	1830 (16.3)	3806 (30.4)	1171 (8.0)	790 (5.0)
Lycium andersonii	293	952	732	322	366	483	205
Machaeranthera tortifolia	0.0	29 (0.5)	37 (0.5)	37 (0.3)	0.0	293 (2.0)	76 (1.2)
Acamptopappus shockleyi	18 (0.2)	0.0	29 (0.4)	0.0	0.0	132 (1.0)	29 (0.9)
Oryzopsis hymenoides	49 (0.6)	102 (1.7)	148 (2.0)	146 (1.4)	0.0	293 (2.0)	132 (0.9)
Psorothamnus fremontii	0.0	0.0	0.0	73 (0.7)	0.0	22 (0.1)	0.0
Coleogyne ramosissima	0.0	0.0	6 (0.1)	415 (4.2)	0.0	0.0	0.0
Salazaria mexicana	73 (0.8)	0.0	0.0	0.0	0.0	0.0	0.0
Mirabilis pudica	0.0	0.0	3 (0.1)	0.0	0.0	0.0	0.0
Opuntia echinocarpa	0.0	0.0	0.0	0.0	0.0	22 (0.1)	0.0
Encelia virginensis	0.0	17 (0.2)	0.0	0.0	0.0	0.0	0.0

*A = *A. dumosa-G. spinosa.*
Ba = *K. parvifolia-L. tridentata.*
Bb = *A. dumosa-K. parvifolia.*
C = *A. dumosa-C. lanada.*
D = *C. lanata-G. spinosa.*
E = *A. dumosa-G. spinosa-E. nevadensis.*
F = *G. spinosa-A. dumosa.*
**Nomenclature according to Beatley 1976.

and identified. At threshold line 2, six clusters (A–F) were identified and named after two or more of the species with the highest density values. Stand number 6, dominated by *Grayia spinosa* (Hook.) Moq. (density = 41 percent), being dissimilar to all other stands, remained as a separate unit. At a slightly higher level of dissimilarity this stand, however, fused with a neighboring grouping codominated by *G. spinosa* and *Ambrosia dumosa* (A. Gray) Payne.

The following is a description of the vegetational groupings:

GROUPING A (A. dumosa-G. spinosa): This grouping is represented by 12 stands (Fig. 1) covering most of the northern part of the study area (Fig. 2). The two most abundant species are *A. dumosa* and *G. spinosa*. The area occupied by this grouping represents about 21 percent (10 ha) of the whole area.

The soil supporting this grouping is characterized by deeper horizons and a relatively more favorable moisture regime. Detailed physical and chemical attributes of the soil profile sampled within one of the representative stands of this grouping (Table 2) indicate predominance of coarse materials, relatively high percentage of water-soluble cations and anions, and low exchangeable sodium percentages.

GROUPING B (*A. dumosa-Krameria parvifolia* Benth.): Most of the stands (50) belong to the grouping. Inspection of Figure 1 shows that this grouping is not a natural one, and at a slightly higher similarity level (threshold line 1) there would be grounds for the identification of two subgroupings, Ba and Bb (Table 1).

SUBGROUPING BA [*K. parvifolia-Larrea tridentata* (Sesse & Moc. ex DC.) Cov.]: The area occupied by this subgrouping covers about 19 ha representing about 40 percent of the study area (Fig. 2). Properties of soil profiles collected from two representative stands within this community indicate high lime content, low values for water-soluble cations, and a moderate exchangeable sodium percentage (Tables 3 and 4).

TABLE 2. Physical and chemical attributes of soil profile at the northwest corner of the study area.

Area	Elevation feet	Slope %	Aspect	Physiography	Erosion
Rock Valley	3340	2	NE	Bajada	Moderate

Horizon	Depth cm	Color dry	Color wet	Phase	Consistence dry
A1	000–009	10YR5/4	10YR4/3	Smooth	Soft
A2	009–021	10YR7/3	10YR5/4	Smooth	Sltly hard
C1	021–032	10YR7/3	10YR5/4	Gravelly	Soft
C2	032–050	10YR7/3	10YR6/4	Cobb & Gravl	Sltly hard

Horizon	Percent moisture retention 0 Sat.	1/3 Bar	1 Bar	15 Bar	pH Paste	pH Sat. Ext.	Ec 25 (mmhos /cm)
A1	27.1	8.2	7.1	6.4	8.3	8.8	1.93
A2	22.0	13.5	11.9	8.1	8.7	8.9	0.70
C1	27.3	14.1	11.3	8.3	8.7	9.0	0.49
C2	29.1	15.4	13.0	7.8	8.7	8.9	0.65

Horizon	Organic carbon %	Exchangeable cations (MEQ/100 gm) Na	K	Ca + Mg	Exch. Na %	Cation Exch. Cap. (MEQ/100gm)
A1	1.18	1.56	3.40	7.90	1.2	12.9
A2	0.42	1.41	4.27	10.57	8.7	16.3
C1	0.36	1.22	4.27	9.51	8.1	15.0
C2	0.28	2.05	4.77	7.68	14.1	14.5

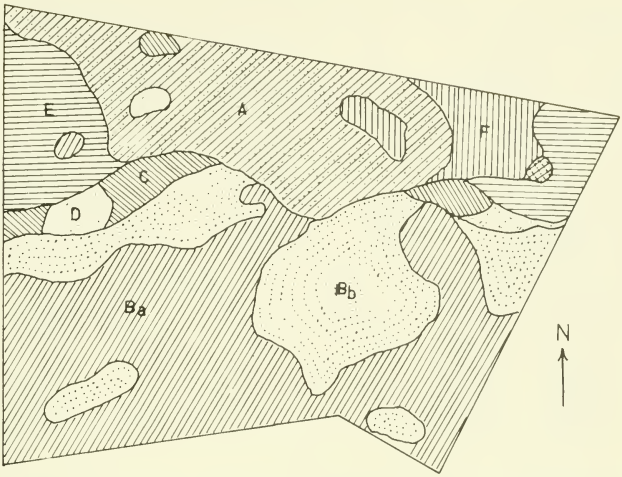


Fig. 2. Vegetation map of the Rock Valley validation site. The vegetation is divided according to the classification derived from the agglomerative clustering analysis. The groupings are: Grouping A (*A. dumosa-G. spinosa*); Grouping B (*A. dumosa-Krameria parvifolia* Benth.); Subgrouping Ba (*K. parvifolia-Larrea tridentata*); Subgrouping Bb (*A. dumosa-K. parvifolia*); Grouping C (*A. dumosa-Ceratoides lanata* Pursh J. T. Howell); Grouping D (*C. lanata-G. spinosa-A. dumosa*); Grouping E (*A. dumosa-G. spinosa-Ephedra nevadensis* S. Wats.); Grouping F (*G. spinosa-A. dumosa*).

Table 2 continued.

% Surface stoniness	Soil origin	Relief	Drainage	Permeability
20–40%	Alluvium	Smooth	Well	Moderate

Consistence moist	Consistence wet	Particle size distribution (mm) % Coarse sand 2–0.25	Fine sand 0.25–0.05	Silt 0.05–0.002	Clay <0.002
Friable	Nonsticky	40.3	51.2	4.7	3.8
Friable	Sltl sticky	45.4	33.9	13.4	7.3
Very friable	Nonsticky	43.4	40.3	10.2	6.1
Friable	Nonsticky	55.4	34.7	7.5	2.4

Percent lime (<2.0 mm)	Sat. extract soluble Na (MEQ/liter)	K	Ca	Mg	Cations and anions Cl (MEQ/liter)	NO3	SO4	Sat. Ext. Boron ppm
4.0	7.05	3.75	28.18	18.76	9.80	0.00	1.03	0.00
6.5	1.75	1.50	8.05	2.63	1.30	0.00	0.21	0.00
6.4	1.20	0.92	4.02	4.03	0.60	0.00	0.15	0.00
20.0	2.70	1.00	2.68	1.23	1.10	0.60	0.14	0.00

P (NaHCO3) ppm	DTPA-extractable micronutrients Fe ppm	Zn ppm	Cu ppm	Mn ppm	Organic N %	Structure	
3.80	1.2	0.49	0.19	4.35	.081	Wk.Fine	Sub.Ang.Bl
1.08	1.0	0.49	0.10	2.35	.048	Mod.Med.	Sub.Ang.Bl
0.80	1.5	0.57	0.13	8.10	0.27	Wk.Fine	Sub.Ang.Bl
0.52	0.8	0.55	0.18	3.20	.048	Mod.Med.	Sub.Ang.Bl

TABLE 3. Physical and chemical attributes of soil profile at the northeast corner of the study area.

Area	Elevation feet	Slope %	Aspect	Physiography	Erosion
Rock Valley	3360	1	NE	Bajada	Slight

Horizon	Depth cm	Color dry	Color wet	Phase	Consistence dry
A1	000–009	10YR4/3	10YR3/3	Smooth	Soft
A2	009–019	10YR7/3	10YR4/4	Smooth	Sltly hard
B	019–037	10YR6/4	7.5YR4/4	Gravelly	Soft
C1	037–047	10YR7/3	10YR6/4	Gravelly	Sltly hard

	Percent moisture retention						
Horizon	0 Sat.	1/3 Bar	1 Bar	15 Bar	pH Paste	pH Sat. Ext.	Ec 25 (mmhos /cm)
A1	33.0	9.4	8.0	4.4	8.1	8.2	2.27
A2	27.6	14.2	12.8	7.9	8.6	8.9	0.69
B	28.8	13.0	11.3	8.1	8.7	9.0	0.53
C1	29.3	15.2	12.7	7.3	8.7	8.8	0.53

		Exchangeable cations (MEQ/100 gm)				
Horizon	Organic carbon %	Na	K	Ca + Mg	Exch. Na %	Cation Exch. Cap. (MEQ/100gm)
A1	1.95	1.36	1.54	10.35	10.3	13.3
A2	0.25	1.43	2.93	12.64	8.4	17.0
B	0.21	1.22	2.93	12.85	7.2	17.0
C1	0.18	1.71	1.57	9.22	13.7	12.5

TABLE 4. Physical and chemical attributes of soil profile at the southwest corner of the study area.

Area	Elevation feet	Slope %	Aspect	Physiography	Erosion
Rock Valley	3360	1	NE	Bajada	Slight

Horizon	Depth cm	Color dry	Color wet	Phase	Consistence dry
A1	000–005	10YR5/3	10YR4/3	Gravelly	Soft
A2	005–018	10YR7/3	10YR5/3	Smooth	Sltly hard
A3	018–038	10YR6/3	10YR5/4	Gravelly	Soft
C1	038–063	10YR7/3	10YR5/4	Gravelly	Loose

	Percent moisture retention						
Horizon	0 Sat.	1/3 Bar	1 Bar	15 Bar	pH Paste	pH Sat. Ext.	Ec 25 (mmhos /cm)
A1	33.0	9.6	8.3	6.1	7.9	8.5	1.21
A2	17.5	12.9	11.0	7.0	8.6	8.8	0.45
A3	28.8	14.2	10.4	7.0	8.7	8.8	0.45
C1	34.5	13.2	10.9	6.4	8.6	8.9	0.62

		Exchangeable cations (MEQ/100 gm)				
Horizon	Organic carbon %	Na	K	Ca + Mg	Exch. Na %	Cation Exch. Cap. (MEQ/100gm)
A1	1.07	1.05	1.81	6.14	11.7	9.0
A2	0.24	1.24	0.99	9.02	11.0	11.3
A3	0.34	1.35	1.36	8.54	12.0	11.3
C1	0.27	1.28	0.65	7.57	13.5	9.5

Table 3 continued.

% Surface stoniness 20–40%	Soil origin Alluvium	Relief Smooth	Drainage Well	Permeability Rapid

Consistence moist	Consistence wet	Particle size distribution (mm) % Coarse sand 2–0.25	Fine sand 0.25–0.05	Silt 0.05–0.002	Clay <0.002
Friable	Nonsticky	46.0	45.8	3.6	4.6
Friable	Sltl sticky	33.3	39.5	17.7	9.5
Friable	Nonsticky	43.6	42.5	8.3	5.6
Friable	Nonsticky	51.0	36.9	8.3	3.8

Percent lime (<2.0 mm)	Sat. extract soluble Na	K	Ca	Mg	Cations and anions Cl	NO3	SO4	Sat. Ext. Boron ppm
	(MEQ/liter)				(MEQ/liter)			
3.1	2.85	4.19	25.49	9.71	5.10	0.00	0.89	0.00
5.5	0.95	1.13	8.05	2.38	1.40	0.00	0.30	0.00
3.2	0.90	0.73	4.22	4.91	1.00	0.00	0.18	0.00
3.6	1.20	0.25	4.02	1.20	2.30	0.00	0.09	0.00

P (NaHCO3) ppm	DTPA-extractable micronutrients Fe ppm	Zn ppm	Cu ppm	Mn ppm	Organic N %	Structure	
4.36	2.0	0.90	0.20	14.00	.193	Wk.Fine	Sub.Ang.Bl
1.20	0.8	0.55	0.20	3.05	.030	Wk.Med.	Sub.Ang.Bl
0.52	1.0	0.25	0.17	4.35	.023	Wk.Fine	Sub.Ang.Bl
0.24	0.6	0.28	0.19	2.10	.036	Mod.Fine	Sub.Ang.Bl

Table 4 continued.

% Surface stoniness 60–80%	Soil origin Limestone	Relief Smooth	Drainage Well	Permeability Rapid

Consistence moist	Consistence wet	Particle size distribution (mm) % Coarse sand 2–0.25	Fine sand 0.25–0.05	Silt 0.05–0.002	Clay <0.002
Friable	Nonsticky	11.6	77.9	5.8	4.7
Friable	Sltl sticky	10.0	65.6	16.5	7.9
Friable	Nonsticky	21.0	64.1	8.6	6.2
Loose	Nonsticky	24.4	62.7	6.6	6.3

Percent lime (<2.0 mm)	Sat. extract soluble Na	K	Ca	Mg	Cations and anions Cl	NO3	SO4	Sat. Ext. Boron ppm
	(MEQ/liter)				(MEQ/liter)			
5.0	1.00	4.10	20.13	13.77	1.60	0.00	0.40	0.00
13.5	0.70	0.29	4.69	1.83	0.60	0.00	0.10	0.00
21.7	0.90	0.65	3.35	1.87	1.50	0.00	0.15	0.00
19.0	3.00	0.13	4.02	1.26	1.40	0.00	0.16	0.00

P (NaHCO3) ppm	DTPA-extractable micronutrients Fe ppm	Zn ppm	Cu ppm	Mn ppm	Organic N %	Structure	
3.04	2.0	1.20	0.24	14.50	.120	Wk.Fine	Platy
0.52	0.7	0.70	0.32	2.75	.030	Str.Med.	Platy
0.52	0.7	0.80	0.20	5.60	.032	Wk.Fine	Sub.Ang.Bl
0.06	1.2	0.70	0.15	5.90	.030	No Str.	Single.Gr

SUBGROUPING BB (*A. dumosa-K. parvifolia*): This subgrouping links together 17 stands in five patches scattered in a mosaic fashion. The total area occupied by this subgrouping represents about 21 percent of the area. Inspection of Figure 2 indicates that parts of the vegetational zones constituting this subgrouping occupy transitional positions between the southern and northern halves of the study area.

GROUPING C [*A. dumosa-Ceratoides lanata* (Pursh) J. T. Howell]: This grouping comprises four stands occupying intermediate positions between most of the identified groupings. The most significant difference in floristic composition between grouping C and the neighboring groupings is the very low density of *Coleogyne ramosissima* Torr. in these later groupings, though its density in grouping C exceeds 400 plants per ha. The area occupied by grouping C represents about 2 percent of the study area.

GROUPING D (*C. lanata-G. spinosa-A. dumosa*): This is also a transitional grouping comprising two stands and occupying a tiny area covering about 1 percent of the study site. The distinction between this grouping and the neighboring ones is principally based on the relatively high abundance of *C. lanata* (Table 1).

GROUPING E (*A. dumosa-G. spinosa-Ephedra nevadensis* S. Wats.): This grouping comprises seven stands, mostly linked together at relatively low similarity levels. The area representing this grouping covers about 12 percent of the study area in two patches (Fig. 2).

The properties of soil collected from one of the representative stands of this grouping (Table 5) are characterized by relatively high phosphorus and low lime content.

GROUPING F (*G. spinosa-A. dumosa*): This grouping comprises two patches covering about 3 percent of the north-eastern part of

TABLE 5. Physical and chemical attributes of soil profile at the southeast corner of the study area.

Area	Elevation feet	Slope %	Aspect	Physiography	Erosion
Rock Valley	3360	3	NE	Bajada	Slight

Horizon	Depth cm	Color dry	Color wet	Phase	Consistence dry
A11	000–006	10YR5/3	10YR4/2	Gravelly	Loose
A12	006–012	10YR6/3	10YR4/3	Smooth	Soft
C1	012–023	10YR7/3	10YR4/3	Smooth	Soft
C2	023–034	10YR7/3	10YR4/4	Smooth	Soft
C3C	034–057	10YR6/3	10YR4/4	Cobb & Gravl	Soft

Horizon	Percent moisture retention 0 Sat.	1/3 Bar	1 Bar	15 Bar	pH Paste	pH Sat. Ext.	EC25 (mmhos /cm)
A11	31.5	8.9	7.7	5.8	8.3	8.9	1.37
A12	28.8	8.1	6.9	5.2	8.7	8.9	0.61
C1	27.6	10.5	9.3	5.6	8.8	9.0	0.44
C2	27.5	12.2	9.3	5.4	8.8	9.0	0.42
C3C	27.4	12.6	9.2	5.7	8.7	8.8	0.42

Horizon	Organic carbon %	Exchangeable cations (MEQ/100 gm) Na	K	Ca + Mg	Exch. Na %	Cation Exch. Cap. (MEQ/100gm)
A11	0.87	0.83	1.34	7.33	8.7	9.5
A12	0.49	0.74	1.36	7.99	7.4	10.0
C1	0.38	0.97	1.56	8.72	8.6	11.3
C2	0.32	1.07	1.48	6.95	11.3	9.5
C3C	0.30	1.29	1.67	7.04	12.9	10.0

the study area (Fig. 2). The big patch occupies an intermediate position between groupings A, D, and F, and the small patch represents a small island within grouping A.

The most important species of this grouping are *G. spinosa* (4978 plants/ha) and *A. dumosa* (3806 plant/ha). Subordinate species are those of *K. parvifolia* and *L. tridentata*.

It is obvious that the application of the agglomerative clustering technique in vegetation analysis has resulted in identifying distinct vegetational groupings. Although interconnected, they are quite recognizable in the field and could be used in drawing a reliable vegetation map for the study site (Fig. 2).

ORDINATION OF THE VEGETATION DATA: The ordination of stands along the second and third principal component axes is illustrated in Figure 3. The groupings and subgroupings derived from the clustering analysis exhibit a clear pattern on the ordination plane. On this plane three major vegetational zones are immediately obvious, a central zone and two lateral ones. The central zone includes subgrouping Bb and Grouping C; the right-hand side zone includes subgrouping Ba and the left-hand side zone includes groupings A, D, E, and F. The separation between these three vegetational zones is effectuated along the second principal axis. On the other hand the distinction between groupings A, C, E, and F is expressed by the third principal axis (Fig. 3).

It is worth noting that groupings A, C, D, E, and F, which exhibit fusion between their stands at remarkably low similarity levels (Fig. 1), occupy the left-hand side of the ordination plane (Fig. 3) and cover in mosaic fashion the northern half of the study area (Fig. 2). On the other hand, subgroupings Ba and Bb, whose stands fuse together at rela-

Table 5 continued.

% Surface stoniness 40–60%	Soil origin Limestone	Relief Smooth	Drainage Well	Permeability Moderate

Consistence moist	Consistence wet	Particle size distribution (mm) % Coarse sand 2–0.25	Fine sand 0.25–0.05	Silt 0.05–0.002	Clay <0.002
Friable	Nonsticky	9.6	82.8	3.9	3.7
Friable	Nonsticky	8.6	84.5	4.3	2.7
Friable	Nonsticky	8.0	80.2	7.2	4.6
Friable	Nonsticky	10.0	78.8	7.2	4.1
Friable	Nonsticky	26.8	63.8	5.6	3.8

Percent lime (<2.0 mm)	Sat. extract soluble Na	K	Ca	Mg	Cations and anions Cl	NO3	SO4	Sat. Ext. Boron ppm
	(MEQ/liter)				(MEQ/liter)			
11.4	0.60	1.25	13.42	3.53	1.20	0.00	0.35	0.00
5.5	0.25	0.70	8.05	1.08	0.70	0.00	0.16	0.00
15.0	0.30	0.60	3.87	1.34	0.50	0.00	0.14	0.00
16.0	0.40	0.73	4.02	1.19	1.50	0.00	0.14	0.00
36.5	0.45	1.00	2.68	1.23	1.10	0.00	0.14	0.00

P (NaHCO3) ppm	DTPA-extractable micronutrients Fe ppm	Zn ppm	Cu ppm	Mn ppm	Organic N %	Structure	
2.36	1.7	2.75	0.20	12.00	.091	Wk.Fine	Platy
1.64	1.2	1.45	0.15	4.00	.047	Wk.Fine	Sub.Ang.Bl
0.40	0.6	1.10	0.20	3.85	.041	Wk.Fine	Sub.Ang.Bl
0.00	0.6	0.85	0.18	4.30	.034	Wk.Fine	Sub.Ang.Bl
0.00	0.7	1.70	0.18	4.10	.032	Wk.Fine	Sub.Ang.Bl

tively high similarity levels, occupy the right-hand side of the ordination plane and cover extensive patches in the southern half of the study area.

In Figure 4 (A–F) an indication of the abundance of some common species is plotted on the stand ordination to illustrate some aspects of their phytosociological behavior. For each species, the range of density values was divided into quartiles (I-IC) in order of increasing density. Stands in which a given species concur with density values in the fourth quartile are surrounded by pecked line. For some species these stands occur in one grouping (e.g., *C. lanata* and *G. spinosa*), but for others they are distributed among two or more groupings (e.g., *L. tridentata*, *L. andersonii*, and *K. parvifolia*). It is equally clear that none of these species can be considered as leading dominant (species with the highest density value) for the whole sectors of the study area. Instead, each species exerts local dominance or is distinctly more important in certain grouping of stands.

In a previous study (Turner and McBrayer 1974), The Rock Valley validation site was subjectively divided into six vegetational zones. These zones, although differing in the relative abundance of the various species, were all characterized by having *A. dumosa* as a leading dominant species. Five of these vegetation zones occupy the northern half of

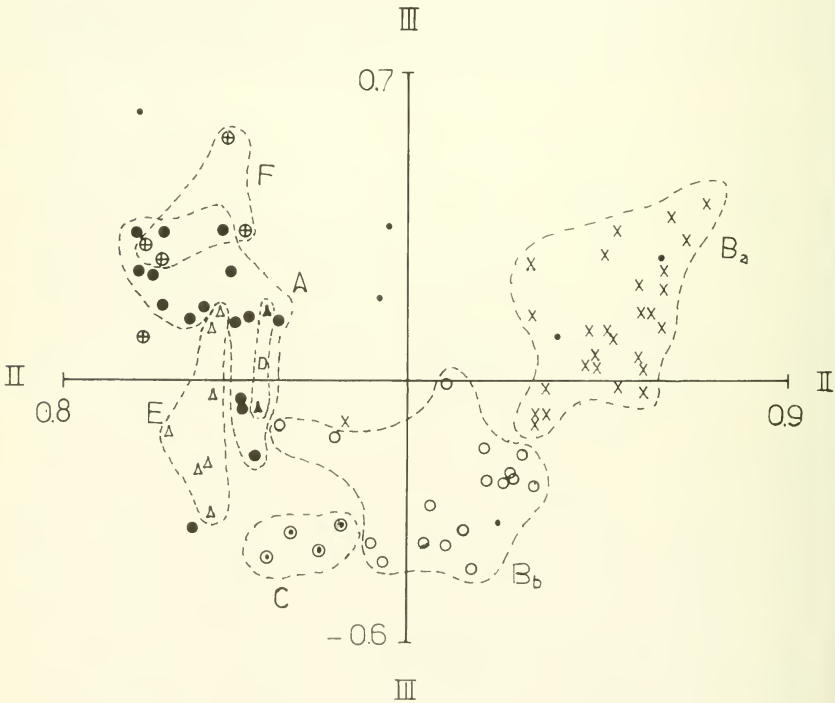


Fig. 3. Ordination plane of stands of the Rock Valley validation site in the plane of the second and third principal component axes. Pecked lines encircle stands belonging to each of the groupings and subgroupings derived from the agglomerative clustering analysis (Fig. 1).

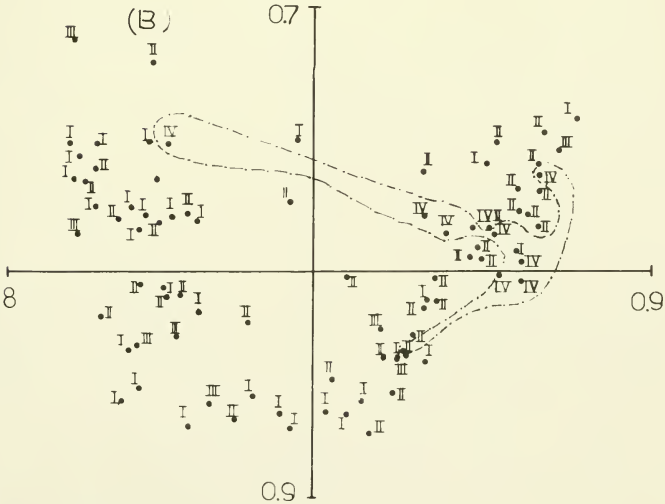


Fig. 4 (A–F). Stand ordination showing density quartiles (I–IV) on an increasing scale of density for selected spe-
es. Pecked lines surround stands in which the species is represented with a density value in the fourth quartile. (A)
mbrosia dumosa, (B) *Lycium andersonii*, (C) *Larrea tridentata*, (D) *Grayia spinosa*, (E) *Ceratoides lanata*, (F) *Kra-*
eria parvifolia.

Fig. 4 continued.

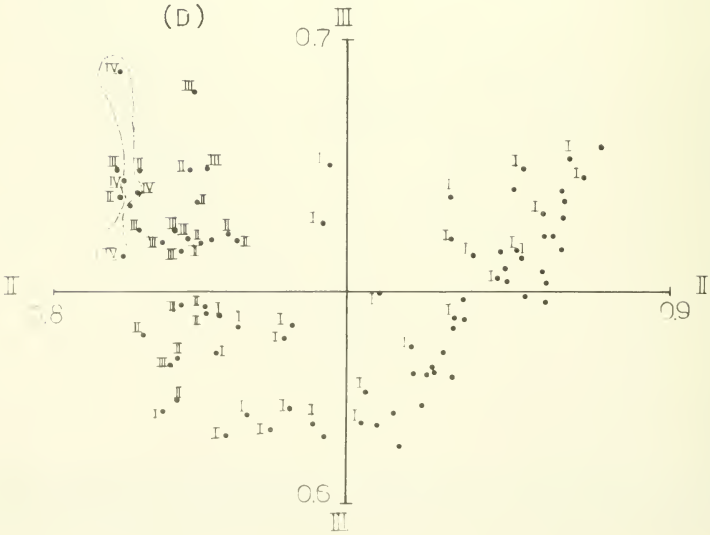
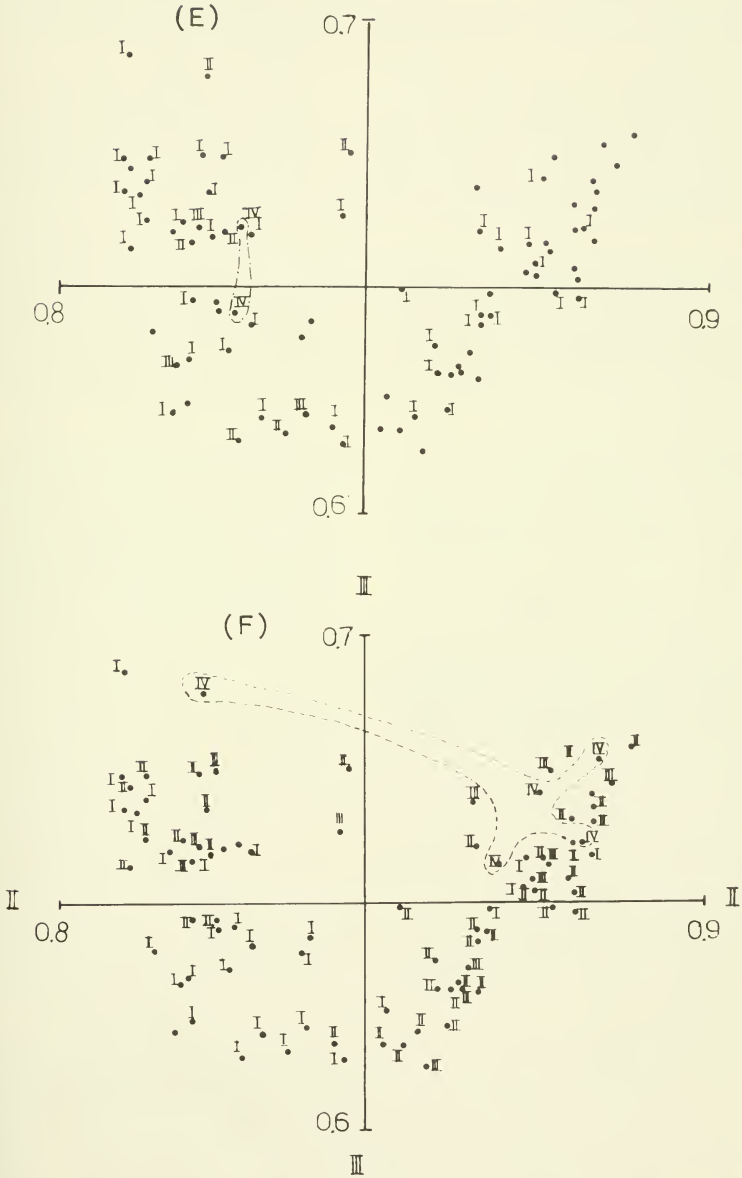


Fig. 4 continued.



the validation site; the southern half is occupied by zone six. In the present study the application of the agglomerative clustering approach in vegetation analysis, substantiated by the principal component analysis, resulted in the identification of seven vegetational groupings segregated among 20 vegetation zones (Fig. 2). In these zones the leading dominant species is not necessarily *A. dumosa*. Other species such as *K. parvifolia* and *G. spinosa* are also leading dominants in fairly extensive patches of the vegetational cover.

We arrived at the following conclusions:

1. Classification and ordination techniques have proved to be compatible, at least in a general way, and have resulted in better analysis for the vegetation date collected from the Rock Valley validation site.

2. Each species has its own distributional pattern; certain species may have similar patterns, but no two are identical.

3. Improved vegetation mapping for the study area was possible, based on vegetational groupings identified through the application of the agglomerative clustering analysis.

ACKNOWLEDGMENTS

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SOCIOECOLOGICAL AND SOIL-PLANT STUDIES OF THE NATURAL VEGETATION IN THE NORTHERN MOJAVE DESERT-GREAT BASIN DESERT INTERFACE

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ABSTRACT.— The purpose of this study is to further describe the distribution, habitats, and ecological characteristics of the natural vegetation in the northern sector of the northern Mojave Desert. Sixty-six stands were classified on the basis of shared leading dominant species. Each of these groupings is well defined and represents a sociologically distinct entity quite recognizable in the field. The relationships between each vegetational grouping and several environmental variables were statistically analyzed. Significant differences were found among plant groupings with respect to soil moisture tension, absolute and relative amounts of exchangeable Na, exchangeable K, cation exchange capacity, and elevation.

The analysis of the relationship between the phytosociological behavior of the major leading dominant species and the environmental variables shows that some of the simple, or multiple, linear correlations obtained with regard to *Larrea tridentata* (Sesse & Moc. ex DC.) Cov. were highly significant. *Atriplex confertifolia* (Torr. & Frem.) S. Wats. and *Atriplex canescens* (Pursh) Nutt. showed the highest number of significant correlations obtained.

Diversity varies from one vegetational grouping to the other as well as between stands of the same grouping. The grouping of *L. tridentata* has proved to be the most widespread, diversified, and, consequently, the most stable vegetation cover in the study area; it, therefore, represents a climax community. The vegetational grouping dominated by *A. confertifolia*, on the other hand, appears not to be a climax community.

The patchiness of the earth's surface in terms of climate, edaphic factors, and physiography extends from large areas to minute areas; that is, the difference may be major, as, for example, between desert and grassland ecosystems, or minor, as between the soil surface under a shrub and the surface a few centimeters away.

The most basic relation between the patchiness of the environment and the forms and distribution of organisms is that of plants. In given climate and soil conditions, certain plant species can survive. In addition, all plants that can survive a particular set of environmental conditions themselves contribute to local climate and microclimatic conditions; all interact to form a characteristic recognizable ecological system.

The relationship between the biotic and abiotic components of a given ecosystem is complicated, and data available that relate the behavior of the whole biotic components to a biotic factor are scarce. This paucity of data is understandable in view of difficulties involved in collection, particularly when matters are related to such large-scale ecosystems as deserts.

Additional ecological investigations in the northern Mojave Desert areas destined for various exploitations are needed. Many important studies have already been made in the general area (Allred et al. 1963, Beatley 1963, 1969, 1974, 1975, 1976, Wallace and Romney 1972, Romney et al. 1973), but much yet remains to be explained.

Special stress should be laid on the study of the natural vegetation and its synecology, with special attention to soil-vegetation relationships. This paper has an aim of providing a quantitative description of the vegetation and environment for certain sites in the northern sector of the Mojave Desert. It includes an assessment of the relationship between the distributional behavior of some vegetational groupings and local environmental variations.

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Study Area Physiography and Soil Characteristics

The physiography of the study area is described in the above references. Briefly it is characterized by low-lying, sparsely vegetated, rugged mountain ranges and intervening valleys into which the erosional material has been deposited over ages, creating extensive alluvial fanlike deposits. These deposits, extending from the bases of the mountains and hills, comprise the bajadas, or foothills. The composition of the bajadas is reflected in the source from which the erosional material was derived and the degree of incline and deposition.

Another characteristic feature of the northern Mojave Desert is those valleys in which moisture is trapped when runoff occurs from the surrounding terrain. The silt-laden waters, which eventually reach the lowest elevation in such valleys, concentrate as ephemeral bodies which, upon elevation, leave a deposit of fine silt and clay that becomes very hard when dry. These lake beds are termed playas and for the most part lack conspicuous vegetation. These physiographic features of the Mojave Desert are in some respects similar to the Arabian inland deserts in Syria, Jordan, Iraq, and Saudi Arabia.

The principal geographic areas in which the present study was conducted are located in two closed and three open drainage basins, located on the Nevada Test Site in southern Nevada. Two of the five valleys in this area, Frenchman and Yucca valleys, are closed catchment basins in which large playas exist. They, particularly Yucca, represent transition to Great Basin vegetation. The other valleys, generally known as Rock Valley and Jackass Flats and Mercury Valley, are not landlocked basins. They all have transitional Great Basin–Mojave Desert vegetation. They drain to the southwest into the Amargosa drainage system terminating in Death Valley. The northernmost flat in the study is Yucca Flat, south of which is Frenchman Flat, separated from the former by a low ridge called Yucca Pass. The alluvial thickness toward the central part of Yucca Flat is about 250–300 m, and about 200 m in the playa in Frenchman Flat (Allred et al. 1963). Most of the soils in the different study sites are calcareous, but some are low in lime because of the influence of alluvial materials of volcanic origin.

Climate

The climate of the area is also described in the above references. The study sites lie to the east and leeward side of the Sierra Nevada, which forms a massive barrier to the prevailing winds from the west. This barrier to moist air has resulted, at least in part, in a vast desert region of which the northern Mojave Desert is a part. Annual rainfall averages from 10 to 15 cm, most of which occurs in late winter. Summer rainfall is principally due to convective showers associated with thunderstorms, which in turn are induced by high humidity. This phenomenon results in considerable annual variation in precipitation, with some microgeographical variation within a given year. There is also a pronounced difference in mean annual rainfall. Snowfall is sparse in the lower valleys and usually only present for short winter periods.

The average temperatures vary with the location, from 18 to 25 C, maximum, and 4 to 11 C, minimum. The highest temperature recorded was 44 C in July 1959 at Jackass Flats; the minimum was −16 C in January 1955 at Yucca Flat.

The relative humidity varies from 2 percent to approximately 90 percent, the highest occurring in predawn hours and the lowest during daylight hours. The average is about 21 percent in summer as contrasted with 30 percent in winter.

MATERIALS AND METHODS

Selection of Stands and Vegetation Sampling

To encompass a broad spectrum and diversity of vegetation types, 66 stands were selected along the various environmental gradients encountered in the different study sites. Maps prepared by Beatley (1969) assisted in the selection. The number of stands varied according to the complexity of the vegetation from 27 in Frenchman Flat to 6 in Yucca Flat. In selecting each stand, a reasonable degree of physiognomic and physiographic homogeneity was secured by visual

judgment. Some cogent ecological attributes of perennial vegetation at each stand were determined by nondestructive, dimensional measurements. Procedural details and calculations involving this method have been reported (Wallace and Romney 1972, Romney et al. 1973). Briefly, two 2 × 25 m quadrats were laid out in undisturbed vegetation at right angles to each other. All perennial plants within each quadrat were identified to the species level and measured for height and width and size (mean of two dimensions). Shrubs with canopies overlapping the quadrat boundary were counted inside only when their root crown was inside the boundary line. Calculations using these dimensional measurements were made for each species to estimate absolute density, cover, and volume. The corresponding relative values for density and cover were then calculated and summed to give a stand-importance value ranging between 0.0 and 200.

Treatment of the Vegetation Data

When a many-species population is sampled, it is interesting to inquire whether the units are naturally classifiable into distinct groups. Pielou (1969) suggested that it was always possible to subdivide a collection of quadrats in one way or another (i.e., classify them), but it does not follow that the vegetation they represent is classifiable into well-defined separate parts. From the theoretical point of view, there are two main concepts concerning the nature of the vegetation: the association concept and the continuum concept. According to the association concept, vegetation is composed of well-defined, discrete, integrated units that can be combined to form abstract associations reflective of natural entities in the real world. According to the continuum concept, on the other hand, vegetation changes continuously and is not differentiated, except arbitrarily, into sociological entities.

In the present study, it was found that a fruitful way to proceed with vegetation study was to apply a simple approach to account for vegetation structure and then evaluate the consequences of this approach by more sophisticated mathematical arguments.

The technique adopted was originally used by Brown and Curtis (1952) as an approach for expressing the continuum nature of the upland conifer-hardwood forests of northern Wisconsin. More recently Karboush et al. (1975) have applied the same approach for classifying the fungal flora in some parts of the Egyptian desert.

According to this technique, an importance value was calculated for each species in each of the 66 stands examined. By inspection of the importance values, each stand in turn is assigned a leading dominant, i.e., that species with the highest importance value. Stands with the same leading dominant are then grouped. Obviously, some of the subordinate species in any one stand will be the leading dominants of other stands. Average importance values are then calculated for each species in each group of stands. The group of stands (or group of species) with the same leading dominant is conveniently referred to as a vegetational grouping somewhat like the ecological grouping of Whittaker (1967).

Soil Sampling and Analysis

At each stand a trench was dug extending across a representative shrub clump for a given site and out into the bare area between shrub clumps. This was done to permit an examination and sampling soil profile under both shrub and bare areas in order to investigate the modifying influence of perennial vegetation on desert soils. The depth of each trench was to the caliche hardpan, or, if no restricting layer existed, to an arbitrary depth well into the C horizon. Soil samples were taken from each profile horizon under both shrub and bare areas. These samples were screened in the field to pass a 6.3 mm sieve, and the rock and gravel contents were estimated and discarded. The remaining samples were transported to the laboratory, where they were oven dried and then further screened to pass a 2 mm sieve. Available phosphorus was extracted with sodium bicarbonate and determined colorimetrically using the method of Olsen et al. (1954) as described by Chapman and Pratt (1961). Lime content was determined by the manometric method of Williams (1948). The available iron, zinc, copper, and manganese were ex-

tracted with DTPA (diethylene triamine pentaacetic acid) chelate and determined by atomic absorption as described by Lindsay and Norvell (1969). Organic nitrogen analysis was by the Kjeldahl method (Bremner 1965). Analytical methods used to determine other physical and chemical properties were those of the USDA Salinity Laboratory Staff (1954).

In the present paper, unless otherwise mentioned, correlation is made between properties of soils collected under the shrub and plant. Data for all soil profile variables have been adjusted through a computer program to mean values for the 2.5 to 30 cm soil depth.

RESULTS

Spatial Variations in Vegetation Cover

The data from the phytosociological analysis that aim at providing a picture of the general composition of the perennial vegetation of the study areas are given in Table 1. Thirty-five species were encountered. None of these species can be considered as a leading dominant of the whole study area; instead, some exhibit local dominance or are distinctly more important in certain groups of stands. Six major vegetational groupings have been defined (Table 1). The number of stands for each grouping varies between 15 for the most representative species (*L. tridentata*) and 5 for the least (*Grayia spinosa* (Hook.) Moq. and *Acamptopappus shockleyi* A. Gray). Each of the leading dominant species of these groupings, i.e., *L. tridentata*, *Ambrosia dumosa* (A. Gray) Payne, *G. spinosa*, *A. shockleyi*, *Atriplex confertifolia*, and *Atriplex canescens*, attained a maximum stand-importance value of more than 100 out of 200 and an average group-importance value, based on the structure of the stands in each group of that particular species, of more than 66 (Table 1).

Another five vegetational groupings of minor representation have also been identified. Each of the leading dominant species of these groupings, viz., *Coleogyne ramosissima* Torr., *Lycium shockleyi*, *Menodora spinescens* A. Gray, *Ephedra nevadensis* S. Wats., and *Krameria parvifolia* Benth. attained an absolute maximum importance value of more than 60 and an average value of more than 50. Each of these groupings is represented by a minimum of two stands and a maximum of four.

Some other species, such as *Lepidium fremontii* S. Wats., *Ceratoides lanata* (Pursh) J. T. Howell, *Hymenoclea salsola* Torr. and Gray, *Lycium andersonii* A. Gray, *Psorothamnus fremontii* (Torr.) Barneby, *Lycium pallidum* A. Gray, and *Oryzopsis hymenoides* (Roem. & Schult.) Ricker, though important and common species, are not dominant and accordingly are not included in the provisional arrangement of leading dominant species.

An ecotonal grouping has also been identified (Table 1). It includes six stands in which the dominance is shared by two or more species of the nonleading dominants. Thus, almost 10 percent of the stands did not fit into the system.

It is clear from Table 1 that, in the vegetational grouping dominated by *L. tridentata* (I.V. = 87) (I.V. is importance value), the subordinate species are *A. dumosa* (I.V. = 31) followed by *L. andersonii* (I.V. = 17). Other species associated with *L. tridentata* are mostly of minor importance because their average importance values are generally below 10. In the *A. dumosa* grouping (I.V. = 80) the next highest importance value to that of *A. dumosa* is 31 for *L. tridentata* and 15 for *G. spinosa*. Other species of some importance are *K. parvifolia* (I.V. = 12) and *E. nevadensis* (I.V. = 11). In the *G. spinosa* grouping (I.V. = 79), the subordinate species were *L. andersonii* (I.V. = 27) and *L. tridentata* (I.V. = 20). Other important species in this grouping are *A. dumosa* (I.V. = 16) and *E. nevadensis*. In the *A. shockleyi* grouping (I.V. = 66), the species second in importance is *L. tridentata* (I.V. = 31) followed by *G. spinosa* (I.V. = 22), *L. andersonii* (I.V. = 16), and *A. dumosa* (I.V. = 15). *Ceratoides lanata* (I.V. = 13) is also of some significance in this grouping. The vegetational groupings of *A. confertifolia* (I.V. = 129) and *A. canescens* (I.V. = 137) are of some interest. In the first grouping only one species, *L. tridentata*, seems of some importance (I.V. = 25). All other species are of very low importance value and consequently of minor significance in community structure. In the vegetational

grouping, the species second in importance is *A. confertifolia*, but its very low importance value of 13 makes it of minor significance in this grouping. Another point of interest is the relatively very low number of species in these two groupings. In either grouping the number of species does not exceed 10, compared with about 20 in the other vegetational groupings. It is also obvious from Table 1 that *L. tridentata*, which is an integral component of all other vegetational groupings identified, is missing from the *A. canescens* grouping.

The structure of the vegetational groupings defined as being of minor representation is also given in Table 1. *Larrea tridentata* can be considered as a common species in all groupings. It is, however, particularly well represented in the *M. spinescens* and *A. shockleyi* groupings. Its importance values in these two groupings are 47 and 31, respectively. The high (112) importance value of *C.*

TABLE 1. Average importance values of plant species in provisionally defined vegetational groupings.

	VEGETATIONAL GROUPINGS											
	Major						Minor					
SPECIES	*L. trid*	*A. dum.*	*G. spin.*	*A. shock.*	*A. conf.*	*A. can.*	*C. ram.*	*L. shock*	*M. spin.*	*E. nev.*	*K. par.*	Ecotonal
A. LEADING DOMINANTS												
Larrea tridentata (15)*	87	31	20	31	25	—	17	31	47	22	19	17
Ambrosia dumosa (10)	31	80	16	15	4	0.6	0.2	8	3	15	29	18
Grayia spinosa (5)	10	15	79	22	—	0.5	7.5	—	1.5	—	23	18
Acamptopappus shockleyi (5)	6	9	8.6	66	2	—	—	21	3.5	—	—	6
Atriplex confertifolia (6)	5	—	—	—	129	13	—	—	—	—	—	4.4
Atriplex canescens (6)	3	1	—	—	9	137	3.2	33	2	15	—	—
Coleogyne ramosissima (4)	—	7	—	—	—	—	112	6	—	—	—	—
Lycium shockleyi (3)	—	—	—	—		—	—	88	—	—	—	—
Mendora spinescens (2)	3	5	—	—	0.6	—	1.2	5	79	26	—	0.2
Ephedra nevadensis (2)	5	11	10	5	—	—	16	—	16	73	25	9
Krameria parvifolia (2)	6	12	—	5	—	—	—	3.6	11	38	54	11
B. COMMON												
Lepidium fremontii (1)	1	0.2	0.4	0.6	—	—	—	—	—	—	—	17.3
Ceratoides lanata	5	3.5	9	13	7	7	1.8	—	5	5.5	4.6	23
Hymenoclea salsola	1	—	4	3	4	4	—	0.3	—	—	—	4
Lycium andersonii	17	8.7	27	16	—	—	15	—	4	—	32	21
Dalea fremontii	1	1.4	—	0.1	—	—	0	1.2	—	—	—	25
Lycium pallidum	3	5	5	3	—	—	—	—	—	—	15	14.4
Oryzopsis hymenoides	6	9	9	11	2	2	—	2.7	9	5	1.9	6.4
C. INFREQUENT OR OF MINOR IMPORTANCE												
Sphaeralcea ambigua	3	1.4	—	1.4	0.5	0.5	1.3	1.5	3.5	—	—	1
Yucca schidigera	4	—	—	1.3	—	—	—	—	—	—	—	—
Ephedra funerea	1.4	1	—	—	—	—	—	1.5	0.3	—	—	—
Hilaria rigida	—	—	—	—	—	—	—	—	—	—	—	—
Stanleya pinnata	—	—	—	—	—	—	—	—	—	—	—	15.8
Mirabilis pudica	—	—	—	—	—	—	—	0.2	—	—	—	0.3
Tetradymia axillaris	—	—	1	0.6	—	—	2.2	—	—	—	—	1.2
Stipa speciosa	—	—	5.2	—	—	—	11	—	—	—	—	1.5
Artemisia spinescens	—	—	1	—	—	—	—	—	—	—	—	1.1
Dalea polyadenia	1	—	—	—	—	—	—	—	—	—	—	—
Cactus sp.	0.7	—	0.1	—	—	—	—		0.8	—	—	1.1
Prunus fasciculata	—	—	—	—	—	—	—	—	—	—	—	0.5
Salazaria mexicana	—	0.1	—	—	—	—	—	0.9	—	—	—	—
Yucca brevifolia	1.5	—	—	—	—	—	7.5	0.7	—	—	—	—
Thamnosma montana	0.2	—	—	—	—	—	—	—	—	—	—	—
Haplopappus cooperi	—	—	3.1	1.2	—	—	—	—	—	—	—	—
Machaeranthera tortifolia	—	—	1	—	1	—	—	3	—	—	—	—

*Number of stands in which the species is the leading dominant.

ramosissima reflects the nonsignificance of other associated species except for *L. tridentata* (I.V. = 17) and *E. nevadensis* (I.V. = 16). In the *A. shockleyi* (I.V. = 88) grouping the subdominance is shared by *A. canescens* (I.V. = 33), *L. tridentata* (I.V. = 31), and *A. shockleyi* (I.V. = 21). In the *M. spinescens* (I.V. = 79) grouping, which is only represented by two stands, *L. tridentata* plays an important role in community structure (I.V. = 47), followed by *E. nevadensis* (I.V. = 16) and *K. parvifolia* (I.V. = 11). Other species are of minor significance. In the vegetational groupings of *C. ramosissima*, *A. shockleyi*, and *M. spinescens*, the number of species is quite high. Each community is represented by at least 14 species. On the other hand, in the two minor groupings of *E. nevadensis* and *K. parvifolia* the number of species in either community is generally below 10. In these last two groupings subdominance is shared by many species. In the *E. nevadensis* grouping the subdominant species are *K. parvifolia* (I.V. = 38), *M. spinescens* (I.V. = 26), *L. tridentata* (I.V. = 22), *A. dumosa* (I.V. = 15), and *A. canescens* (I.V. = 15). In the *K. parvifolia* grouping (I.V. = 54), *Lycium andersonii* is of great significance in community structure (I.V. = 32), followed by *A. dumosa* (I.V. = 29) and *E. nevadensis* (I.V. = 25). In fact, the relatively low importance value of *K. parvifolia* brings this group close to certain ecotonal communities. In the arbitrarily designated ecotonal grouping (Table 1) the dominance is shared by many species. This grouping is characterized by a number of species, a character generally associated with transitional zones or effects.

Nature of Relationships between Groupings

Relations between different vegetational groupings may be expressed in terms of similarity indices for pairs. Some of these depend on the number of species common to the two groupings in relation to the total number present, and others depend on quantities present.

In the present study, the similarity between different groupings identified was assessed with the use of Spatz's (1970) formula as given by Dombois and Ellenberg (1974).

"Index of similarity (I.S.) =

$$R \times \frac{Mc}{Ma + Mb + Mc} \times 100$$

The first component (R) is an expression of the relative similarity of the two groupings being compared, and is calculated by dividing the smaller quantitative value of the species common to the two groupings by the greater quantitative value. The resulting fractions for each of the species in common are added and divided by the total number of species in the two groupings. Mc is the sum of importance values of the species common to both groups, Ma is the sum of importance values of species restricted to grouping (a) and Mb is the sum of importance values of species restricted to grouping (b)."

According to Dombois and Ellenberg (1974) this index has greater sensitivity to quantitative difference than any other index.

In Table 2 are represented the coefficients of similarities between the different group-

TABLE 2. Similarity indices between different vegetational groupings.

VEGETATIONAL GROUPINGS	*L. tri.*	*A. dum.*	*A. can.*	*A. conf.*	*G. spin.*	*A. shoc.*	*C. ram.*	*L. shoc.*	*M. spin.*	*E. nev.*	*K. par.*
L. tridentata	—	38	6	16	31	44	13	13	29	17	22
A. dumosa			9	9	34	33	21	18	32	17	24
A. canescens				4	6	2	1	1	2	2	4
A. confertifolia					7	8	6	14	18	16	4
G. spinosa						43	11	3	18	11	33
A. shockleyi							3	15	17	12	23
C. ramosissima								3	7	7	8
L. shockleyi									9	9	5
M. spinescens										24	16
E. nevadensis											23

ings identified. It is clear that similarity coefficients between groupings are generally low. Among the highest coefficients are those between the *L. tridentata* grouping and those of *A. shockleyi* (44), *A. dumosa* (33), and *G. spinosa* (31). The *A. dumosa* grouping also has some relatively high similarity indices with those of *G. spinosa* (34), *A. shockleyi* (33), and *M. spinescens* (32). *Grayia spinosa* grouping has high similarity indices with those of *A. shockleyi* (43) and *K. parvifolia* (33). It is interesting to notice that the lowest similarities obtained are those between the grouping of *A. canescens* and all other groupings.

Distribution of Stands with Leading Dominants among the Different Study Sites

In Table 3, stands are grouped according to leading dominant species and the different sites are investigated, viz., Mercury Valley, Frenchman Flat, Rock Valley, Jackass Flats, and Yucca Flat. The average density of the leading dominant species in each of these sites is also presented. *Larrea tridentata* was dominant in 15 stands, 9 of which were in Frenchman Flat (Table 3). The average density of *L. tridentata* within its stands in this site is 1244 plants/ha. The only site in which *L. tridentata* is not represented by stands in which it is a dominant species is Yucca Flat, although *L. tridentata* does occur in the transitional basin (Beatley 1974).

Ambrosia dumosa, on the other hand, is poorly represented in Frenchman Flat and is not dominant in Yucca Flat. In Jackass Flats, where *A. dumosa* is well represented (4 stands out of 10), its average density is 5875 plants/ha. *Grayia spinosa* is also well represented in Yucca flat with an average density of 5600 plants/ha.

Acamptopappus shockleyi shows its dominance in Mercury Valley (3 stands) and Jackass Flats (2 stands). Its average density in these two sites is 7400 and 6300 plants/ha, respectively.

Atriplex confertifolia and *A. canescens* reach maximum dominance in Frenchman Flat. One stand with *A. confertifolia* as a leading dominant has been reported in Mercury Valley. The average density per hectare for either of the two species (in Frenchman Flat) is about 3400 plants.

Grayia spinosa is mostly represented in Yucca Flat, and *L. shockleyi* is represented only as a leading dominant species in Frenchman Flat. Stands in which *M. spinescens* and *E. nevadensis* are dominants are equally distributed between Frenchman flat and Jackass Flats, but the stands in which *K. parvifolia* is dominant are highly localized.

Soil Characteristics in Relation to Major Vegetational Groupings

Horizontal variations in some of the soil characteristics among different major vegetational groupings are summarized in Table 4.

TABLE 3. Distribution of stands with leading dominant species among the different study sites, and the average absolute density for each species (no. of plants/ha). (No. of stands in which each species is dominant.)

	SITE				
LEADING DOMINANT SPECIES	Mercury Valley	Frenchman Flat	Rock Valley	Jackass Flat	Yucca Flat
Larrea tridentata	3 (1233)*	9 (1244)	2 (1850)	1 (700)	—
Ambrosia dumosa	3 (3962)	1 (4800)	2 (4400)	4 (5875)	—
Grayia spinosa	1 (3500)	1 (3900)	1 (4800)	—	2 (5600)
Acamptopappus shockleyi	3 (7400)	—	—	2 (6300)	—
Atriplex confertifolia	1 (2900)	4 (3370)	—	—	—
Atriplex canescens	—	6 (3430)	—	—	—
Coleogyne ramosissima	—	—	—	1 (1410(	3 (5370)
Lycium shockleyi	—	3 (5130)	—	—	—
Menodora spinescens	—	1 (7700)	—	1 (4400)	—
Ephedra nevadensis	—	1 (3300)	—	1 (600)	—
Krameria parvifolia	—	—	2 (2500)	—	—

*Number between parentheses indicates average density (plants/ha).

A general idea about the magnitude of variation in each of these soil variables can be gained if the average and range are examined. A more precise judgment, however, may be achieved by examining the results of analysis of variance given in Table 5. In this table the ordered means of soil variables that show significant variations among major vegetational groupings are presented. Six soil variables out of 16 (given in Table 4) show significant variations: soil moisture retention capacity at 0.0 bar, exchangeable Na, ex-

TABLE 4. Average and range of soil variables in different major vegetational groupings (for statistical difference see Table 5).

	VEGETATIONAL GROUPINGS					
SOIL VARIABLE	*L. tridentata*	*A. dumosa*	*G. spinosa*	*A. shockleyi*	*A. confertifolia*	*A. canescens*
Soil moisture retension at 0.0 bar	12.7 7.6–20.6	9.7 4.8–16.0	12.4 8.8–17.8	12.5 5.1–18.9	13.5 10.4–17.0	19.3 8.8–33.5
pH	8.64 8.3–8.8	8.5 7.8–8.8	8.5 8.4–8.7	8.3 8.4–8.8	8.66 8.3–8.9	8.65 8.5–8.8
E.C. mmhos/cm	1.84 1.0–3.3	1.17 0.39–2.5	1.65 1.2–2.6	1.15 1.1–2.6	1.45 0.3–3.0	1.88 0.55–3.2
Lime %	13.3 0.9–30	6.0 0.1–14.3	8.1 1.0–22.9	10.0 0.2–20.7	12.5 5.7–24.4	13.8 2.4–30
Ex. Na^+ meq/100 gm	0.41 0.2–1.0	0.33 0.22–0.6	0.41 0.2–0.73	0.42 0.3–0.53	2.22 0.2–0.4	0.55 0.4–0.8
Ex. K^+ meq/100 gm	4.47 2.5–8.1	3.38 2.1–5.6	4.66 2.8–8.7	2.89 2.6–3.6	7.56 3.2–13.5	5.66 0.9–9.1
Ex. Ca^{++} + Mg^{++} meq /100 gm	7.86 4.1–11.8	7.52 2.6–13.4	9.11 7.4–11.3	8.72 3.5–12.9	9.08 2.6–18.0	7.31 5.7–10.9
Ex. Na^+ %	3.39 1.7–8.4	3.18 1.5–7.6	4.76 1.7–3.8	3.68 2.5–5.6	12.1 2.6–22.1	3.42 1.9–6.2
Cat. Ex. Cap. meq/100 gm	12.8 9.5–15.8	11.3 6–17	14.2 11.2–18.8	12.4 6.9–16.0	15.3 8.4–19.3	17.2 12.6–22.5
($NaHCO_3$) phosphorus ppm	1.88 0.2–4.3	1.56 0.5–3.3	2.2 1.1–5.7	1.8 0.7–3.4	0.52 0.2–1.2	1.5 0.8–2.3
(DTPA) Iron ppm	0.33 0.1–0.7	0.31 .02–0.6	0.33 0.3–0.6	0.38 0.2–0.5	0.16 0.1–0.3	0.23 0.1–0.3
(DTPA) Zinc ppm	0.67 0.3–1.33	0.46 0.2–0.67	0.52 0.31–0.8	0.6 0.3–1.3	0.51 0.3–0.7	9.44 0.16–0.73
(DTPA) Copper ppm	0.13 0.1–0.22	0.126 0.05–0.2	0.23 0.13–0.45	0.15 0.1–0.26	0.16 0.1–0.2	0.22 0.1–0.27
(DTPA) Manganese ppm	2.58 1.2–3.8	2.51 0.9–5.1	2.6 1.6–3.8	3.0 1.3–6.1	1.96 1.2–3.0	2 1.0–2.55
Org. nitrogen %	0.07 0.04–0.095	0.062 0.026–0.12	0.07 0.04–0.1	0.09 0.02–0.13	0.03 0.02–0.04	0.06 0.03–0.08
Elevation m	1030 960–1134	1007 910–1085	1199 991–1463	1070 1037–1104	997 939–1207	955 945–979

changeable K, exchangeable Na expressed as percentage of the total cations, cation exchange capacity, and elevation. The vegetational grouping of *A. dumosa* occupies the stands with the lowest level of soil moisture retention. Groupings of *A. canescens*, on the other hand, occupy stands with the highest moisture retention. Other groupings occupy intermediate positions along the soil moisture retention gradient. Along the exchangeable sodium gradient, the grouping of *A. confertifolia* occupies a significantly high position. The response of the different vegetational groupings to exchangeable K is rather significant. The two groupings of *A. shockleyi* and *A. dumosa* occupy the lower end of the gradient; *A. canescens* occupies the highest portion, and the other groupings are of intermediate positions. In exchangeable Na, expressed as percentage of the total cations, the grouping of *A. confertifolia* occupies soils having the highest levels. It is of interest to notice that the grouping of *A. canescens* occupies an intermediate position along the sodium percent gradient. On the other hand, when we consider the gradient of the total cation exchange capacity, we find that the grouping of *A. canescens* occupies the highest level. *Atriplex canescens* does populate low-lying areas that have accumulated clay and silt. The distribution of the different vegetational groupings along the elevation gradient presents another point of interest. There is a stepwise segregation of groupings with altitudinal zonation. The grouping of *A. canescens* occupies the lower level of the gradient, and *G. spinosa* occupies the highest level.

Behavior of Leading Dominant Species along an Environmental Gradient

According to Dagnelle (1965), correlation of species with particular environmental variables has much potential as a tool for explanation of plant distribution though, as always with correlation or regression studies based on observational data, conclusions regarding causation must be hedged with reservation. In this case, the reservations are most likely to concern doubts whether the environmental variable studied is directly responsible or whether it is merely associated with the variable to which the effect observed should be properly ascribed.

In the present study the simple linear correlation between the soil variables and both the importance values and the absolute densities (abundance) for the six major leading dominant species has been calculated (Table 6). The number of significant correlations obtained are very few for most of the species. The results are to be interpreted with caution. The importance value of *L. tridentata* shows one positive correlation ($P<0.05$) with electrical conductivity (E.C.). This correla-

TABLE 5. Ordered means for soil parameters that showed significant variations among different major vegetational groupings, according to the analysis of variance for unequal cell sizes.

SOIL VARIABLES						
Soil moisture retention	9.7 (Ad)	12.4 (Gs)	12.5 (As)	12.7 (Lt)	13.5 (Ao)	19.4 (Ac)*
Ex. Na^+ meq/100 gm	0.33 (Ad)	0.41 (La)	0.41 (Gs)	0.42 (As)	0.55 (Ac)	2.22 (Ao)
Ex. K^+ meq/100 gm	2.87 (As)	3.38 (Ad)	4.47 (La)	4.66 (Gs)	5.66 (Ao)	7.56 (Ac)
Ex. Na^+ %	3.18 (Ad)	3.39 (Ld)	3.42(Ac)	3.68 (As)	4.76 (Gs)	12.1 (Ao)
Cation ex. cap. meq/100 gm	11.3 (Ad)	12.4 (As)	12.8 (La)	14.2 (Gs)	15.3 (Ao)	17.2 (Ac)
Elevation m	955 (Ac)	977 (Ao)	1007 (Ad)	1030 (Ld)	1070 (As)	1199 (Gs)

*The means parenthesed are not different from each other; those over different parentheses are. La = *Larrea tridentata*, Ad = *Ambrosia dumosa*, Gs = *Grayia spinosa*, As = *Acamptopappus shockleyi*, Ao = *Atriplex confertifolia*, Ac = *Atriplex canescens*.

tion, however, does not necessarily mean that *L. tridentata* is really increasing its abundance with the progressive increase in E.C. Examining the correlation of the absolute density of the same species with the same soil variable shows that there is no significant correlation and that the trend of correlation present is even negative. Accordingly, the positive correlation of the importance value of *L. tridentata* with E.C. is actually due to

TABLE 6. Simple correlation coefficients (r) between the importance value (a) and the absolute density (b) of major leading dominant species and soil variables. A single asterisk denotes a significant correlation at the 5 percent probability level, and double, triple, and quadruple asterisks denote a highly significant correlation at the 2, 1, and 0.1 percent probability levels.

		SPECIES					
SOIL VARIABLE		*L. tridentata*	*A. dumosa*	*C. spinosa*	*A. shockleyi*	*A. confertifolia*	*A. canescens*
Soil moisture retention at 0.0 bar	a	-0.036	-0.34°°	0.11	0.01	-0.16	0.61°
	b	0.223	-0.39°°°	-0.18	0.01	0.16	0.91°°°°
pH	a	0.19	-0.15	-0.03	-0.41°°	0.05	0.31
	b	-0.10	-0.17	-0.16	-0.16	-0.07	0.18
E.C. mmhos cm	a	0.326°	-0.20	0.23	0.03	0.5°°	0.23
	b	-0.071	-0.21	-0.14	0.02	0.15	-0.12
Lime %	a	0.078	-0.27	-0.18	-0.09	-0.25	0.58°
	b	0.22	-0.33°	-0.15	-0.03	-0.10	0.91°°°°
Ex. Na meq/ 100 g	a	-0.245	-0.31°	-0.17	-0.17	0.45°	-0.35
	b	-0.09	-0.28	-0.10	-0.15	0.63°°°	-0.31
Ex. K meq/ 100 g	a	0.226	-0.19	-0.002	-0.21	0.23	-0.01
	b	-0.027	-0.19	-0.05	-0.23	-.10	-0.39
Ex. Ca + Mg meq/ 100 g	a	-0.17	-0.11	0.08	0.06	0.40	0.45
	b	-0.06	-0.06	-0.004	0.07	0.13	0.78°°°
Ex. Na^+ %	a	-0.27	-0.31°	-0.21	-0.05	0.49°°	-0.4
	b	-0.089	-0.27	-0.14	-0.06	0.56°°°	-0.44
Cat Exc Cap meq/ 100 g	a	0.24	-0.12	0.03	-0.15	0.1	0.32
	b	0.04	-0.13	0.01	-0.15	0.35	0.38
($NaHCO_3$) P ppm	a	0.20	-0.01	0.16	0.19	-0.35	0.02
	b	0.14	-0.02	0.10	0.23	-0.60°°°	-0.06
(DTPA) Fe	a	-0.21	-0.14	0.14	0.19	-0.40	0.5°
	b	-0.10	-0.02	0.31	0.21	-0.053°°	0.43
Zn	a	0.004	-0.33°	-0.17	0.13	-0.16	-0.26
	b	0.009	-0.35°°	-0.11	0.17	0.08	-0.31
Cu	a	-0.02	-0.15	0.39°°	0.06	0.16	0.58°
	b	-0.21	-0.22	0.33°	0.07	0.09	0.55°°
Mn	a	0.02	-0.06	0.04	0.33	0.07	0.06
	b	0.03	-0.03	0.09	0.4°°	0.31	0.34
Total N %	a	0.09	-0.19	0.02	0.35°	-0.31	0.69°°°
	b	0.10	0.02	0.04	0.36°	-0.49°	0.51
Elevation m	a	-0.1	-0.28	0.8	0.17	-0.18	-0.68°°°
	b	-0.2	-0.14	0.39°°	0.20	0.05	-0.7°°°

the decrease in the abundance of its associated species. In fact, all species, including *L. tridentata*, are decreasing their abundance along the E.C. gradient, but *L. tridentata* has the slowest rate.

The correlation between *A. dumosa* and exchangeable Na shows similar results. On the other hand, the abundance of *A. dumosa* shows decidedly significant correlation (negative) with soil moisture retention ($r = -0.39$; $P < 0.01$) and lime ($r = -0.31$; $P < 0.02$). However, the coefficient of determination (r^2) is actually a very low percentage. The abundance and the importance value of *G. spinosa* are positively correlated with copper at 2 percent and 5 percent levels of significance for the two parameters, respectively. The abundance of *G. spinosa* is also positively correlated with altitude ($r = 0.39$; $P < 0.02$). The importance value and abundance of *A. shockleyi* are correlated negatively with pH and positively with total nitrogen, but most of these correlations are at the 5 percent level of significance. The abundance of this species shows also a positive correlation with extractable Cu at the 2 percent level of significance. The highest number of significant correlations obtained are those between *Atriplex* species and the abiotic variables. The abundance of *A. confertifolia* shows positive correlations with both absolute and relative amounts of exchangeable Na at the 0.1 percent level of significance. On the other hand, it shows negative correlations with phosphorus ($P < 0.01$), iron ($P < 0.02$), and total nitrogen ($P < 0.05$). The importance values of *A. confertifolia* show only two positive correlations with both absolute and relative amounts of exchangeable Na at the 5 percent and 1 percent levels of significance. *Atriplex canescens* behaves in a different manner; it shows no correlation with any of the soil variables associated with *A. confertifolia* (Table 6). Four soil variables, namely, soil moisture retention, lime, exchangeable Ca + Mg, and Cu show strong positive correlations with the abundance of *A. canescens*. The high values for the coefficient of determination (r^2) of 0.83 for soil moisture, 0.3 for lime, 0.63 for Ca + Mg, and 0.42 for Cu indicate the significance of the role of these soil variables in affecting the distribution and abundance of *A. canescens*. The negative correlation of the same species with altitude is also highly significant. This may be related to drainage in that the species does occur at the bottom of drainage basins. The importance value of *A. canescens* also shows positive correlations (but mostly at low significance) with soil moisture retention, lime, copper, and total nitrogen.

The multiple linear correlations (R) relating the abundance of the different leading dominant species and the different combinations of soil variables are given in Table 7. *Atriplex confertifolia*, *A. canescens*, and *A. shockleyi* show the greatest number and the highest magnitude of significant relationships with the different combinations of soil variables. *Larrea tridentata*, *A. dumosa*, and *G. spinosa* show smaller numbers of significant correlations.

The following are multiple regression equations relating the absolute density (number of plants/ha of the three species highly correlated with the different combinations of environmental variables: (for the level of significance see Table 7).

A) *Atriplex canescens*

Absolute density = 1.04 moisture retention % + 1.0 lime % - 2.72 ($R = 0.9^{****}$)

Absolute density = 51.3 - 5.5 pH + 1.92 lime % ($R = -0.92^{****}$)

Absolute density = 0.19 - 3.1 Na % + 0.26 K% + 3.32 (Ca + Mg)% ($R = 0.82^{****}$)

Absolute density = 15.3 + 58.2 Fe ppm - 26.7 Zn ppm + 148.4 Cu ppm - 6.7 Mn ppm ($R = 0.72^{***}$)

B) *Atriplex confertifolia*

Absolute density = 10.1 pH - 10.5 P% - 199 N% - 50.1 ($R = 0.7^{***}$)

Absolute density = 9.53 Na% - 0.7 K% + 1.05 (Ca + Mg)% - 0.157 ($R = 0.7^{***}$)

C) *Acamptopappus shockleyi*

Absolute density = 365.7 - 34.3 pH + 1.6 P% + 359.6 N% ($R = 0.6^{****}$)

Diversity in Different Vegetational Groupings

The various ways of defining and measuring diversity have been reviewed and dis-

cussed by Pielou (1969). According to Pielou's definition, diversity is a single statistic in which the number of species and the evenness (uniform distribution of individuals among species) are combined. A collection is said to have high diversity if it has many species and their abundance is fairly even. Conversely, diversity is low when the species are few and their abundance uneven. It should be noted, however, that diversity is sometimes used as a synonym for a number of species; that is not the sense in which it is used here.

In the present study, the Simpson's (1949) measure of diversity as quoted by Pielou (1969) has been used for calculating the diversity in the different major vegetational groupings. This index reads as follows:

$$D = 1 - \frac{1}{N(N-1)} \sum_j N_j(N_j - 1)$$

where D is Simpson's measure of diversity in an S species collection containing N individuals, of which N_j belongs to the jth species

$$(j = 1, 2, 3, -, S; \sum_j N_j = N)$$

The results of this study are given in Table 8. The vegetational groupings studied can be classified into two main categories. The first category is characterized by low diversity (<0.4) as well as by a wide range of variation. This category includes the vegetational groupings of *A. confertifolia* and *A. canescens*. In one of the stands of *A. confertifolia* the whole population is *A. confertifolia* with a consequent zero diversity. The second category includes the groupings *L. tridentata*, *A. dumosa*, *G. spinosa*, and *A. shockleyi*. The diversity in these groupings is fairly high (>0.7) and with a narrow variation range. These results obviously indicate the poverty in species and unevenness in the distribution of individuals among species in stands representative of the vegetational groupings of the first category. Conversely, there are a richness in species and an evenness in individual distribution in stands representative of the vegetational groupings in the second category.

DISCUSSION

Since climatic, topographic, edaphic, and biotic conditions vary to a greater or lesser degree within a landscape, numerous habitats and plant communities are formed and become manifest in a mosaic or zonation of vegetation. An important feature of vegetation, therefore, is change. The causal factor or factors behind this change is of primary concern to biologists, soil scientists, and even to geologists.

Environmental variations generally occur in the form of gradients on different scales. Some of those gradients are described as microgradients (Hanson and Churchill 1965). They may be caused by soil variations in microrelief, texture, organic content, phosphorus content, or any other conditions that might be of direct or indirect influence on plant life and existence. The soil sampling program was not intensive enough to reflect all these.

TABLE 7. Multiple correlation (R) between the absolute density of each of six leading dominant species and variations in multiple combination of soil variables. A single asterisk denotes a significant correlation at the 5 percent probability level, and double, triple, and quadruple asterisks denote high significant correlation at 2, 1, and 0.1 percent probability levels.

	SPECIES					
COMBINED SOIL VARIABLES	*L. tridentata*	*A. dumosa*	*G. spinosa*	*A. shockleyi*	*A. canescens*	*A. confertifolia*
All variables	0.51°°°°	0.67°°°°	0.74°°°°	0.93°°°°	1.0°°°°	0.95°°°°
Fe, Zn, Cu, Mn	0.37°°	0.31	0.42°°	0.49°°	0.72°°°	0.62°°°
pH, P, N	0.19	0.30°	0.18	0.60°°°°	0.67°°	0.70°°°°
Na, K, Ca + Mn	0.15	0.27	0.16	0.23	0.82°°°°	0.7°°°°
E.C., Na%, Cat. ex. cap	0.11	0.31°	0.2	0.18	0.64°°	0.6°°°
Moisture, lime	0.32°	0.34°	0.18	0.05	0.93°°°°	0.29
pH, lime	0.28	0.38°°	0.15	0.39°	0.92°°°°	0.09
pH, P	0.18	0.17	0.18	0.44°°	0.11	0.63°°°

The behavior of the biotic communities in the Mojave Desert in general or in some of its sectors has attracted the attention of many biologists. Shreve and Wiggins (1964) have described the Mojave Desert as showing its most distinctive development between 600 and 1200 m elevation (2000–4000 ft). When it is followed thence toward the northeast or southeast, it loses some of its characteristic vegetational features and much of its distinctive flora. The basic structure of the vegetation throughout the Mojave Desert is very open stands of *L. tridentata* and *A. dumosa*. On the western edge these plants are joined and, to some extent, replaced by *Artemisia* sp., *G. spinosa*, *Tetradymia*, and some suffrutescent perennials, and at higher elevations on the north *C. ramosissima* and *G. spinosa* are dominant.

In the northern sector of the Mojave Desert, particularly in the Nevada Test Site and its surroundings, detailed phytosociological and autoecological studies have been carried out by many authors. Among them are Beatley (1963, 1969, 1974, 1975), Allred et al. (1963), Rickard and Beatley (1965), Brown and Mason (1968), and Wallace and Romney (1972). In these studies some vegetational units have been defined and named by various terms as associations, types, and subtypes. The correlation between these vegetational units and certain environmental variables has been discussed also.

In the present study it has proved useful to segregate the stands into several vegetational groupings according to leading dominant species (species with the highest importance values). However, these groupings are not absolutely discrete. The members of each pair of groupings are, in various degrees, linked together by having one or more of the dominant species in common. This, however, does not preclude the fact that these vegetational groupings are well defined and represent sociologically distinct entities quite recognizable in the field. Six major and five minor vegetational groupings have been defined. In a wider ecological study these minor groupings may prove to be of major importance.

Several edaphic factors were analyzed statistically in relation to the distribution of each of the major vegetation types. Significant differences were found among the plant groupings with respect to soil moisture tension, absolute and relative amounts of exchangeable Na, exchangeable K, cation exchange capacity, and elevation. However, no one grouping is restricted in its distribution by a narrow tolerance range for any specific soil factor. Overlapping of the vegetational groupings occurred for all the soil variables measured. This overlapping, however, does not preclude the fact that, within the overall structure of the vegetation dealt with, each vegetational grouping studied has a significant association with a particular combination of environmental variables.

The analysis of the relationship between the phytosociological behavior of the major leading dominant species and the environmental variables studied is of certain interest. Only one of the simple linear correlations between the relative or absolute abundance of *L. tridentata* and any of the environmental variables is highly significant. This might be explained by the fact that *L. tridentata* may be so well adapted to the conditions in the study area that its behavior is not noticeably affected by the changes within the limits of any of the factors studied. Other factors could be more important. The coefficient of determination (r^2) of 0.25, as determined from the multiple correlation analysis, indicates that only 25 percent of the total variation in abundance of *L. tridentata* along its range of distribution in the study area is due to the combined effect of the different environmental variables investigated.

TABLE 8. Simpson's measure of diversity in different vegetational groupings.

	Vegetational Grouping					
Diversity	*L. tridentata*	*A. dumosa*	*G. spinosa*	*A. shockleyi*	*A. canescens*	*A. confertifolia*
Mean	0.75	0.725	0.706	0.703	0.390	0.33
Range	0.61–0.84	0.64–0.84	0.7–0.8	0.64–0.81	0.18–0.55	0.0–0.73
S.D.	± 0.067	± 0.05	± 0.048	± 0.075	± 0.206	± 0.34
S.E.	± 0.017	± 0.0175	± 0.0214	± 0.034	± 0.08	± 0.155

That *L. tridentata* has a very wide range of distribution has been discussed by many authors. As reviewed by Barbour (1968), it dominates a desert area of 358,000 km² in the southwestern United States; occurs in 183,000 km² in adjacent vegetation; and covers a range that differs widely in climates, soils, elevations, and communities. However, within this distribution range, *L. tridentata* is so ubiquitous that Benson and Darrow (1954) have used its range limits to define the boundaries of the warm desert. More recently Beatley (1974) has suggested that the prevailing low minimum air temperatures and their extremes in the lowlands of drainage basins of Nevada are inferred to be the primary cause of the absence of *L. tridentata* in three discrete vegetation zones. Wallace and Romney (1972) have suggested that the lack of *L. tridentata* in dry lake areas of closed basins in southern Nevada is due to periodic flooding. This species is sensitive to poor root aeration (Lunt et al. 1973).

The analysis of correlation between species behavior and site variables also shows that the concentration of the different ions has a significant role in determining the abundance of some of the different species studied. On the other hand, total salinity as reflected by electrical conductivity or as total soluble cations is of limited significance as a controlling factor. Similar results are obtained by Gates et al. (1956) and Ayyad and El-Ghareeb (1972). In a study on some of the alkali desert soils in Utah, Gates et al. (1956) concluded that total salinity is not a wholly satisfactory criterion and that future work should involve specific ions. Chapman (1960) concluded that the roles of the cations and anions or their combination in relation to vegetation zonation may have far greater importance than has previously been suggested.

On the basis of subjective and qualitative argument, it was for many years believed by the majority of ecologists (Odum 1959, Hanson and Churchill 1965, Pielou 1975) that the more complex a community (that is, the more numerous its species and the more intricate their relationships), the greater the community's system stability would be; for, if each species would rely on many rather than few food sources and be regulated by many rather than few predators, the eggs-in-basket effect would be minimized. As a result, a high diversity would cause a high community stability.

However, acceptance of this theory has wavered since May (1973) pointed out that community stability is not a mathematical consequence of high species diversity and that the contrary is true. May's theory is still, so far, in its infancy, is a matter of controversy, and may not apply to deserts. As Pielou (1975) suggests, many species models that make no allowance for certain vegetational parameters, such as spatial heterogeneity, are totally unrealistic.

In the present study, the relative stages of community stability for the different vegetational groupings has been discussed on the basis of the assumption that community stability and high diversity are positively correlated (Pielou 1975). It is also based on the assumption that the diversity of an abstract community should be expressed as an average of the diversity measures for the different concrete units of that particular community, and consequently the lower the standard error of the diversity measure, the greater the homogeneity of the community. The vegetational grouping of *L. tridentata*, showing both high diversity and greater homogeneity, may be considered, therefore, as the most stable community in the study area, consequently representing its climatic climax vegetational cover. The vegetational grouping of *A. dumosa* is also characterized by both high diversity and homogeneity, but it has a relatively narrower distribution range.

The view that the *L. tridentata* grouping represents the most stable community in the study area has been supported by the study of Beatley (1969), who described the *L. tridentata* type as the one with the highest floristic diversity in the region, and by Shelford (1963), who described the *L. tridentata* community as representing the bush desert climax. However, the position of the *L. tridentata* community along the successional ladder is a matter of great controversy, and views vary according to phytogeographical regions. According to Stebbins and Major (1965), *L. tridentata* has been described in the Mojave Desert as representing a relict species. On the other hand, in Sampson Valley in southeastern Arizona, Chew and Chew (1965)

have described *L. tridentata* as a pioneer species that has been recently dispersed in the study area at the expense of *Flourensia*. Gardner (1951) concluded also that *L. tridentata* is expanding its distribution and dominance into areas occupied by *Flourensia* in the Rio Grande Valley, New Mexico, probably as the result of changes in the complex of soil factors, especially the loss of surface soil.

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FREQUENCY DISTRIBUTION OF THREE PERENNIAL PLANT SPECIES TO NEAREST NEIGHBOR OF THE SAME SPECIES IN THE NORTHERN MOJAVE DESERT

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Abstract.— Frequency distribution patterns were developed for distance to nearest neighbor of the same species for *Larrea tridentata* (Sesse & Moc. ex DC.) Cov., *Ephedra nevadensis* S. Wats., and *Acamptopappus shockleyi* A. Gray. The distances between shrubs had been determined previously in another study. About one-third or more of the nearest neighbor of its own kind was within less than one meter for each species, indicating that it was usually within the same shrub clump, which in turn is indicative of an aggregating effect. For *L. tridentata* and *E. nevadensis* much of this could be from the same original plant by crown diffusion (*L. tridentata*) or underground spreading (*E. nevadensis*). None of the three gave evidence of spacing at regular intervals when the nearest neighbor of a single individual within a shrub clump was outside that clump. Rather, they appeared to be randomly distributed under this condition, except possibly for *A. shockleyi*.

Nearest neighbor information among perennial plants is of considerable importance in desert environments. Involved is the tendency of a given system to have regulatory mechanisms that can space plants at quite regular intervals. This is observed with *Larrea tridentata* (Sesse & Moc. ex DC.) Cov. with limited rainfall (Barbour 1969); the more sparce the rainfall, the greater is the spacing. In our previous studies of plant populations in the northern Mojave Desert some entire populations had been subjected to a census, and from the data nearest neighbor relationships had been calculated (Wallace and Romney 1972d). In the previous work, the mean distance and standard deviation to the nearest neighbor of any species and of the same species were reported for 23 perennial shrubs. In general the coefficient of variation for the distance to nearest neighbor of the same species of the perennial plants was around 100 percent.

Barbour's (1969) work indicated that *L. tridentata* spacing could be random, clumped or at regular intervals depending on the climate. The purpose of this report was to determine how this species was spaced in part of the Nevada Test Site and to get similar data for other species.

Materials and Methods

The site of the study area is Mercury, Nevada, near waste water ponds from the local sewage processing system. The soil at this site is underlain by a virtually impervious hardpan layer at depths varying from 15 to 75 cm.

Perennial plants grow both singly and in clumps, separated by bare areas of desert soil (Fig. 1). The size and spacing of the clumps is irregular, and several different species may grow together in a single clump (Fig. 2). A census was made in the summer of 1968 of all perennial plants (including shrubs, grasses, herbs, and their seedlings) in 25 circular experimental plots, each plot being 30.5 m in diameter. Each plant was categorized as to its species and its vegetational unit membership. This census effort involved more than 19,000 individual plants representing 28 different species.

A special method was devised for locating and cataloging each plant in each plot. A permanent standpipe for mounting a surveyor's transit was installed at the center of each plot, with a marker located on magnetic north at a distance of 15.25 m. Orientation for each vegetational unit was the measured

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Fig. 1. View of northern Mojave Desert study site with typical shrub clumps separated by bare areas of desert pavement.

Fig. 2. Typical clumps of shrubs in group association (vegetational unit). Present are *Acamptopappus shockleyi* (3), *Ambrosia dumosa* (8), *Ceratoides lanata* (5), *Grayia spinosa* (1), *Krameria parvifolia* (1) and *Lycium andersoni* (1).

distance from the plot center to the vegetational unit center. The azimuth for each unit was measured from magnetic north to the center of the vegetational unit. The unit's greatest and smallest width and its species content were recorded. Each species within a unit was measured in like manner, and it was further identified by height. These data were recorded and transferred to punch cards for computer processing.

The method for calculating distance to nearest neighbor is given in detail in the previous publication (Wallace and Romney 1972d).

RESULTS AND DISCUSSION

Frequency distribution histograms for distance to nearest neighbor of the same species for *L. tridentata* Sesse & Moc. ex DC. (1241 individuals), *Ephedra nevadensis* S. Wats. (386 individuals), and *Acamptopappus shockleyi* A. Gray (3470 individuals) are in Figures 3, 4, and 5. The three species were chosen for their different growth habits. All three, however, tend to exist in clumps with individuals of other species as well as with other individuals of the same species, as is observed in each of the histograms. A high proportion of the nearest neighbor of the same species lies within a distance of 1.5 meters. A near normal type of frequency distribution existed within the clumps for the first 1.5 meters or so according to each of the figures.

About one-third of the *L. tridentata* plants were within about two-thirds meter distance of one another. Part of this may be due to the breakup of crowns into more than one plant (Wallace and Romney 1972b). No attempt was made in the census to identify these as one plant, so a crown diffusion phenomenon existed within the first meter in the histogram in Figure 1.

Beyond the first clump or beyond a dis-

Fig. 3. Histogram of frequencies of distance to nearest neighbor of the same species in meters of 1241 individual *Larrea tridentata* plants in the northern Mojave Desert.

tance of one meter there was almost a constant number of individuals within each cell width out to 4 or 5 meters. There was a very slight tendency for a number of nearest neighbors to occur in the next adjacent clump, but data generally show distribution with different distances up to about 5 meters to the nearest neighbor within the study plots. This would imply that the clumps are very randomly distributed.

The mean distance of one *L. tridentata* to another *L. tridentata* was 2.15 meters. The mode was at 0.6 meters and, being left of the mean, is indicative of some aggregation. The skewness was –0.27 and the kurtosis was –15.77.

The *E. nevadensis* had the smallest population of the three species studied, and it was chosen for this reason. About one-half of the individuals were nearest neighbor within less than one meter. This may be related to the habit of propagation by underground roots (Wallace and Romney 1972a). These groups would be aggregated. In the census no attempt was made to separate such plant groups from those that were truly individual, so this may account for the large proportion of close neighbors. Beyond one meter the distribution appeared to be mostly uniform with distance and therefore random. There did seem to be a small distribution peak at about 3.6 meters, however.

The overall mean to nearest neighbor of *E. nevadensis* of the same species was 3.35 meters, with a skewness of 1.36 and kurtosis of 4.68. The mode was at 0.6 meters, which is to the left of the mean and would indicate aggregation as explained above.

The largest population of the three species was with *Acamptopappus shockleyi*. It has the tendency to grow both in groups within clumps of other species and as individuals in the space between clumps (Wallace and Romney 1980, this volume). This latter habit is the reason for its more negative association with other species (Wallace and Romney

Fig. 4. Histogram of frequencies of distance to nearest neighbor of the same species in meters of 386 individual *Ephedra nevadensis* plants in the northern Mojave Desert.

972c). The frequency distribution for *A. hockleyi* is almost exponential, with numbers apidly dropping off with distance. This is, of ourse, related to its relatively dense popuation. The data can be interpreted as the pecies being to a large extent aggregated. he mean distance between neighbors was .18 meters. The mode was at 0.6 meters. he skewness of the frequency distribution as 2.47 and kurtosis was 12.54.

The varied nature of the distribution of the ndividuals for each species may indicate that e site in question is not extremely limited n rainfall. Other sites in the northern Mojave Desert can be found that are more limited in ainfall, and spacing at regular intervals may e more likely at such sites. Because the udy site involves a mixture of vegetation, it quite unlikely that the forces that result in egular spacing have been in operation in this udy area.

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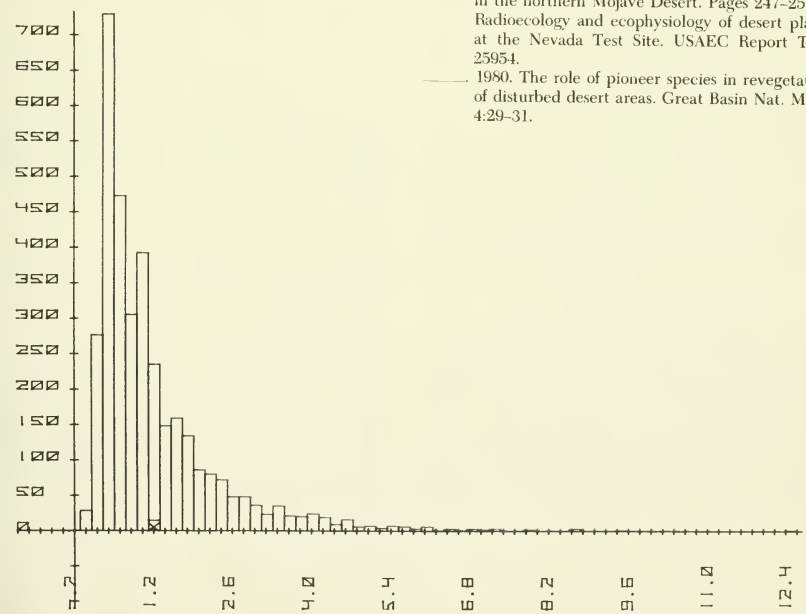

Fig. 5. Histogram of frequencies of distance to nearest neighbor of the same species in meters of 3470 *Acamptoppus shockleyi* plants in the northern Mojave Desert.

RELATIONSHIP OF SMALL WASHES TO THE DISTRIBUTION OF *LYCIUM ANDERSONII* AND *LARREA TRIDENTATA* AT A SITE IN THE NORTHERN MOJAVE DESERT

A. Wallace[1], E. M. Romney,[1] and R. B. Hunter

Abstract.— At a site near Rock Valley, Nevada, dominated by volcanic rocks, both *Larrea tridentata* (Sesse & Moc. ex DC.) Cov. and *Lycium andersonii* A. Gray were restricted in distribution. *Larrea tridentata* did not grow in the many small washes in the area, but *L. andersonii* grew only in the washes. *Ambrosia dumosa* (A. Gray) Payne was more dense and more dominant in wash areas than in nonwash areas.

The vegetation mosaic of the Rock Valley area of the northern Mojave Desert has a high degree of variability and changes considerably from site to site (Beatley 1976, Romney et al. 1973, Turner and McBrayer 1974, Turner 1975, 1976). The dominant species are *Larrea tridentata* (Sesse & Moc. ex DC.) Cov., *Ambrosia dumosa* (A. Gray) Payne, and *Lycium andersonii* A. Gray on some sites and *L. tridentata*, *Lycium pallidum* Miers, and *Grayia spinosa* (Hook.) Moq. on others. *Ambrosia dumosa* and *L. pallidum* are of lesser importance on these latter sites. The study was made because of the impression that the small washes in the area were free of *L. tridentata* and that *L. andersonii* grew only in the washes. In other studies conducted here, *L. tridentata* and *L. andersonii* have been highly associated, whereas, *L. tridentata* and *L. pallidum* tend to be negatively associated (Romney and Wallace 1980, Wallace and Romney 1972).

Materials and Methods

The study site was located off Road 40 near the east entrance to Rock Valley at the Nevada Test Site. It is near Site No. 58 of the soils-plant study made by Romney et al. (1973). The area is above the main part of the valley and near Skull Mountain (Beatley 1976). It has a slope of 2 percent to the south and the area is crossed by many small washes, often 10 to 15 m apart.

Two belt transects, each 50 m × 2 m, were sampled in both the wash and nonwash areas. An inventory was made of all plants falling more than 50 percent in the transect in order to determine numbers and relative dominance (Wallace and Romney 1972).

Mineral analyses were made of the plants to determine if the location differences could be explained by variations in nutrient element distribution.

Results and Discussion

The numbers and relative dominance of plant species are reported in Table 1. The high species diversity seen elsewhere in Rock Valley (Beatley 1976, Romney et al. 1973) is apparent. No *L. tridentata* were observed in the transects in the washes and no *L. andersonii* were observed in the transects in the nonwash areas. The density of *L. pallidum* was not different in and out of washes. There were more total plants (greater density) in the wash than out of the wash area, primarily due to variations in the density of *A. dumosa*.

Four possible reasons for the vegetation pattern differences are (1) more water in the washes, (2) different soil texture in the washes, (3) soluble salts had been leached out along the washes, and (4) positive effect of

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the wash on the seed germination of the *L. andersonii*. No seedlings of any of the species were observed either in or out of the washes when sampled in 1976. Soil texture is sandy (Beatley 1976, Romney et al. 1973, Wallace and Romney 1972).

A question of most interest was the salt status of the plants, but the mineral element contents generally did not vary significantly between locations. Some of the mineral analyses are in Table 2. *Lycium pallidum* is known to be more adapted to salt than is *L. andersonii* (Beatley 1976, Romney et al. 1973, Wallace et al. 1973). *Lycium pallidum* is not an obligate halophyte and this may account for its being equally distributed in wash and nonwash areas. The chlorine concentration in *L. pallidum* and *G. spinosa* varied inversely in and out of washes (3.68 percent and 2.73 percent in and out of washes for *L. pallidum* and 1.84 percent and 2.02 percent in and out of washes for *G. spinosa*).

An attempt was made in 1976 to determine differential leaf water potentials in plants in and out of washes as determined with a Scholander bomb (Scholander et al. 1965). Results were inconclusive. Leafwater potentials of the species involved were reported earlier (Wallace and Kleinkopf 1974). Given repeated and prolonged measurements in different types of rainfall years, this technique probably could yield important information on the problem of differential plant distribution.

ACKNOWLEDGMENTS

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TABLE 1. Numbers of shrubs and their relative dominance in wash and nonwash areas*.

	Wash 1		Wash 2		Hill 1		Hill 2	
SPECIES	No.	Rel. dom.	No.	Rel. dom.	No.	Rel. dom.	No.	Rel. dom.
Psorothamnus fremontii	1	0.4	3	0.8	2	3.1	7	5.1
Ephedra nevadensis	1	2.1	0	0.0	0	0.0	0	0.0
Ceratoides lanata	1	0.1	0	0.0	0	0.0	5	1.5
Ambrosia dumosa	57	30.4	72	27.6	40	14.0	29	9.6
Grayia spinosa	34	39.2	33	50.6	29	37.0	31	39.5
Hymenoclea salsola	1	0.9	0	0.0	0	0.0	1	0.6
Larrea tridentata	0	0.0	0	0.0	10	24.0	4	16.7
Lycium andersonii	5	5.6	4	4.7	0	0.0	0	0.0
Lycium pallidum	15	18.6	10	15.8	16	21.7	16	26.9
Tetradymia axillaris	2	2.3	0	0.0	0	0.0	0	0.0
Machaeranthera tortifolia	2	0.4	3	0.4	1	0.2	1	0.1
Oryzopsis hymenoides	0	0.0	3	0.1	0	0.0	0	0.0
	119	100.0	128	100.0	98	100.0	94	100.0

*Relative dominance is calculated as: $\frac{\text{Total basal area of species}}{\text{Total basal area all species}} \times 100.$

TABLE 2. Mineral composition of leaves of plants in and out of washes.

Species and location	P %	Na %	K %	Ca %	Mg %	Cu μg/g
Lycium pallidum						
In wash—mean	0.288	0.954	4.393	3.643	1.312	6.6
Out of wash—mean	0.250	1.193	3.955	4.497	1.275	4.5
In wash vs. out of wash F value	2.529	0.424	1.917	8.606	0.167	3.85
Lycium andersonii						
All in wash—mean	0.232	0.0269	3.650	10.695	1.111	3.5
F value between species	93.76	22.50	3.68	8.46	16.01	14.68
Grayia spinosa						
In wash—mean	0.248	0.0497	7.711	2.440	1.462	4.0
Out of wash—mean	0.312	0.0667	8.618	2.231	1.351	3.4
In wash vs. out of wash F value	0.582	1.030	0.829	0.406	0.985	1.148

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Table 2 continued.

Fe μg/g	Mn μg/g	B μg/g	Al μg/g	Si μg/g	Mo μg/g	Sr μg/g	Ba μg/g	Li μg/g
296	63.3	33.5	271	1056	2.4	426	23.3	25.4
259	55.4	38.2	231	954	2.1	414	19.8	34.6
2.364	1.774	1.339	0.862	0.927	0.575	0.133	3.386	0.413
311	48.9	28.3	299	958	1.6	751	48.7	56.6
6.76	26.65	23.01	8.87	5.99	146.0	5.41	15.98	93.3
342	250	44.1	463	1529	1.0	268	28.2	–
327	202	36.4	378	1416	1.2	213	22.3	–
0.729	0.830	4.218	2.318	0.478	1.810	1.865	6.399	–

REGULATIVE EFFECT OF DODDER (*CUSCUTA NEVADENSIS* JTN.) ON THE VEGETATION OF THE NORTHERN MOJAVE DESERT

A. Wallace[1], E. M. Romney[1], and R. B. Hunter[1]

Abstract.— On two separate transects in the Rock Valley area of the northern Mojave Desert in the spring of 1976, 4 percent to 17 percent of the perennial plants were infested with the parasite *Cuscuta nevadensis* Jtn. (dodder), and dead pieces of dodder from previous years were on dead plants equivalent to another 5 percent, indicating that the dodder had a regulating effect on the plant population and may be an important cause of perennial plant death.

Dodder (*Cuscuta nevadensis* Jtn.), a yellow-orange parasitic vascular plant, is common in the northern Mojave Desert (Beatley 1976). A previous study indicates its presence on 16 different perennial plant species and its ability to kill the host plant and consequently influence the ecology of an area was recognized (Wallace and Romney 1972). The biological characteristics of the genus *Cuscuta* have been recently reviewed (Ashton 1976).

In a 50 × 2 m transect made near Rock Valley, Nevada, in the spring of 1976, 93 living perennial plants were present: 16 of these were infested with dodder (17 percent). Some of them were so badly infested that death of the host was certain (Fig. 1). Two dead plants were also observed in the transect with pieces of dead dodder attached. The numbers infested by species were: *Grayia spinosa* (Hook.) Moq. (6), *Ambrosia dumosa* (A. Gray) Payne (3), *Ceratoides lanata* (Pursh) J. T. Howell (1), *Lycium pallidum* Miers (5), and *Psorothamnus fremontii* (Torr.) Barneby (1). All these species were found to be infested in the previous study.

Another transect (100 × 2 m) contained 8 plants with live dodder and 10 dead plants apparently killed by dodder because pieces of dead dodder were attached to them. This transect had approximately 4 percent infestation and a 5 percent kill from a previous year.

A 5 percent shrub mortality per year is greater than average if many of the plants live 20 to 100 years, as believed (Wallace and Romney 1972). The effect of dodder then, at least in some years, is important wherever infestations occur. The prevalence of dodder is related to the soil-moisture conditions; therefore, its impact varies from year to year. It grows abundantly in spring seasons with relatively cool temperatures. We had postulated that an intensive kill of shrubs could revert such areas into grassland, at least until the perennial shrubs became reestablished. The incidence of dodder then may favor the establishment of grasses. The relative importance of dodder and rodents as regulators of perennial plant populations is a subject of continuing interest.

Acknowledgments

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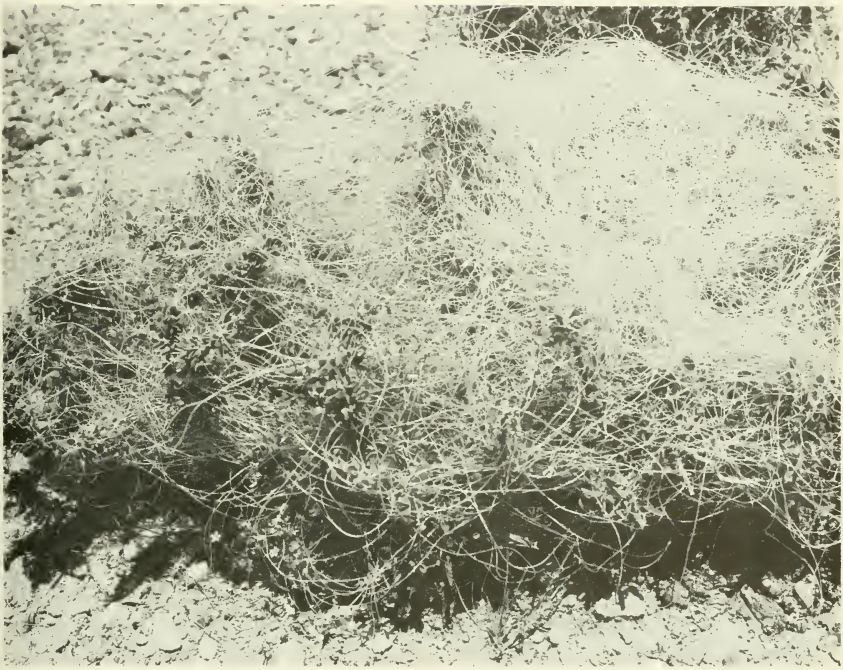

Fig. 1. *Lycium pallidum* plant heavily infested with *C. nevadensis* in the spring of 1976.

PHOTOSYNTHETIC STRATEGIES OF TWO MOJAVE DESERT SHRUBS

G. E. Kleinkopf[1], T. L. Hartsock[1], A. Wallace[1], and E. M. Romney[1]

ABSTRACT.— Photosynthetic production of two Mojave Desert shrubs was measured under natural growing conditions at UCLA. Measurements of photosynthesis, transpiration, resistances to water vapor flux, soil moisture potential, and tissue water potential were made. *Atriplex canescens* (Pursh) Nutt., a member of the C_4 biochemical carbon dioxide fixation group was highly competitive in growth rate and production during conditions of adequate soil moisture. As soil moisture conditions declined to minus 40 bars, the net photosynthetic rate of *Atriplex* decreased to zero. However, the C_3 shrub species *Larrea tridentata* (Sesse & Moc. ex DC.) Cov. was able to maintain positive net photosynthetic production during conditions of high temperature and extreme low soil moisture through the major part of the season. The comparative advantages of the C_4 versus the C_3 pathway of carbon fixation was lost between these two species as the soil moisture potential declined to minus 40 bars. Desert plants have different strategies for survival, one of the strategies being the C_4 biochemical carbon fixation pathway. However, many of the plants are members of the C_3 group. In this instance, the C_4 fixation pathway does not confer an added advantage to the productivity of the species in the Mojave Desert. Species distribution based on comparative photosynthetic production is discussed.

Desert plant species have evolved specialized strategies for coping with extreme environmental conditions. Drought avoidance and drought resistant plant species exist in the same area, although growth and reproduction may occur at different times during the season. In the Mojave Desert, plant species growth response and productivity is governed principally by moisture relationships (Bamberg et al. 1975, 1976). Photosynthetic production is also related to species differences between age, leaf type, and distribution (Cunningham and Strain 1969, Strain 1969, Bjorkman 1971, Wallace and Romney 1972). In addition, desert plants possess special physiological traits such as low leaf tissue moisture and high osmotic pressure (Kozlowski 1968, 1972, Solbrig and Orians 1977) and temperature adaptation (Bjorkman et al. 1971, Pearcy 1977). Many desert plants carry out most of their photosynthesis during favorable periods of the year when moisture relationships are conducive to growth (Hatch and Slack 1970, Jarvis 1971, Caldwell et al. 1972).

Three biochemical pathways for carbon dioxide fixation have been documented rather extensively (Hatch et al. 1971, Burris and Black 1976). These three pathways include C_3, C_4, and CAM photosynthesis. *Atriplex canescens* (Pursh) Nutt., one of the plant species of interest, is a member of the C_4 photosynthesizing group. The second plant, *Larrea tridentata* (Sesse & Moc. ex DC.) Cov., has the C_3 pathway of photosynthesis. There is some consensus of opinion that the C_4 pathway of photosynthesis has conferred some adaptive advantage to species possessing it, enabling them to be more competitive under extreme conditions such as exist in desert environments. In C_4 species, carbon dioxide is first fixed by PEPcarboxylase into aspartate or malate and then transferred to specialized bundle sheath cells for fixation by ribulose diphosphate carboxylase. In C_3 plants, which lack the specialized bundle sheath tissue, carbon is fixed by ribulose 1;5-diphosphate carboxylase. The affinity of the PEPcarboxylase for carbon dioxide is greater than is the affinity of carboxylase for carbon dioxide in the C_4 pathway. Another advantage is a high water use efficiency intrinsic to those plants that have the C_4 pathway. This higher rate of photosynthesis and higher water use efficiency, coupled with higher light saturation and lack of photorespiration, should confer upon those plant species a bet-

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ter adaptive strategy for survival in extreme conditions of the desert (Hatch et al. 1971, Solbrig et al. 1977). It became of interest to study the photosynthetic strategy of two shrubs, one of the C_4 group, *A. canescens*, and one of the C_3 group, *L. tridentata*. The morphology, distribution, and density of the species have been described earlier (Wallace and Romney 1972, Solbrig et al. 1977).

MATERIALS AND METHODS

This work was done on species from the Nevada Test Site located in a transition zone between the Great Basin desert and the Mojave Desert. Climatic conditions in this area are characteristic of both regions, with extreme summer heat and winter cold. The precipitation generally is less than 125 mm yearly. Both plant species are native to this area, with *L. tridentata* being of higher density than *A. canescens*.

Plant materials as cuttings or whole plants were removed from the desert and transported to the UCLA facility for study. Plants taken from the desert were removed during winter dormancy and transplanted directly into cement-lined growth beds where total soil water availability could be controlled. Plant material, as cuttings, was rooted in a glasshouse and then transplanted into the beds for study. The cement-lined beds were 1 × 4 m and 40 cm deep. These growing conditions provided a means for establishing and monitoring plant growth during several seasons. Four beds were used; 6 to 8 plants of each species were used in the study, and numerous photosynthetic measurements were taken on each plant. Soil moisture was measured with psychrometers purchased from Wescor, Logan, Utah. Plant moisture potential was measured with a pressure bomb (Scholander et al. 1965). Gas exchange was measured using a Seamens Null-point chamber as described by Koller 1970). The Seamens equipment was designed to measure CO_2 exchange and transpiration at controlled or ambient conditions. Plant materials previously established in the beds were maintained in a well-watered condition before measurements were taken. Soil water depletion occurred by allowing the plants to utilize the available soil water. Photosynthesis and transpiration measurements were followed during several drying cycles.

RESULTS AND DISCUSSION

Data presented here are averages of the photosynthetic rates of the two shrub species in two years. Figures 1 and 2 show the comparison of photosynthetic rate and resistance to water vapor diffusion as plotted versus increasing soil water potential for 1974 and 1975. At higher water potentials and higher water availability, *A. canescens* showed higher maximum net photosynthetic rates than *L. tridentata* for both years. The net photosynthetic rate of *A. canescens* was maximum at high soil water content and decreased from near 50 mg CO_2 per square decimeter per hour to near zero as the soil moisture decreased to minus 45 bars. At high soil moisture these data show the *A. canescens* response to be consistent, with C_4 photosynthesis being greater than C_3; however, the C_4 advantage is not as apparent at decreasing soil moisture. Data for *L. tridentata* for the two years show the initial lower maximum rate of photosynthesis, but maintenance of a small but positive net CO_2 uptake as the soil moisture decreased to minus 50 bars. *Larrea tridentata* is capable of small positive net photosynthesis during portions of the day to minus 65 bars of soil water potential (Bamberg et al. 1975).

Figure 3 shows the net carbon dioxide uptake of *A. canescens* and *L. tridentata* during morning and afternoon conditions. The C_4 plant, *A. canescens*, shows a higher maximum and a broader range of morning fixation (Fig. 3b) than the C_3 plant, *L. tridentata*. A decreasing rate of photosynthesis and increasing resistance values characterized both plants as soil moisture decreased. The afternoon carbon fixation by *A. canescens* showed a different pattern, i.e., a decrease from an initial high rate at high water content of the soil to a rather low rate. *Larrea tridentata*, on the other hand, showed very little difference between morning and afternoon fixation rates, starting at a maximum of 30 to 35 mg CO_2 per square decimeter, decreasing with decreasing water potential of the soil, but maintaining a positive net fixation to minus 50

bars. Morning measurements of leaf resistance to water vapor flux showed an increase in the afternoon as temperatures gradually increased. Afternoon temperature measurements are commonly 30 to 40 C at UCLA, where the measurements were made. These data show the opposing photosynthetic strategies of the two desert shrubs. The C_4 plant, *A. canescens*, had a higher photosynthetic rate during conditions of lower morning temperatures and higher soil water potentials. However, the C_3 plant, *L. tridentata*, was capable of maintaining a positive net photosynthetic rate at higher stress levels.

In Figure 4, data are plotted which describe the net carbon dioxide uptake at two temperatures, 25 and 35 C. In both species at 25 C, photosynthesis and transpiration paralleled each other as tissue water potential declined. At 35 C transpiration increased pro-

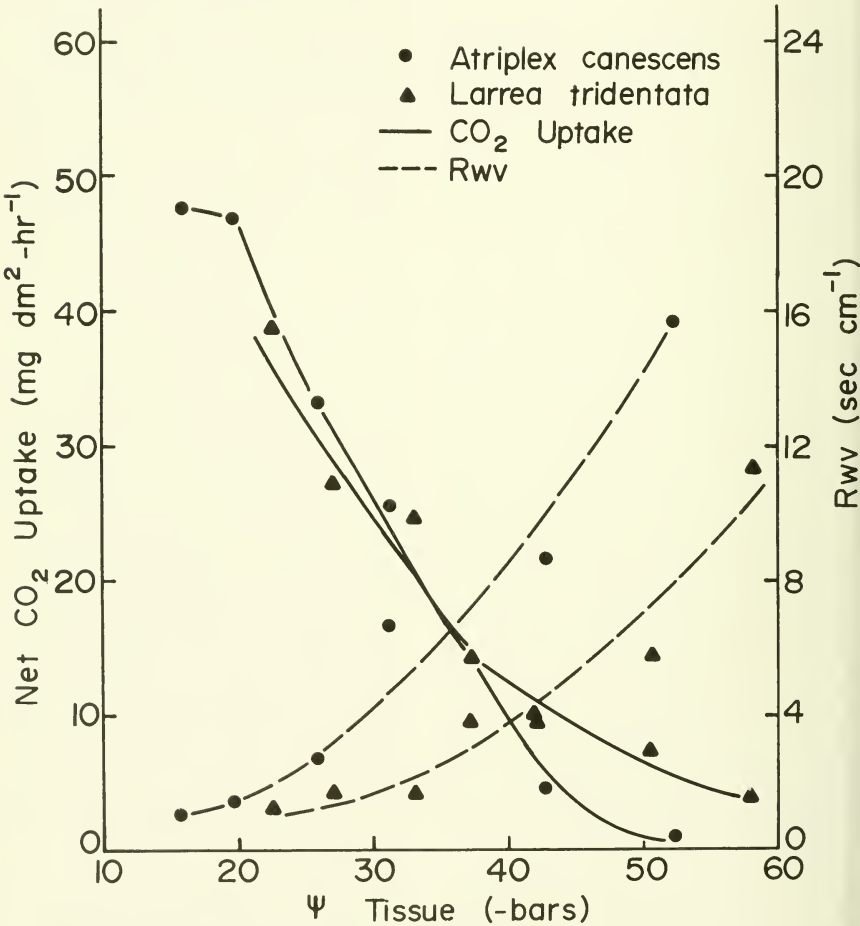

Fig. 1. Daily average rate of photosynthesis and stomatal resistance versus tissue water potential of *Atriplex canescens* and *Larrea tridentata*, 1974. Plants were well established in cement lined beds containing native desert soil. Data represent averages of 20 or more measurements on six plants.

portionately greater than the photosynthetic increase in both species. As the tissue water potential decreased to minus 40 bars at 35 C, the net photosynthetic rate decreased to zero in *A. canescens*. The evergreen shrub, *L. tridentata*, was able to maintain a small but positive net photosynthetic rate as the tissue potential decreased below minus 50 bars.

The photosynthesis to transpiration ratio, as plotted in Figure 5, shows some interesting

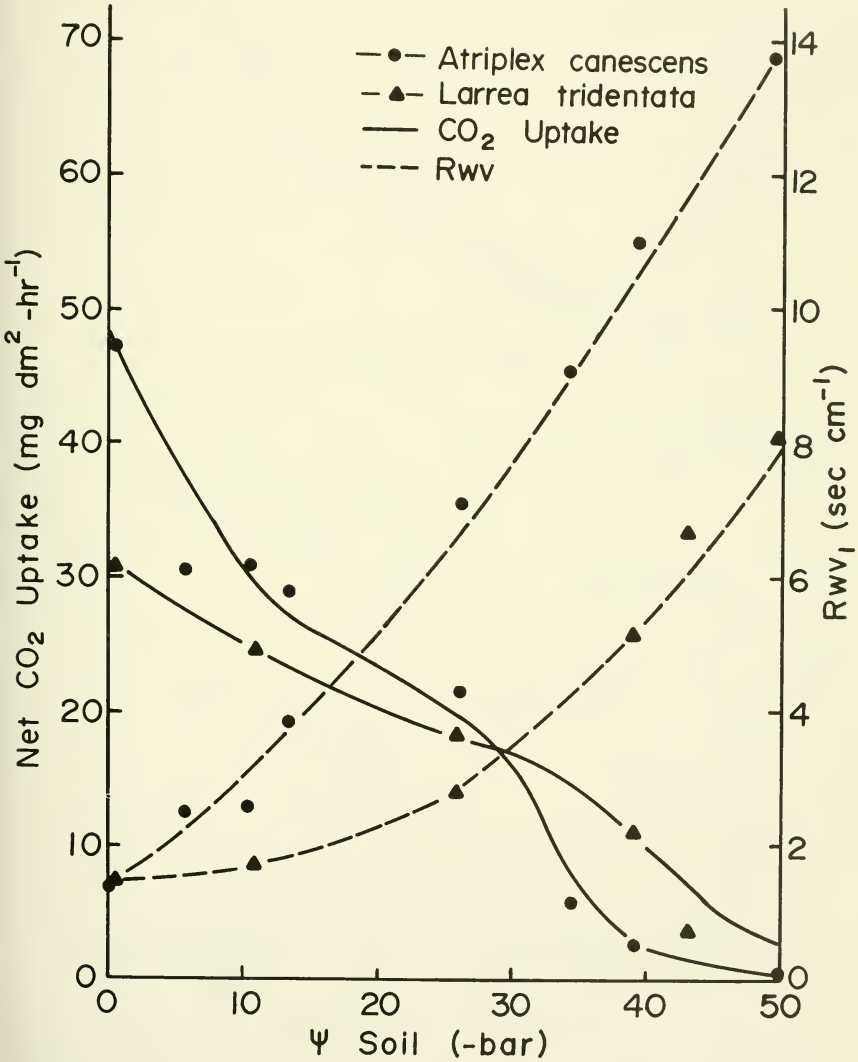

Fig. 2. Daily average rate of photosynthesis and stomatal resistance versus soil water potential of *Atriplex canescens* and *Larrea tridentata*, 1975. Conditions were as described in Figure 1.

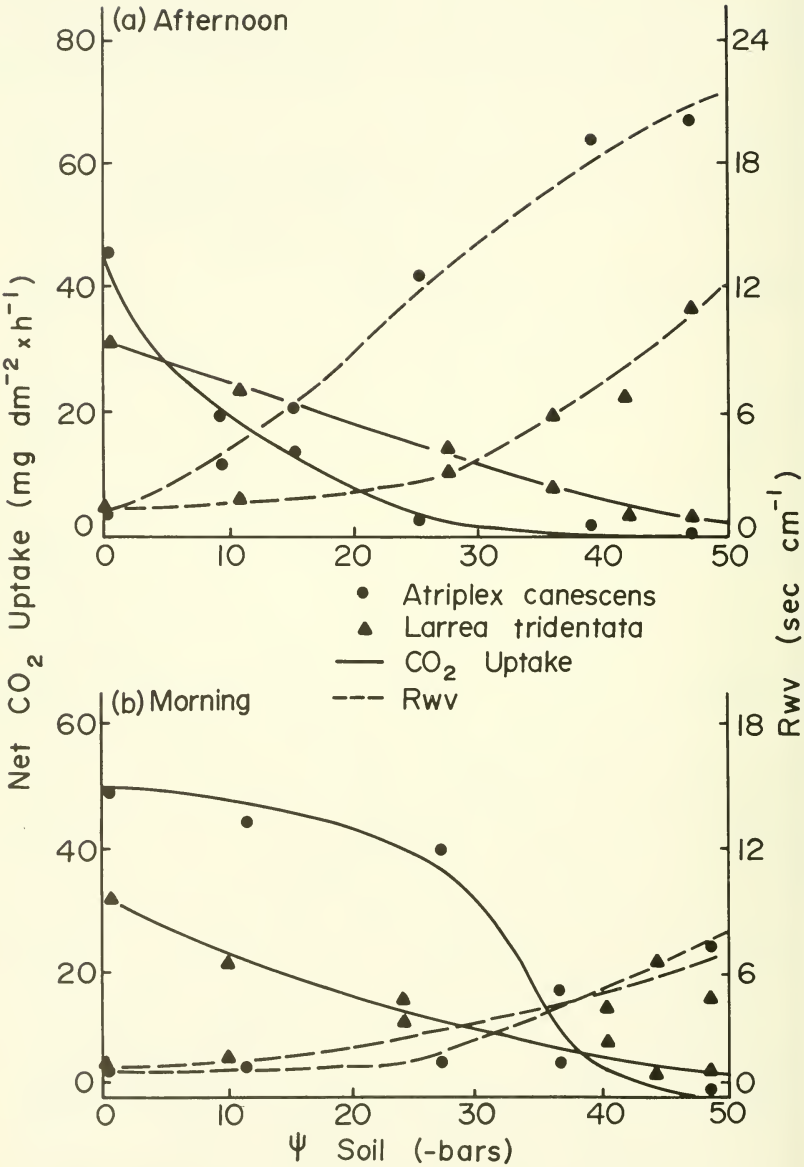

Fig. 3. Photosynthesis and stomatal resistance of two desert shrubs. Data represent averages of plants to morning (cool) conditions and (warm) afternoon conditions as soil moisture declines. Conditions were as described in Figure 1.

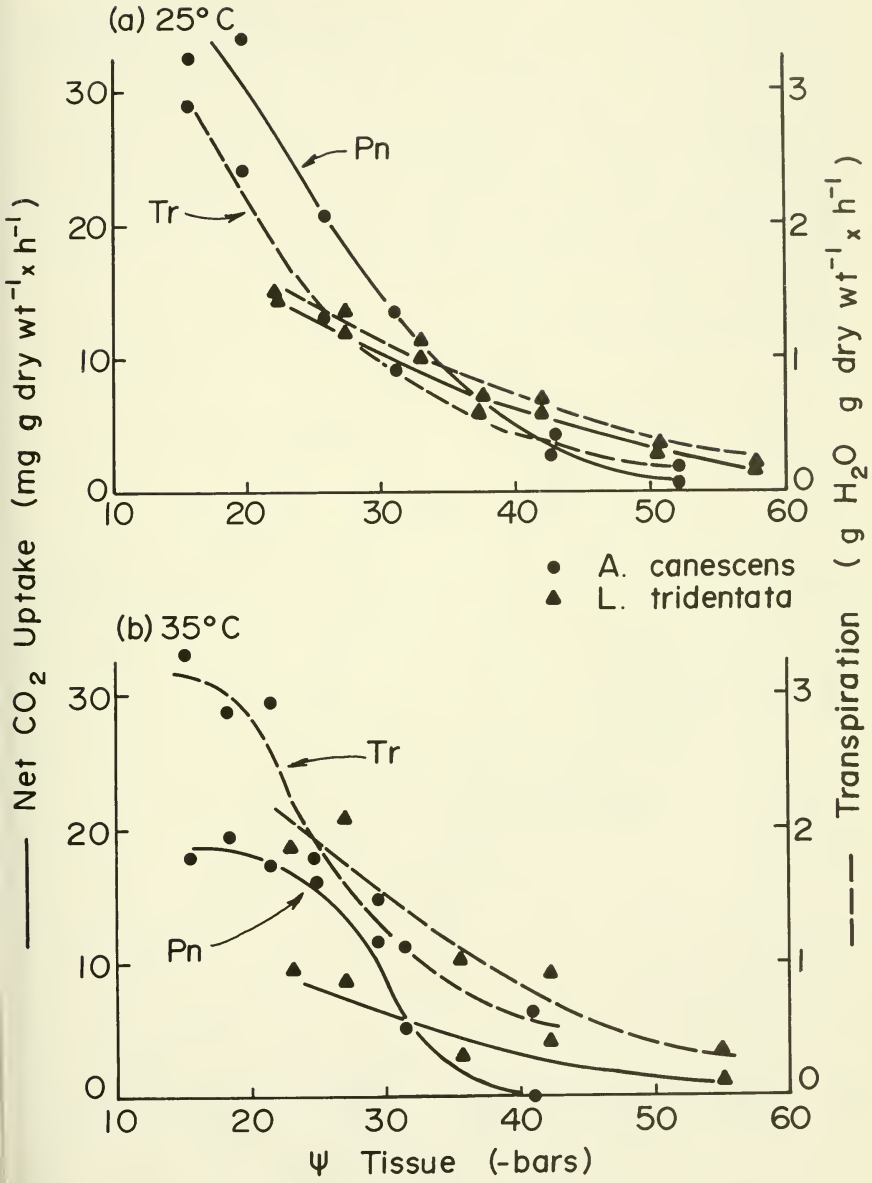

Fig. 4. Daily average rate of photosynthesis and transpiration of two desert shrubs versus tissue water potential at two temperatures. Conditions were as described in Figure 1.

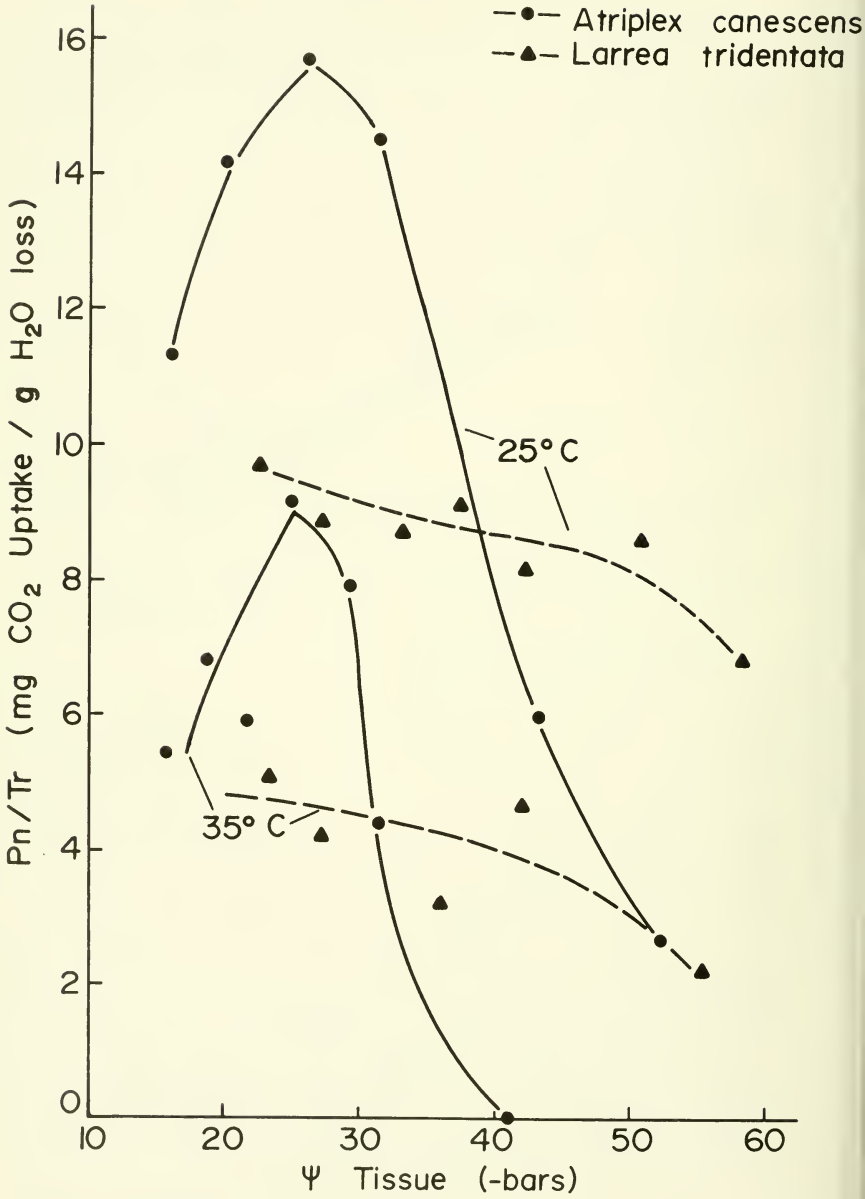

Fig. 5. Water use efficiency versus tissue water potential of two desert shrubs. Experimental conditions are as described in Figure 1.

differences between the C_4 species, *A. canescens*, and the C_3 species, *L. tridentata*. At moderate tissue water potential between minus 10 and minus 30 bars, *A. canescens* showed an increasing water use efficiency at both temperatures 25 C and 35 C. Such is characteristic of a C_4 shrub. However, as the tissue water potential decreased below minus 30 bars, the ratio decreased rapidly. The strategy displayed by the C_3 plant, *L. tridentata*, was somewhat different. The water use efficiency as shown by the photosynthesis: transpiration ratio decreased rather gradually as tissue water potential declined to minus 50 bars.

Figures 6 and 7 show the relationship between the milligrams carbon dioxide fixed on an area basis and a dry weight basis. These two curves indicate that it is possible with a high degree of confidence to make a dry weight measurement on the leaves and convert that to an area base measurement for resistance calculation. These data also imply that the specific leaf weight of *A. canescens*

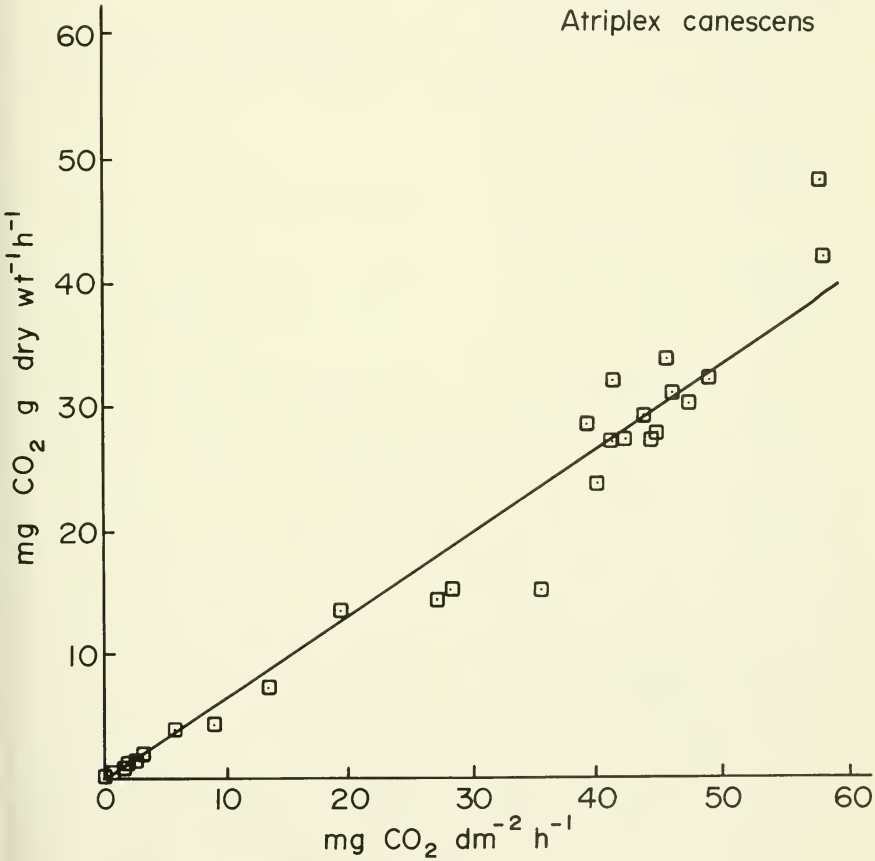

Fig. 6. Photosynthesis of *Atriplex canescens*. Data are plotted to show the correlation between dry weight and leaf surface measurements for a photosynthetic base. Leaf area determinations of numerous small leaves can be time consuming.

and *L. tridentata* do not change as the photosynthetic rates decline due to decreasing water potential of the soil.

These two plant species, one a C_4 carbon fixer and one a C_3 fixer, showed differing strategies in coping with the extreme environment of the desert. The C_4 species, *A. canescens*, appeared to have the higher photosynthetic rate during conditions of moderate moisture and temperature stress. Higher water use efficiency is shown by the C_4 species under conditions of moderate water stress. However, the evergreen shrub, *L. tridentata*, is capable of maintaining small but positive net photosynthetic rates throughout the major portion of the growing season.

These two plant species differ in their biochemical mechanism of photosynthesis and show contrasting strategies for survival in the desert. *Atriplex canescens* is capable of productivity and growth during a more favorable moisture climate and is not competitive

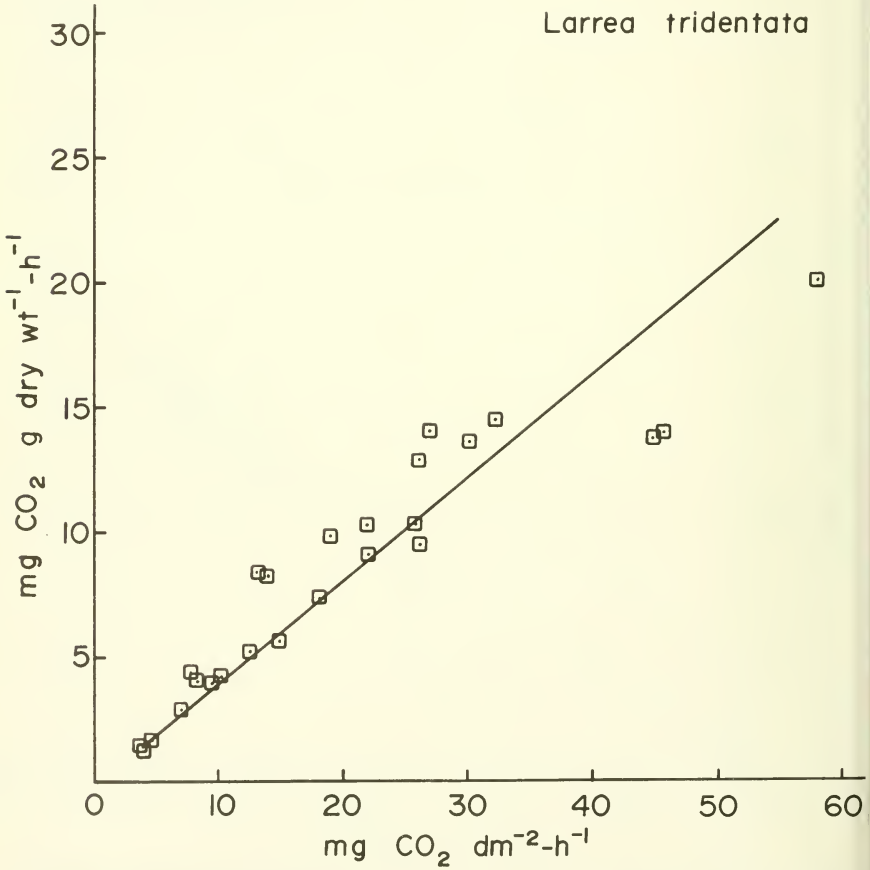

Fig. 7. Photosynthesis of *Larrea tridentata*. Data are plotted to show the correlation between dry weight and leaf surface area.

under soil moisture conditions of less than minus 35 bars. Distribution of the two shrubs in the various desert climates has been described by Wallace and Romney (1972). *Atriplex canescens* appears to be more suitable to the colder, wetter climates provided by the Great Basin desert than does *L. tridentata*. The distribution of *L. tridentata* into the more northern part of the Mojave Desert and into the Great Basin desert appears to be limited by the cold winter temperatures.

ACKNOWLEDGMENTS

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TRANSPIRATION AND CO_2 FIXATION OF SELECTED DESERT SHRUBS AS RELATED TO SOIL-WATER POTENTIAL

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ABSTRACT.— In desert plants, transpiration rates decreased before photosynthetic rates when plants were entering a period of water stress. This may have adaptive consequences. A difference of –5 bars in the soil-moisture potential had considerable importance in reducing the rate of transpiration. In *Helianthus annuus* L. (sunflower) the photosynthetic rate decreased before the transpiration rate in contrast to Great Basin-Mojave Desert plants, and the changes occurred with a –1 bar difference in soil-moisture potential. Morphological changes in three desert plant species [*Artemisia tridentata* Nutt., *Ambrosia dumosa* (Gray) Payne, *Larrea tridentata* (Ses. Moc. ex DC) Cov.] as the soil-moisture potential decreased are given. With a mesic species, *H. annuus*, 20 percent reduction in photosynthesis and transpiration was reached at higher soil-moisture potentials than with the desert plants. Loss of net photosynthesis occurred in *A. dumosa* (a summer deciduous shrub) as Ψsoil reached –48 bars in the field, whereas *L. tridentata* (an evergreen shrub) at the same time was able to maintain a water potential difference betwen soil and plant of –10 to –15 bars and continue net CO_2 gain well into the summer months.

Plants growing in arid regions obviously have the capability of surviving conditions of low soil-water content. The mechanisms differ (Cooper 1975). Transpiration and photosynthesis are two important plant processes that must adapt to the dry conditions for survival. Both processes involve gas exchange between the plant and the atmosphere, and both are known to decrease as soils become drier or as moisture stress increases (Babalola et al. 1968, Cox and Boersma 1967, El-Rahman 1969, Fischer 1970, Heichel and Musgrave 1966, Pallas et al. 1967, Schneider and Childers 1941, Schratz 1937, Shinn and Lemon 1968). Obviously, plants which have very low transpiration rates, thus prolonging the water supply provided that leaf turgor remains in a satisfactory state, would be favored under arid conditions. Also, a relatively high rate of photosynthesis could be advantageous, especially if it could be maintained with decreasing transpiration rates due to drying of soil.

Studies of quantitative relationships among transpiration, photosynthesis, and soil-water potential for desert shrubs have generally been difficult in the past because of technical difficulties. Desert shrubs grow and survive under conditions where the soil-water potential is usually much lower than can be accurately monitored by soil-water potential monitoring devices such as tensiometers or resistance blocks. However, recent developments of thermocouple psychrometers for measuring water potential extended the range that can be measured in soil. More sophisticated instruments that measure water vapor and CO_2 exchange between plants and the surrounding atmosphere have also been developed (Koller 1970, Mork et al. 1972). In particular, a null-point system that maintains a given atmospheric condition is desirable because the exchange is not greatly influenced by the measuring technique (Koller 1970, Mork et al. 1972).

The purpose of the research reported herein was to measure the relationship between transpiration and photosynthesis and soil-water potential of various desert shrubs. One study was conducted on sunflowers to provide comparison with a plant not adapted to desert conditions.

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MATERIALS AND METHODS

Studies were conducted under glasshouse conditions in containers so that the soil-water condition throughout the root zone could be determined. The plant species studied were *Artemisia tridentata* Nutt., *Ambrosia dumosa* (Gray) Payne, *Larrea tridentata* Ses. Moc., and *Helianthus annuus* L. (sunflower).

Rooted cuttings of *A. tridentata* (Wieland et al. 1971), along with seedlings of the other plant species, were grown in either 900 ml (10.5 cm diameter and 15 cm deep) or 2700 ml (10.5 cm diameter and 45 cm deep) containers. A Yolo silt loam soil treated with "krilium" to maintain aggregate stability was used as a growth medium. All containers were watered to approximately 20 percent soil-water content (Ψ soil = –1) and maintained until roots were established throughout the container. After roots were fully established, some of the containers were watered on a regular basis, whereas others were allowed to dry out.

Soil-water potential (Ψ soil) was measured by thermocouple psychrometers. (Commercial psychrometers manufactured by Wescor Inc., Logan, Utah were used. Readout was on a Keithley Nanovoltmeter.) One psychrometer was placed at 10 cm depth in the 900 ml container, and three psychometers were placed at 10, 28, and 42 cm depths in the 2700 ml containers.

Soil-water potential measurements were made early in the morning after plants were taken from the greenhouse into the headhouse to prevent rapid increase in soil temperature that interferes with potential measurement. Plants were allowed to stand in the headhouse for approximately one-half hour before measuring the potential, and then the containers were returned to the greenhouse.

Transpiration and apparent photosynthesis were monitored on both watered and unwatered plants. These measurements were made by a null-point compensating system described by Koller (1970) and further modified by Mork et al. (1972). Briefly, the measuring procedure was as follows: The plant was enclosed in a chamber that was maintained at constant relative humidity, temperature, and carbon dioxide concentrations. The amount of water removed to maintain constant relative humidity was measured and represented the transpirational loss from the plant. The amount of CO_2 added to the chamber to maintain the constant concentration was also measured and represented apparent photosynthesis. The plant chamber was used in the greenhouse; thus light intensity was not maintained constant and represented an uncontrolled variable. Light intensity measurements were made and recorded for the time transpiration, and apparent photosynthesis measurements were made. The plant chamber was maintained at a relative humidity of 28 percent, a CO_2 concentration of 316 μl/liter and a temperature of 25 C.

The time required for the plant to remain in the chamber depended upon the rate of transpiration and apparent photosynthesis. Sufficient water and CO_2 had to be exchanged for significant results. A 20-minute period generally was sufficient when transpiration and apparent photosynthesis were quite rapid, as occurred for nonstressed plants. Monitoring periods of up to an hour were often required for the stressed plants because of the low transpiration and apparent photosynthesis of these plants.

Because of the time involved in making measurements, not many plants could be measured. Because both transpiration and apparent photosynthesis are dependent upon light intensity, day to day variations in light intensity were partially compensated for by reporting only points where major changes occurred. Representative data, however, are shown in Figure 1.

Artemisia tridentata plants were grown in both 900 ml and 2700 ml containers. Apparent photosynthesis and transpiration were measured over two drying cycles. *Larrea tridentata* plants were grown in 2700 ml containers, and the transpiration and apparent photosynthesis were monitored for one drying cycle on two plants. The *A. dumosa* and *H. annuus* plants were grown in 900 ml containers and monitored for one drying cycle.

Gas exchange measurements were made on *L. tridentata* and *A. dumosa* during the months of May and June in the Mojave Desert. Soil-water potential and plant-water potential were monitored simultaneously. The latter was monitored by the pressure

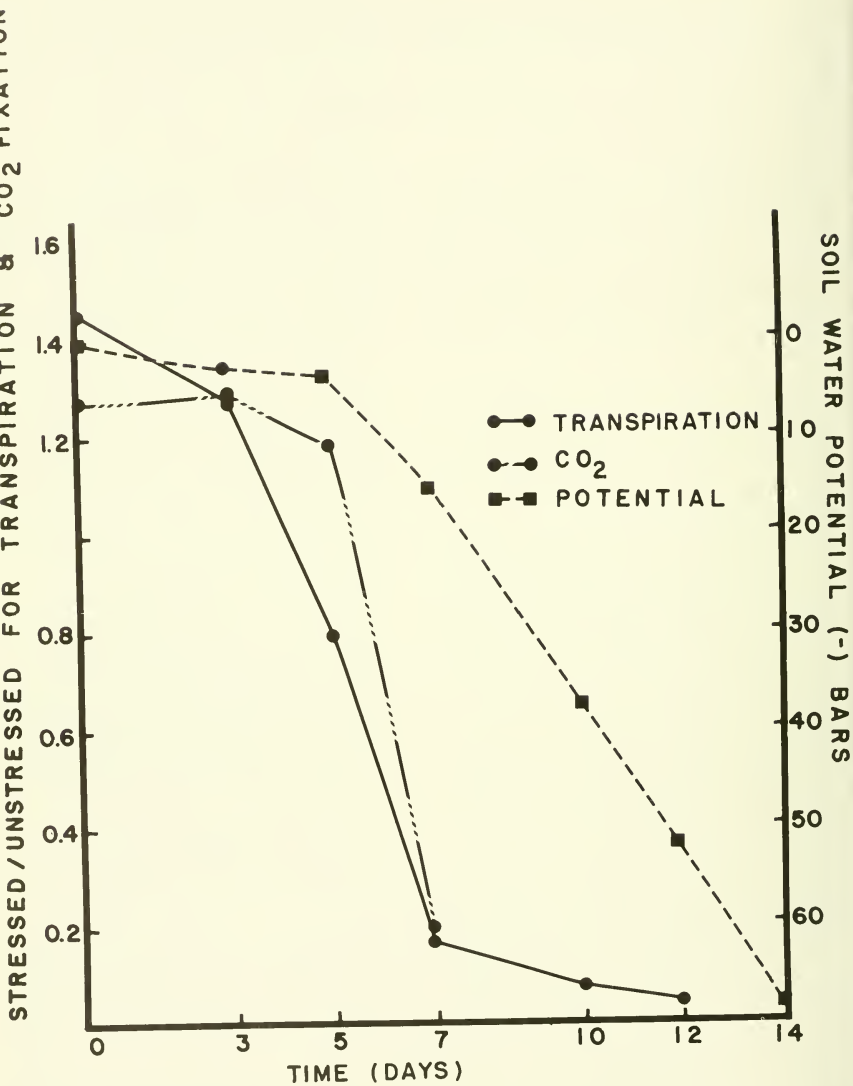

Fig. 1. Representative plot of data obtained, in this case for *A. dumosa*. Data are plotted as a ratio of stressed to unstressed plant conditions. Part of the variation in the ratio for zero time is due to differences in individual plants. Light intensity in 1000s μ Einsteins m^{-2} sec^{-1} in stressed plants for 0, 3, 5, 7, 10, 12, and 14 days, respectively, were 0.4, 1.4, 1.5, 1.2, 1.5, and 1.5, respectively. For unstressed plants for the same number of days they were 0.4, 1.2, 1.6, 1.1, 0.5, 1.3, and 1.5, respectively.

bomb technique (Scholander et al. 1965). Conditions for measuring photosynthesis and transpiration were the same as for greenhouse experiments.

RESULTS AND DISCUSSION

The results for *A. tridentata* are described in Table 1. At the beginning of the measurement, plants were in a vigorous state of vegetative growth; the stems were green and supple, the leaves were approximately 3 cm long, and the internodes approximately 0.5 cm apart. A shoot approximately ½ to 1 cm long was developing at each node. The lobes of the trees were deeply cleft, and the color was green with a slight shade of gray both on the upper and lower surfaces.

First visual indication of water stress on the plant was a gradual yellowing of the leaves attached to the main stem. As soil-water potential decreased over an 11-day period, the leaves turned necrotic and eventually fell off. The earlier symptoms occurred at a Ψ soil of –15 to –20 bars. A sharp reduction in transpiration and CO_2 fixation occurred when the soil was –5 to –10 bars. When the soil was between –20 and –25 bars, the remaining leaves wilted, and the overall color became more gray than green. No measurements on transpiration or apparent photosynthesis were made when Ψ soil was –25 bars; therefore, the plant in the dried soil was rewatered to start a second cycle.

Although the specific plant under test was not carried beyond –25 bars Ψ soil before watering, other plants were carried to lower potentials. The symptoms which occurred were that the shoot tips wilted and, if kept under stress, eventually died. However, the tips can be killed and the plant can recover if it is not held under stress too long.

Having the study plant subjected to 11 days without addition of water caused a noticeable change in plant appearance and characteristics even after irrigation. The stems were woody; internodes were quite close, giving the appearance of a whorl or rosette rather than single leaves alternately spaced as on the first cycle. The longer leaves were still attached, but were either yellow or necrotic.

There was an increase in the relative transpiration and CO_2 fixation rate following irrigation. The transpiration was initially high relative to the CO_2 fixation during the recovery period; however, the CO_2 fixation rate eventually was higher than transpiration. Upon starting the second drying cycle, decrease in transpiration appeared at a higher Ψ soil than did a decrease in CO_2 fixation. There was a steady decrease in transpiration as the Ψ soil decreased below about –2.5 bars. On the other hand, there appeared to be little effect of Ψ soil on CO_2 fixation until the soil-water potential was lower than about –16 bars. Further decrease in Ψ soil caused a decrease in CO_2 fixation. Within limits, a more rapid decrease in transpiration than decrease in CO_2 fixation as Ψ soil decreases may be an important factor in survival of plants adapted to arid environments. The

TABLE 1. Soil-moisture potential at which various changes occurred in the plants (–bars).

	H. annuus	*A. dumosa*	*L. tridentata* Plant No. 1	*L. tridentata* Plant No. 2	*A. tridentata*
20 percent reduction of photosynthesis rate	1	6	20	16	15
20 percent reduction of transpiration rate	2.5	3.5	5	26	5
Stress at CO_2 reduction of 75 percent	6	13	40	30	30
Stress at minimum CO_2 exchange	17	38	62	54	52

plant can be conserving water while still effectively producing carbohydrates. A recent review by Fischer and Turner (1978) on productivity in arid and semiarid environments suggests that plants tend to maintain high gas exchange rates as long as possible, thus maximizing both photosynthesis and transpiration.

Following are visual descriptions of the stressed plant as the Ψ soil decreased after the second irrigation. There were no visible symptoms of stress until Ψ soil was about –22 bars. This observation related quite closely to the CO_2 fixation but not to transpiration, as there had been a curtailment of transpiration well before visible symptoms occurred. The changes noted in the plant at –22 bars were an inward curling of the outer edge of the leaves; added stress induced by Ψ soil of –27 bars caused a very slight wilting. The change in plant appearance at –32 bars was a pronounced wilting and leaf color change from greenish to gray. When Ψ soil reached –52 bars, no apparent photosynthesis was measurable. Leaf tips became darker in color and severely curled. Soil-water potentials lower than about –61 bars were not measurable by the psychrometers in use (psychrometers more recently developed can measure below –61 bars). Thus, further observations on the plant refer to number of days following the time Ψ soil reached –61 bars.

After 5 days, the plant was under very severe stress, but there were no signs of necrosis except on leaves that had been damaged during the previous irrigation cycle. The method for measuring apparent photosynthesis was to monitor the amount of CO_2 required to maintain a constant CO_2 content in the plant chamber. Because there was no net CO_2 use at this high stress, the CO_2 concentration in the chamber was monitored with no air flow. With this change, the CO_2 concentration increased slightly and covering the chamber caused a threefold increase in rate of CO_2 production, indicating that some photosynthesis occurred at this time, even though it was not equal to the rate of respiration.

Seven days following the –61 bar potential readings, visible symptoms were about the same. CO_2 did increase slightly in the chamber, indicating respiration; however, the rate of CO_2 production did not change when the chamber was covered to eliminate light, thus indicating that photosynthesis had completely ceased.

Necrosis started to appear on lobes and margins of the leaves nine days following the –61 bar stress. Twelve days following the –61 bar Ψ soil reading the plant had a dull slate-gray appearance, the lower leaves were generally necrotic, and the upper leaves were flaccid. There was no change in CO_2 concentration within the chamber, indicating respiration had ceased. The plant was then irrigated, but it did not recover. It appears, therefore, that the plant can recover following irrigation at any time that measurable metabolism such as respiration can be found. Apparently, after the plant reaches a stage in which respiration completely ceases, it is irreversibly damaged.

In general, there were similarities between the results observed for plants grown in the 2700 ml container as compared to the 900 ml container even though the drying times to achieve the same level of stress were different. Transpiration decreased at a higher Ψ soil than did apparent photosynthesis during both the first and second irrigation cycles. However, during the second irrigation cycle, more time was required for the plant to recover in both photosynthesis and transpiration after having been subjected to water stress. The increase in apparent photosynthesis and transpiration following irrigation cannot be attributed completely to an increase in plant size because of growth. Although the drying period extended over a longer period of time in the 2700 ml container, the visual symptoms of the plant were very similar to those reported for the 900 ml container. During the first drying cycle, the longer leaves on the main stem curled and turned yellow. As drying continued, the other leaves changed to a grayer color with some curling. During the second drying cycle, there was no great appearance of chlorosis or necrosis of the leaves, but the leaves became a dull color and rolled.

The results for *A. dumosa* are also summarized in Table 1. This plant was carried over one drying cycle only. As was observed with *A. tridentata*, the transpiration appeared to decrease at a higher Ψ soil as compared to

CO_2 fixation. Transpiration noticeably decreased at Ψ soil less than –5 bars. A marked decrease in CO_2 fixation occurred when Ψ soil decreased from about –4 bars to about –15 bars. Apparent photosynthesis had ceased when the Ψ soil was –38 bars, however; CO_2 production was enhanced by covering the chamber, indicating that some photosynthesis was occurring at that Ψ soil even though respiration was at a higher rate than photosynthesis.

Some of the visual symptoms of *A. dumosa* are as follows: plants showed no symptoms of wilt, but the leaves were grayer than the control at a Ψ soil of –15 bars. As with *A. tridentata*, decrease in metabolic processes such as transpiration and photosynthesis occurred before visual symptoms appeared. Severe chlorosis on all but the leaves toward the growing tip occurred when the Ψ soil reached –38 bars. At this point there was no apparent photosynthesis, although some transpiration was still occurring. When the Ψ soil was –60 bars, the foliage was completely necrotic except for some color in the axils of leaves. This plant recovered if watered at this stage.

Soil in the containers of two separate *L. tridentata* plants was allowed to dry out. The *L. tridentata* plants were grown from seed and there was large variation between individual plants. One plant will be referred to as *Larrea 1*. Similar to other species, transpiration tended to decrease at a higher Ψ soil than did CO_2 fixation. However, the other plant (referred to as *Larrea 2*) showed an opposite trend that CO_2 fixation decreased at a higher Ψ soil than did transpiration. Differences between the two individual plants, however, go beyond these observations. The *Larrea 1* plant responded to drying out by having 50 to 60 percent of the leaves on the plant turn yellow and fall off when the Ψ soil was approximately –20 bars. The trend toward defoliation and yellowing of leaves continued as the water potential decreased. On the other hand, the *Larrea 2* plant had very little yellowing and defoliation under stress. Leaves tended to wilt and turn to a gray-green color. With continued soil drying, the leaves became desiccated. Some yellowing of leaves did occur, but the plant appeared completely different from the *Larrea 1* plant.

Results for the *H. annuus* plant are also in Table 1. One noticeable difference between *H. annuus* and the desert shrubs was that a slight decrease in Ψ soil down to –1 bar greatly reduced CO_2 fixation and did not have any significant effect on transpiration. Most of the desert shrubs behaved quite oppositely where transpiration was reduced much more significantly than CO_2 fixation at low soil. This may be of competitive advantage for the desert species. It has been reported that halophytes have lower transpiration rates than nonhalophytes (Schratz 1937), and this may be true also of other plants growing in harsh environments. A Ψ soil of –6 bars caused a great reduction in both transpiration and CO_2 fixation in *H. annuus* plant, but neither process could be monitored at a soil-water potential of –24 bars. When the Ψ soil reached –6 bars, the lower leaves were severely wilted and other leaves moderately wilted. When Ψ soil reached –20 bars, all leaves were severely wilted and the lower leaves complete necrotic. At Ψ soil of –33 bars the stem was shriveling.

The *H. annuus* experiment was conducted as an indicator of our procedure. Many studies have been conducted on drying soil in which *H. annuus* plants are growing, and –15 bars has often been quoted as the permanent wilting percentage for *H. annuus*; our results are in reasonable agreement with that value. Transpiration and photosynthesis measured on *H. annuus* also appear to be reasonable. This provides some degree of confidence in accepting the results measured on the desert shrubs.

The results of a field experiment where both soil-water potential and tissue-water potential (Ψ plant) (Scholander et al. 1965) were measured are shown in Table 2. Gas exchange measurements on *A. dumosa* during May and June showed decreasing photosynthesis and transpiration rates as Ψ soil decreased. Positive carbon dioxide exchange ceased on *A. dumosa* as Ψ plant reached –47 bars. However, *L. tridentata*, an evergreen desert shrub, continued photosynthesis until Ψ plant reached –65 bars. This difference between species is in agreement with greenhouse studies reported in Table 1 and also with results of Odening et al. (1974). *Larrea tridentata* has a distinct advantage of being

TABLE 2. Ψ soil and Ψ plant (–bars) as measured on two desert shrubs under field conditions.*

		Ambrosia dumoa		*Larrea tridentata*	
		Ψsoil	Ψplant	Ψsoil	Ψplant
May	1	22	39	22	51
	9	28	40	28	54
	31	42	—	42	56
June	1	48	47	48	63
	6	48	dormant	48	—
	12	50	dormant	50	63
	12	52	dormant	52	65

*Maximum rates of gas exchange for *A. dumosa* and *L. tridentata* were net photosynthesis 35 and 10 mg/g dry wt –h and transpiration 45 and 13 g/dry wt –h, respectively.

able to maintain productivity well into the summer months. In both shrub species, maximum gas exchange activity occurred during the early spring months when favorable moisture conditions existed.

ACKNOWLEDGMENTS

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EFFECT OF CERTAIN PLANT PARAMETERS ON PHOTOSYNTHESIS, TRANSPIRATION, AND EFFICIENCY OF WATER USE

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ABSTRACT.— Rates of gaseous exchange were measured on selected desert shrubs native to the northern Mojave Desert to determine effects of varying chamber temperature, CO_2 concentration, relative humidity, and root temperature in preliminary studies. Results indicate that changes in these parameters produced differences in the rates of photosynthesis and transpiration. *Ceratoides lanata* (Pursh) took up CO_2 almost equally at 25 and 39 C. Doubling the CO_2 concentration in the below-ambient range roughly doubled photosynthesis rates in *C. lanata*. Very small changes in relative humidity had marked changes in the photosynthesis and transpiration rates of four species studied, with greater effect on transpiration. Photosynthesis and transpiration increased, and water-use efficiency decreased in two species as soil temperature was increased from 9 to 29 C.

The subject of photosynthesis has been discussed and reviewed thoroughly by Sestak et al. (1971), Troughton (1975), and Cooper (1975). These reviews indicate that it is very difficult to predict or explain the photosynthetic rate of a plant because it is influenced by the simultaneous action of many external and internal factors that affect the rate of photosynthesis.

For this reason a study was undertaken with objectives to determine how sensitive the rates of CO_2 exchange and water loss are to variations in chamber temperature, CO_2 concentration, relative humidity, and the root temperature of the plant (i.e., how much variation can be tolerated in these parameters without adversely affecting the validity of gas exchange rates in desert plants). This technique has been described by Koller (1975).

Rates of photosynthesis and transpiration were measured using the Null-point Compensating System (Koller 1970) with the Improved Feedback Mechanism (Mork et al. 1972). The principle of this system is based on maintaining essentially constant conditions in the chamber; i.e., the CO_2 concentration, the relative humidity, the chamber temperature, and the bath temperature must be constant to make valid measurements of compensation rates.

MATERIALS AND METHODS

Five species of desert shrubs were tested in February and March 1972: *Ephedra nevadensis* S. Wats., *Larrea tridentata* (Sesse & Moc. ex DC.) Cov., and *Lycium pallidum* Miers in the field, and *Atriplex hymenelytra* (Torr.) S. Wats., *Ceratoides lanata* (Pursh) and *L. tridentata* in the glasshouse.

Field plants were tested at various levels of CO_2 concentration. Plants in the glasshouse were tested at various chamber temperatures and root temperatures. Initially, a more complete and extensive study was envisioned, particularly with regard to the effect of varying the root temperature. All the necessary equipment was on hand: the plants were growing in water-jacketed lucite cylinders, so the root temperature could be adjusted by running heated or cooled water through the jacket. In each case one parameter was varied, and the rates of photosynthesis and transpiration were measured using the Null-point Compensating System with the Improved Feedback Mechanism. The light intensity was measured with a portable Weston meter. Air temperature has complex interactions with photosynthetic rate (Bauer et al. 1975, Mooney et al. 1975), but a study of them is not the purpose of this report.

The photosynthesis and transpiration rates

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were calculated using the method of Koller (1970) and expressed as mg CO_2 per g dry tissue per h (or as mg CO_2 per sample per h) and g H_2O per g dry tissue per h (or as g H_2O per sample per h), respectively.

Efficiency of water use is a ratio of photosynthesis (g CO_2 fixed per unit time) to transpiration (g water lost per unit time) × 100 (percent).

RESULTS AND DISCUSSION

Increasing the chamber temperature about 25 C tended to increase the rate of water loss up to 46 C for *C. lanata* at field capacity soil moisture (Table 1). The rate of photosynthesis was decreased at 46 C but not at 39 C relative to 25 C. A wide optimum range was indicated for these glasshouse-grown plants.

The CO_2 concentration in the chamber had significant effects on the plant process rates as expected (Table 2). Increasing the CO_2 concentration (range 90–375 ul/l air) increased the CO_2 exchange for *L. pallidum* almost tenfold while reducing the water loss by about 10 percent. About the same range of increases in CO_2 increased the CO_2 exchange about fourfold for *L. tridentata*, with a reduction in water loss of about 10 percent. Doubling the concentration of CO_2 in these low ranges roughly doubled the rate of CO_2 exchange. Decreasing the relative humidity even by very small increments for *L. tridentata* and *E. nevadensis* tended to reduce the CO_2 uptake (r = +0.68 and +0.99, respectively, for the two species) and increase the water loss rate (Table 3). In contrast, the net result of a slight decrease in relative humid-

TABLE 1. Effects of chamber temperature on photosynthesis and transpiration rates and on efficiency of water use of *Ceratoides lanta* grown in the glasshouse (3-9-72).

Hour of day	Chamber temperature C	Light intensity μ Einsteins m^{-2} sec^{-1}	Photosynthesis mg CO_2/g-h*	Transpiration g H_2O/g-h*	Efficiency percent
1230–1250	24.8	1206	6.89	0.46	1.50
0953–1013	30.8	446	3.45	1.31	0.26
1128–1148	37.0	1296	7.38	1.23	0.60
1023–1043	38.8	782	8.90	1.30	0.68
1100–1120	46.3	1229	3.10	1.84	0.17

*Measurements made on potted plant, continuing study.
Chamber conditions: CO_2 concentration 320 μliters/liter air; relative humidity 27.7 percent; root temperature 28 C.

TABLE 2. Effect of CO_2 concentration on photosynthesis and transpiration rates, and on efficiency of water use of *Lycium pallidum* (3-18-72) and *Larrea tridentata* (3-10-72) in the field (Rock Valley).

Hour of day	CO_2 concentration μliter liter air	Light intensity μ Einsteins m^{-2} sec^{-1}	Photosynthesis mg CO_2/g-h*	Transpiration g H_2O/g-h*	Efficiency percent
		Lycium pallidum			
1020–1040	90	2410	4.39	3.34	0.13
1100–1120	132	2460	13.6	3.37	0.60
1200–1220	172	2410	17.8	3.32	0.54
1240–1300	215	2370	25.2	3.22	0.78
1320–1340	260	2370	28.9	3.16	0.94
1420–1440	375	2280	38.3	2.90	1.32
		Larrea tridentata			
1110–1120	90	2460	6.25	1.19	0.52
1130–1140	132	2410	6.97	1.17	0.60
1200–1140	172	2370	8.00	1.11	0.72
1300–1310	215	2370	9.25	1.10	0.84
1330–1340	368	2370	26.3	1.03	2.55

Chamber conditions: Temperature 25 C; relative humidity 28.0 percent; root temperature 18–19 C.

ity on *C. lanata* was an increase both in photosynthesis (r = –0.94) and in water loss (r = –0.99). For *L. pallidum* the effect on the rates was somewhat the same (r = +0.26 for photosynthesis and –0.84 for transpiration with decreasing relative humidity).

In the experiment with root temperature, the range should have been extended up to perhaps 40 C or higher. The data in Table 4 (for the range 10 to 29 C) showed increases in

TABLE 3. Effect of relative humidity on photosynthesis and transpiration rates, and on efficiency of water use of *Lycium pallidum* (3-17-72), *Larrea tridentata* (3-19-72), *Ephedra nevadensis* (3-21-72) and *Ceratoides lanata* (2-3-72) in the glasshouse.

Hour of day	R.H. percent	Light intensity μ Einsteins m^{-2} sec^{-1}	Photosynthesis mg H_2O/g-h	Transpiration g H_2O/g-h	Efficiency percent
		Lycium pallidum			
1413–1433	27.9	2370	28.1	3.55	0.79
1457–1507	26.8	2270	32.2	4.09	0.79
1537–1547	25.5	2010	26.9	4.08	0.66
		Larrea tridentata			
1530–1540	27.8	2270	14.3	0.90	1.58
1558–1608	26.8	2010	9.25	0.95	0.97
1610–1620	25.0	2010	10.7	1.07	1.00
1630–1640	24.2	2010	9.25	1.14	0.81
		Ephedra nevadensis			
1550–1600	28.3	1880	4.09	0.12	3.30
1628–1724	27.8	1250	3.32	0.13	2.57
		Ceratoides lanata			
1330–1350	27.5	693	2.98	0.08*	3.77
1255–1315	26.6	850	3.12*	0.11*	2.96
1220–1240	25.5	890	4.02*	0.17*	2.34
1145–1205	24.0	1200	4.18*	0.20*	2.07

*Values for *Ceratoides lanata* are mg CO_2/sample-h and g H_2O/sample-h.
Chamber conditions: Temperature 25 C; CO_2 concentration 330 μliters/liter air.

TABLE 4. Effect of root temperature on photosynthesis and transpiration rates, and on efficiency of water use of *Larrea tridentata* (3-9-72) and *Atriplex hymenelytra* (2-29-72) in the glasshouse.

Hour of day	Root temperature C	Light intensity μ Einsteins m^{-2} sec^{-1}	Photosynthesis mg CO_2/g-h*	Transpiration g H_2O/g-h*	Efficiency percent
		Larrea tridentata			
1550–1600	10–11	1030	2.94	0.27	1.09
1530–1540	12–14	1120	4.45	0.54	0.83
1500–1510	16–19	540	3.81	0.73	0.52
1430–1440	23–26	1030	4.83	0.71	0.69
1350–1400	28–29	1030	5.65	0.70	0.80
		Atriplex hymenelytra			
1432–1442	9.2	715	11.4	0.52	2.19
1410–1420	10.0	625	13.1	0.67	1.96
1315–1325	16.8	1210	21.6	0.93	2.32
1305–1315	20.0	1270	21.7	1.02	2.14
1240–1250	23.1	1340	20.6	1.05	1.97
1225–1235	27.7	985	22.9	1.13	2.02
1125–1135	29.0	1340	26.1	1.14	2.29

*Measurements made on potted plants, continuing study.
Chamber conditions: Temperature 25 C; CO_2 concentration 322 μliters/liter air; relative humidity 27.7 percent.

both photosynthesis and transpiration for both *L. tridentata* and *A. hymenelytra* grown in the glasshouse. Water-use efficiency decreased as soil temperature increased, as has been observed elsewhere (Wallace 1970). The C_4 plant, *A. hymenelytra*, had a 4.6-fold greater photosynthetic rate, a 2.9-fold greater water-use efficiency, and a 1.6-fold greater transpiration rate at 29 C root temperature than the C_3 plant *L. tridentata*. At 10 C root temperature the C_4 plant had 2.9-fold greater photosynthesis, 2.4-fold greater water use efficiency, and 1.24-fold greater transpiration. The apparent advantages of the C_4 characteristics seem to decrease as soil temperature is decreased.

Changes in the CO_2 concentration, the chamber temperature, the relative humidity, or the root temperature of the plant may produce tenfold differences in the gas exchange rates. Therefore, it is important to maintain each of these parameters as constant as possible when making observations in experimental tests.

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CARBON FIXED IN LEAVES AND TWIGS OF FIELD *LARREA TRIDENTATA* IN TWO-HOUR EXPOSURE TO $^{14}CO_2$

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ABSTRACT.— Six *Larrea tridentata* (Sesse & Moc. ex DC) Cov. plants were exposed to $^{14}CO_2$ in a field experiment r 2 h. Three of the plants had been irrigated regularly in the preceding year. Ten small twigs from each plant were moved and counted for ^{14}C activity at the end of 2 h. The stem portion of the twigs was of equal dry weight for e two sets of plants, but those irrigated had a greater weight of leaves per twig. The activity of ^{14}C in leaves was ual for the two groups, but was higher in stems for watered plants than for unwatered plants. The results were st expressed as ratios. Dry weight of leaves ÷ dry weight of stems was high for watered plants; cpm/g dry weight leaves ÷ cpm/g dry weight of stems was higher for unwatered plants. In another experiment in which leaves ere removed before exposing stem portions of twigs to $^{14}CO_2$, small green stems accounted for about ⅛ the total notosynthesis for a plant; the coefficient of variation was around 100 percent.

INTRODUCTION

Larrea tridentata (Sesse & Moc. ex DC) Cov. is a perennial well adapted to the hot, ry summers of the Mojave Desert. It is a C-3 lant with a relatively low rate of photonthesis (Barbour, 1977). It is an evergreen ith an ability to fix CO_2 in every month of e year (Bamberg et al. 1973, 1975). Its naller stems have chlorophyll, particularly oung stems, and they also are capable of hotosynthesis. The purpose of this report as to show the relative importance of leaves nd stems for photosynthesis of this species in e field in the northern Mojave Desert. Part f the plants used in this study were also inolved in a shoot-root carbon budget study Vallace et al. 1980, this volume) and data ere available from which the present results ere obtained.

MATERIALS AND METHODS

Six *L. tridentata* were exposed to $^{14}CO_2$ for h on the morning of 14 May 1974 by techiques previously used (Bamberg et al. 1973, 974; Wallace et al. 1977). Briefly, 5 ml of a .5 *M* solution of $KH^{14}CO_3$ was mixed with ICl inside a plastic bag which was tied at e base of the plant. The ^{14}C activity was 5 Ci/ml. After exposure the bags were removed, and ten small twigs containing leaves and stems were removed from each plant and assayed with Q-gas counting for ^{14}C fixed. Each leaf and stem sample was counted in triplicate. Three of the six plants used had been irrigated regularly in the previous year. Since translocation from leaves to twigs was possible during the 2-h test, a second experiment was conducted in which leaves were first removed from green stems. These stems were then subjected to the same type of test as twigs previously.

RESULTS AND DISCUSSION

The weight of leaves per twig was higher for the three plants previously irrigated than for those not irrigated (Table 1). The coefficient of variation (C.V.) for within the watered plants was low enough to indicate that that group was a separate population. The weights of stems per twig, however, were similar for both groups of plants.

The amount of ^{14}C fixed per g dry weight of both leaves and stems was variable with a C.V. of about 100 percent. However, for leaves the means of each group were essentially identical. For stems the watered plants had about 60 percent more ^{14}C than the nonwatered plants (Table 1). When the data were considered as ratios with cpm/g dry

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weight of leaves ÷ the cpm/g dry wt of stems (Table 2) it is apparent that this observation is statistically significant. The C.V. for ratios with unwatered plants was only 7.6 percent and only 5.5 percent for watered plants. When all six plants were grouped together the C.V. was 23.8 percent.

The ratio of dry weight of leaves to dry weight of stems was 40 percent larger for the watered plants than for the nonwatered ones. The C.V. of both groups was low (1.7 and 13.2 percent), indicating that they are separate populations. The previous irrigation then was reflected in a larger growth of leaves on the plants.

In the second experiment in which leaves had been removed from green stems before the $^{14}CO_2$ was started, it was shown that approximately ⅛ (the coefficient of variation was around 100 percent) of the photosynthesis for *L. tridentata* could be by way of the green stems (Table 3). On the dry weight basis the amount of ^{14}C in green stems was 51 percent that of leaves. Green stems with leaves attached contained more ^{14}C than did green stems with leaves removed, so it can be assumed that there was some translocation from leaves to stems during the 2 h test. There was also some ^{14}C translocated to small branches during the 2 h.

Stem photosynthesis is very likely one of the adaptive mechanisms of this drought-tolerant, heat-resistant desert plant species.

TABLE 1. Dry weight of twigs and ^{14}C in twigs of *L. tridentata* exposed for 2 h to $^{14}CO_2$.

	Dry wt of twigs		^{14}C	
	Leaves	Stems	Leaves	Stems
	mg/twig		cpm/g dry wt	
	Unwatered (n = 3)			
Mean	67.1	29.8	67547	41900
S.D.	19.4	8.3	59103	33710
C.V.%	28.9%	27.7%	87.5%	80.5%
	Watered (n = 3)			
Mean	85.2	27.1	69753	66380
S.D.	9.4	1.4	72615	66021
C.V.%	11.1%	5.2%	104.1%	99.5%
	All plants (n = 6)			
Mean	76.2	28.5	68650	54140
S.D.	16.9	5.5	59227	48763
C.V.%	22.2%	19.3%	86.3%	90.1%

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TABLE 2. Ratios of leaf and stem portions of the twigs for dry weight and ^{14}C fixed in *L. tridentata*.

	Dry wt of leaves / Dry wt of stems	cpm/g dry wt leaves / cpm/g dry wt stems	cpm/twig-leaves / cpm/twig-stems
	Ratio	Ratio	Ratio
	Unwatered (n = 3)		
Mean	2.26	1.56	3.49
S.D.	0.038	0.12	0.21
C.V.%	1.7%	7.6%	6.0%
	Watered (n = 3)		
Mean	3.18	1.02	3.19
S.D.	0.42	0.056	0.30
C.V.%	13.2%	5.5%	9.3%
	All plants (n = 6)		
Mean	2.71	1.29	3.34
S.D.	0.58	0.31	0.28
C.V.%	21.3%	23.8%	8.5%

TABLE 3. ^{14}C fixation of green stems of *L. tridentata* from which leaves had been removed compared with stems with leaves attached.*

	Relative Dry wt	^{14}C cpm/g	CV %	Relative cpm/g
Leaves	1.00	88,127	88.0	1.00
Green stems (leaves attached)	0.45	45,233	104.0	0.51
Small branches	0.26	13,773	72.4	0.16
Green stems (without leaves attached)	0.45	32,910	114.1	0.37

*Relative photosynthesis for the green stems for the per plant basis would be (0.45 × 0.37) + 1 + (0.45 × 0.51) + (0.26 × 0.16) = 0.134 or about ⅛. All values in the calculation are in Table 3. Since the CV is around 100%, its value of ⅛ must be considered also as possibly in error by as much as 100%.

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THE ROLE OF SHRUBS ON REDISTRIBUTION OF MINERAL NUTRIENTS IN SOIL IN THE MOJAVE DESERT[1]

E. M. Romney[2], A. Wallace[2], H. Kaaz[2], and V. Q. Hale[2]

ABSTRACT.— Soil profiles underneath shrub clumps and bare desert pavement were examined at 62 study sites located in both open and closed drainage basins of the northern Mojave Desert. Highly significant differences occurred in the root zone underneath shrub clumps with higher concentrations of the following soil properties: electrical conductivity (EC25°), Na, K^+, Ca^{++}, Mg^{++}, Cl^-, NO_3^-, and $SO_4^=$; exchangeable K^+; cation exchange capacity; organic C and N; available P, and DTPA-extractable Fe and Mn. These differences reflect differential cycling caused by different plant species. The decomposition and mineralization of litter deposited underneath the perennial vegetation can account for these differences in soil properties which, collectively, increase the fertility of the soil underneath the vegetation canopy. Aboveground biomass of shrubs was measured and the nitrogen and mineral element composition of new photosynthetic tissue was determined. Estimates from a representative study site indicate that the reservoir of nitrogen and mineral nutrients in new leaf material of shrubs available for litter deposition could contribute 3.64 kg N, 0.31 kg P, 0.57 kg Na, 5.20 kg K, 4.95 kg Ca, 31.82 g Fe, and 4.30 g Mn per hectare. This source probably represents about one-third of the total amount of nutrients involved in annual turnover for the study area during a normal production year. The remaining contribution would be supplied from the standing dead wood in shrubs and as litter from annual plant species.

Efforts to develop the potential benefits of wildland shrubs have increased with man's needs to make arid and semiarid lands more productive and useful. An extensive world literature produced from studies on production and mineral cycling in terrestrial vegetation was summarized in the work of Rodin and Bazilevich (1965), which considers several aspects of mineral involvement in plant production between vegetation types representing the broad climatic zones of the world. A review of available literature on the biology and utilization of wildland shrubs in arid and semiarid lands was one of the main objectives of a recent international symposium (McKell et al. 1971). At that symposium Charley (1971) discussed the role of shrubs in nutrient cycling, with emphasis upon the nitrogen conditions encountered in a perennial saltbush ecosystem. The principles governing important transformation processes involved in shrub production, litter fall, and subsequent decomposition and mineralization in natural ecosystems have been well covered in these and other recent reviews (Rennie 1955, Ovington 1962, 1965, Egunjobi 1969).

This paper reports on the influence of shrubs on cycling or redistribution of mineral nutrients in zones near roots in the Mojave Desert. Edaphic factors are important in the distribution of plant species, but plants also are important in determining soil characteristics. For example, an accumulation of nitrogen and mineral elements in plant foliage results in the cycling of these elements from litter to the soil underneath the plant canopy (Roberts 1950, Fireman and Haywood 1952, Beadle et al. 1957, Rickard 1965b, Charley and Cowling 1968, Chatterton and McKell 1969, Jessup 1969, Garcia-Moya and McKell 1970, Charley 1971, Sharma and Tongway 1973, Tiedemann and Klemmedson 1973). The extent to which this process occurs under northern Mojave Desert conditions was one aspect of concern in studies undertaken in southern Nevada.

[1]Findings in this paper appeared, with slight modifications, in The belowground ecosystem: a synthesis of plant-associated processes. Pages 303–310 in Range Science Department Science Series report No. 26. Colorado State University, Fort Collins 1977. We present these findings again for convenience and accessibility to readers interested in the several related papers in this issue.

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DESCRIPTION AND METHODS

Investigations were conducted at the USAEC Nevada Test Site to obtain more information on soil and plant relationships in the desert ecosystem to better understand the impact of nuclear testing on the natural environment. The findings presented herein were synthesized from preliminary raw data reported by Romney et al. (1973).

The perennial vegetation of the study areas exists as solitary shrubs or as discrete clumps consisting of several different shrub species. Sharp ecotonal demarcation zones are prevalent among some of the more dominant shrub species. Most of the soils examined have developed on alluvium consisting of limestone or mixed limestone and volcanic material. Except in areas of recent sedimentary deposition, many are now underlaid by layers of restrictive hardpan formed from the processes of alkaline hydrolysis at depths varying from 30 to 70 cm. Study sites were selected in both open and closed drainage basins. Details of the study areas involved in these investigations have been reported (Wallace and Romney 1972, Romney et al. 1973).

At each of 62 study sites a trench was dug with a backhoe extending across a shrub clump and out into the bare desert pavement to a distance of at least 3 m. This was done to permit an examination and sampling of the soil profile underneath both shrub and bare areas in order to investigate the modifying influence of perennial vegetation on the profile horizons. The soil profiles were described according to the USDA Soil Conservation Service nomenclature (Soil Survey Staff 1951). Represented among these study sites were soil belonging to several subgroups, including Typic Torripsamments, Haplic Nadurargids, Entic Durorthids, and Typic and Duric Camborthids.

Physical and chemical properties were determined on soil samples screened to pass a 2 mm sieve. Sand fractions were measured by mechanical separation on standard testing sieves. Silt and clay fractions were determined by the pipette method described by Day (1965). Available phosphorus was extracted with sodium bicarbonate and determined colorimetrically using the method of Olsen et al. (1954) as described by Chapman and Pratt (1961). Lime content was determined by the manometric method of Williams (1948). The available micronutrients were extracted with DTPA chelate and determined by atomic absorption analysis (Lindsay and Norvell 1978). Organic nitrogen analysis was by the Kjeldahl method (Bremner 1965). The analytical methods used to determine other physical and chemical properties were those of the USDA Salinity Laboratory Staff (1954).

Some of the ecological attributes of the perennial vegetation were determined by nondestructive dimensional measurements (Wallace and Romney 1972:250). Briefly, 2 m × 25 m quadrats were laid out at right angles to each other in undisturbed vegetation in the proximity of the soil sampling trench. All shrubs within the quadrats were identified by species and measured for height and width (mean of two dimensions). These measurements were used to determine shrub density, frequency, relative dominance, cover, and volume. Biomass estimates were derived from regressions of dry weight on volume indexes developed from the destructive sampling of shrubs in nearby areas (Romney et al. 1973). Measurements of new photosynthetic production were made for the more prominent shrub species by destructive sampling at selected study sites during the peak of seasonal leaf flush.

Samples of clean foliage were collected in the vicinity of each soil sampling trench for chemical analysis. Oven-dried (70 C) samples were separated into leaf and stem material and finely ground for analysis by optical emission spectrometry (Wallace and Romney 1972:363). Total nitrogen contents were determined on leaf tissue using the Coleman Model 29A Nitrogen Analyzer.

RESULTS AND DISCUSSION

Soil Profile Characteristics

Most of the soil profiles examined in this study have developed on relatively coarse alluviums low in clay content under conditions of high temperature and low rainfall. Many profiles clearly indicate an acceleration of the soil-forming processes underneath shrub clumps. Distinct differences also occur in the

amounts of wind-blown material deposited underneath shrubs and on bare soil. Loess blankets a major portion of the study area (Ekren 1968); volcanic ash falls and wind action are responsible for its wide distribution. Other prominent characteristics evident under shrubs include better developed A horizons containing higher concentrations of salt and organic matter, and some decomposition of the underlying hardpan when present. Table 1 contains the profile description for study site No. 5, which is representative of soils with an underlying hardpan developed on alluvium parent material of mixed limestone and quartz. Detailed descriptions and properties of other soil profiles are given in Romney et al. (1973).

Physical and chemical properties of the soil profile at site No. 5 are listed in Table 2. They reflect the kinds of change generally found between different horizons underneath shrub clumps and bare areas. These properties most notably modified in zones near roots include the salts of sodium, potassium, calcium and magnesium, available phosphorus, organic carbon and nitrogen, and available iron and manganese. The particle size distribution, water-holding capacity, pH, and lime content essentially remained unaltered within the depth of the root zone. Electrical conductivity (EC25°) of the saturation extract reflected the concentrations of soluble cations and anions in the profile horizons. Highest salt concentrations were found in the A horizons underneath shrubs. No evidence was found of an accumulation of soluble salts in the bare soil areas between shrub clumps as reported by Charley and McGarity (1964) for perennial saltbush communities growing on saline soils of the Australian arid zone. The soils examined here are moderately permeable and subject to leaching by rainfall. Except for a few sites located on sediments of closed-drainage basins, most profiles examined were nonsaline-nonalkali within the root zone, i.e, the EC25° was less than 4 mmhos/cm and the exchangeable sodium percentage was less than 15 (U.S. Salinity Laboratory Staff 1954).

Several other investigators have described sharp changes in the chemical properties of soil underneath shrub canopies resulting from an accumulation of salts as the result of litter deposition (Roberts 1950, Fireman and Hayward 1952, Rickard 1965a, 1965b, Charley and Cowling 1968, Sharma and Tongway 1973). Similarly, significant accumulations of nitrogen and organic matter have occurred as the result of litter decomposition (Garcia-

TABLE 1. Soil profile description at Mercury Valley Study Site No. 5.

Area: Mercury Valley, Nye County, Nevada

Perennial vegetation: *Acamptopappus shockleyi* A. Gray, *Atriplex confertifolia* (Torr. & Frem.) Wats., *Ambrosia dumosa* (A. Gray) Payne, *Ephedra funerea* Cov. & Mort. *Ephedra nevadensis*, Wats., *Ceratoides lanata* (Pursh) J. T. Howell, *Grayia spinosa* (Hook) Moq., *Krameria parvifolia* Benth., *Larrea tridentata* (Sesse & Moc. ex DC.) Cov., *Lycium andersonii* A. Gray., *Yucca schidigera* Roezl ex Ortgies.

Parent material: alluvium from limestone and quartz.

Topography: 3 percent southwest slope, smooth relief; well-drained moderate erosion; surface about 80 percent rock and gravel; well-developed desert pavement; elevation 1096 m.

Profile under shrub clump: (*C. lanata, L. tridentata, L. andersonii*)

A1	0–9 cm	Brown (10YR5/3) loamy fine sand, brown to dark brown (10YR4/3) moist; weak fine subangular blocky structure; soft, friable, nonsticky, violently effervescent; few micro roots; pH 8.0; abrupt smooth boundary.
A2	9–13 cm	Very pale brown (10YR7/3) sandy loam, yellowish brown (10YR5/4) moist; moderate medium platy; slightly hard, friable, slightly sticky; violently effervescent; few medium, fine, and micro roots; 20 percent gravel; pH 8.4; abrupt irregular boundary; discontinuous.
C1	13–36 cm	Very pale brown (10YR7/3) loamy sand, yellowish brown (10YR5/4) moist; weak fine subangular blocky structure; soft, friable, nonsticky, violently effervescent; few medium, fine, and micro roots; 20 percent gravel; pH 8.4; clear wavy boundary.
C2sicam	36+ cm	Cemented pan.

Profile under bare area:

C1		Horizon description is the same as C1 under shrub.
C2sicam	34+ cm	

Moya and McKell 1970, Charley 1972, Tiedemann and Klemmedson 1970, Holmgren and Brewster 1972, Nishita and Haug 1973). The work of Charley and Cowling (1968) indicates that biologically increased vertical salt gradients in soil seem to become sharper with increased aridity.

Perennial Vegetation Characteristics

Some of the ecological attributes of shrubs at study site No. 5 are given in Table 3. Beatley (1969a) described the vegetation type and association for the area in which this site was located as *Larrea-Franseria* (*Ambrosia*). Nondestructive dimensional measurements indicate *Acamptopappus shockleyi* A. Gray and *Ambrosia dumosa* (A. Gray) Payne were of highest density and frequency. The relative dominance index for basal area was highest for *A. dumosa* followed closely by *Lycium andersonii* A. Gray and *Krameria parvifolia* Benth. Greatest aboveground standing biomass was contributed by *Yucca schidigera* Roezl ex Ortgies (927 kg/ha). *Lycium andersonii* and *A. dumosa* contributed essentially the same biomass (458 and 456 kg/ha) followed by *Ephedra funerea* Cov. and Mort. (228 kg/ha), *Larrea tridentata* (Sesse & Moc ex DC.) Cov. (162 kg/ha) and *K. parvifolia*

TABLE 2. Physical and chemical properties of soil profile horizons under shrub and bare areas of site no. 5.

Profile horizon properties	Shrub clump			Bare area
	A1	A2	C1	C1
Horizon depth, cm	0–9	9–13	13–36	0–34
Particle size distribution (% < 2mm)				
coarse sand (2.0–0.25)	28.8	26.2	21.0	25.5
fine sand (0.25–0.05)	53.9	41.3	56.7	50.2
silt (0.05–0.002)	10.9	23.4	16.2	16.9
clay (< 0.002)	6.4	9.1	6.1	7.4
Percent moisture retention				
saturation	44.7	26.6	32.8	26.2
–0.3 bar	15.7	17.7	19.5	16.5
–1 bar	13.4	14.5	15.3	14.7
–15 bar	9.6	8.7	7.8	8.1
pH (saturated paste)	8.0	8.4	8.4	8.3
EC (mmhos per cm, 25 C)	4.74	1.49	0.55	0.40
Saturation extract soluble cations and anions				
Na, meq/1	2.50	8.32	1.84	0.56
K, meq/1	13.20	2.95	1.65	0.63
Ca, meq/1	19.69	5.14	0.56	0.76
SO_4, meq/1	1.00	0.14	0.02	0.07
B, ug/g	5.10	3.60	0.10	2.90
Exchangeable cations (NH_4OAc-extraction)				
Na, meq/100 g	0.27	0.71	0.42	0.47
Na, %	1.50	4.10	2.50	3.00
K, meq/100 g	4.06	3.92	3.45	1.78
Ca + Mg, meq/100 g	13.17	12.87	13.01	13.38
C.E.C., meq/100 g	17.50	17.50	16.88	15.63
Percent lime (< 2mm)	16.00	17.00	17.00	17.00
P, ($NaHCO_3$-ext.) ug/g	3.26	0.36	0.04	0.24
Organic carbon, %	2.12	0.48	0.38	0.33
Organic nitrogen, %	0.211	0.050	0.044	0.035
DTPA-extractable micronutrients				
Fe, ug/g	0.5	0.1	0.2	0.1
Zn, ug/g	0.80	0.80	0.80	0.95
Cu, ug/g	0.20	0.30	0.20	0.25
Mn, ug/g	5.00	1.50	1.15	0.95

(148 kg/ha). These shrubs accounted for more than 95 percent of the perennial plant biomass. In this particular area, dead wood often accounts for a significant portion of the standing biomass of perennial vegetation. It remains standing for many years and probably contributes about as much mass in annual litter-fall as does new leaf material.

Leaf/plant ratios were measured for most shrubs at this site during peak leaf flush in 1968. *Yucca schidigera* was ignored because of its lack of contribution to mobile leaf litter

TABLE 3. Characteristics of perennial vegetation at study site no. 5.

Plant species	Density No/ha	Frequency %	Relative dominance*	Biomass** kg/ha	Leaf/Plant ratio**
Acamptopappus shockleyi	3589	25.6	8.4	26.1	0.137 (19)***
Ambrosia dumosa	3274	23.3	23.9	456.5	0.689 (38)
Atriplex confertifolia	356	2.5	1.4	61.6	0.156 (8)
Ephedra funerea	452	3.2	7.9	228.6	—
Ephedra nevadensis	561	4.0	4.0	63.0	0.010 (10)
Eurotia lanata	863	6.2	2.6	52.5	0.080 (22)
Grayia spinosa	123	0.9	0.6	15.3	0.135 (18)
Krameria parvifolia	1178	8.4	15.5	148.6	0.188 (17)
Larrea tridentata	561	4.0	7.0	162.7	0.081 (13)
Lycium andersonii	1000	7.1	19.3	458.6	0.054 (13)
Yucca schidigera	109	0.8	5.7	927.1	—

*Index of basal area occupied by species. Ground cover estimate from nondestructive, dimensional measurements was 24.8 percent.
**Measurements were made of aboveground parts of shrubs at peak of new leaf flush, 1968.
***Number of shrubs from which mean ratio was determined.

TABLE 4. Nitrogen and mineral element composition of perennial vegetation from study site no. 5.

Plant species	Plant part*	N %	P %	Na %	K %	Ca %
Acamptopappus shockleyi	leaf	2.98	0.25	0.161	4.43	1.68
	stem		0.17	0.110	3.32	1.52
Ambrosia dumosa	leaf	4.16	0.37	0.114	5.48	2.98
	stem		0.24	0.111	4.07	1.58
Atriplex confertifolia	leaf	2.96	0.39	4.414	6.84	3.95
	stem		0.27	1.960	2.21	2.52
Ephedra funerea	shoot	2.32	0.12	0.028	1.17	2.55
Ephedra nevadensis	shoot	2.94	0.32	0.008	2.37	1.18
Ceratoides lanata	leaf	3.62	0.22	0.037	3.69	1.42
	stem		0.09	0.005	3.99	0.52
Grayia spinosa	leaf	2.23	0.09	0.175	10.13	4.25
	stem		0.08	0.009	6.06	1.23
Krameria parvifolia	leaf	2.10	0.31	0.316	2.13	1.23
	stem		0.24	0.127	2.12	0.87
Larrea tridentata	leaf	2.56	0.16	0.103	2.13	1.53
	stem		0.07	0.088	1.18	1.10
Lycium andersonii	leaf	3.26	0.12	0.013	5.58	11.64
	stem		0.10	0.010	2.12	2.65

*Samples harvested at peak of leaf flush, 1969.

due to growth habit. There was no significant increase of new shoots on *E. funerea* in 1968. It should be noted here that annual photosynthetic production in this ecosystem differs markedly from year to year, depending upon seasonal rainfall and temperature conditions (Beatley 1969b, Wallace and Romney 1972). New leaf production in 1968 was considered to be about normal for this area. Calculations based upon these biomass and leaf/plant ratios indicate that the total contribution of new leaf material available for litter deposition from shrubs was 107.4 kg/ha in 1968. The biomass of annual plants was not measured at this site, but Beatley (1969b) reported total winter annual plant biomass values for a nearby study plot of 60.58, 21.73, and 174.16 kg/ha for 1964, 1965, and 1966, respectively.

The nitrogen and mineral element composition of perennial vegetation sampled at the peak of leaf flush in 1969 is shown in Table 4. The nitrogen composition of leaf tissues varied among species but fell within the range commonly found in cultivated pasture crops (2.5 to 3.5 percent). Phosphorus contents varied within the range of 0.10 to 0.40 percent, and higher levels usually occurred in leaf than in stem tissues. Sodium concentrations were relatively low in plant tissues grown at this site; however, *A. dumosa*, *Grayia spinosa* (Hook.) Moq., *L. andersonii*, and, of course, the *Atriplex* species have the capacity to concentrate much higher levels of sodium than is present in the soil (Wallace and Romney 1972, Romney et al. 1973). Potassium is one of the most variable of the nutrient elements in these desert shrubs; its concentration in stem tissues often reaches or exceeds that found in leaf tissues. *Ambrosia dumosa*, *Ceratoides lanata* (Pursh) J. T. Howell, and *L. andersonii* consistently contain relatively high levels of potassium, and *G. spinosa* usually contains exceptionally high concentrations. High concentrations of calcium and strontium are normally found in

Table 4 continued.

Mg	Si	Zn	Cu	Fe	Mn	B	Sr	Ba
%	μg	μg	μg	μg	μg	μg	μg	μg
0.48	0.47	22	8	164	51	46	29	1
0.20	0.04	7	5	48	12	17	43	7
0.54	0.15	28	7	256	23	100	56	9
0.54	0.07	13	4	141	19	42	50	14
0.61	0.17	9	5	362	32	73	130	50
0.37	0.07	7	7	237	86	21	131	47
0.34	0.17	7	6	186	68	10	197	52
0.26	0.03	22	2	92	18	24	61	11
0.56	0.05	21	4	110	66	41	45	5
0.23	0.02	6	3	79	28	14	37	6
2.15	0.07	37	5	150	139	65	32	5
0.51	0.01	16	3	20	15	20	25	5
0.37	0.18	17	6	261	43	39	99	17
0.28	0.10	16	5	168	15	27	88	15
0.22	0.45	26	2	585	41	88	44	11
0.21	0.40	16	4	1091	33	28	54	16
1.44	0.05	41	4	162	33	65	648	18
0.24	0.04	9	3	90	5	12	77	11

leaf tissues of *L. andersonii*. Stem tissues usually contain less calcium than do leaf tissues of most shrub species. Both *G. spinosa* and *L. andersonii* leaves often contain higher contents of magnesium than do those of other species from the same location. The micronutrients and trace metals vary considerably among the various shrub species, and leaf tissues usually contain higher amounts than are concentrated in stem tissues. One striking exception to this was the consistently high iron content of leaf and stem tissues of *Larrea tridentata*, wherever sampled (Romney et al. 1973). Boron contents generally ranged from 10 to 100 ug/g.

Modifying Effects of Vegetation on the Soil Properties Near Root Zones

Inasmuch as soil properties were characterized from existing horizons of varied depths, it was necessary for statistical analysis to normalize all values to assess differences underneath shrubs and bare sites. This was done by computer synthesis to a common depth of 30 cm because most of the active root zone lies within this depth in our study areas. Comparisons were made of the statistical significance of differences between the values of properties measured underneath shrubs and bare surfaces at 62 study sites. Bare site values were subtracted from shrub site values, and the means and standard deviations for each of 22 variables were derived from these differences. For each of these variables, the mean differences were divided by the standard deviations and then multiplied by the square root of the sample number to derive a t-value. The null hypothesis that the means are not significantly different from zero was rejected if t was less than –2.000 or greater than 2.000 ($p = 0.05$). With this test means that were significantly different from each other could be identified and the conclusion reached that the presence of shrubs modified the soil properties when their mean difference was positive (Table 5).

The soil properties which tended to have higher values underneath shrubs, but which were not significantly different, included water-holding capacity, pH, and exchangeable sodium. The exchangeable calcium and magnesium, lime, and DTPA-extractable zinc and copper contents tended to be higher in bare soil, but their differences were not significant. All the other soil properties tested were significantly higher under shrub clumps including the saturation extract conductivity (EC25°), the soluble cations and anions, exchangeable potassium, the cation exchange capacity, organic carbon and nitrogen, available phosphorus, and the DTPA-extractable iron and manganese.

The cycling and redistribution of carbon, nitrogen, and mineral elements from the decomposition and mineralization of litter deposited underneath perennial vegetation can account for these differences in soil properties that, collectively, increase the fertility of the soil underneath the vegetation canopy. These shrub clumps also act as catchments for windblown litter and serve as shelters for most of the annual plant species. The shrub

TABLE 5. A measure of the difference in soil properties underneath shrub and bare areas at 62 study sites.

Soil properties	Mean difference (shrub minus bare)	t-statistic*
Moisture, –0.3 bar	0.48	1.534
pH (paste)	0.08	0.528
EC_{25} mmhos/cm	1.06	10.435
Saturation extract soluble cations and anions:		
Na, meq/l	1.64	3.067
K, meq/l	2.96	9.466
Ca, meq/l	8.75	7.921
Mg, meq/l	5.06	8.131
Cl, meq/l	3.43	5.090
NO_3, meq/l	1.98	2.669
SO_4, meq/l	0.64	4.046
Exchangeable cations (NH_4OAc-extractable):		
Na, meq/100 g.	0.09	1.127
K, meq/100 g.	1.44	8.327
Ca + Mg, meq/100 g.	–0.21	–0.682
C.E.C, meq/100 g.	1.21	3.813
Lime, % < 2 mm	–0.18	–0.482
Organic C, %	0.46	11.078
Organic N, %	0.041	12.601
P($NaHCO_3$-ext.),ug/g	1.17	8.244
DTPA-extractable micronutrients:		
Fe, ug/g	0.07	4.664
Zn, ug/g	–0.07	–1.094
Cu, ug/g	–0.01	–1.492
Mn, ug/g	1.42	10.477

*t = (mean difference/standard deviation) × $\sqrt{N}$, N = 62; difference is significant ($p = 0.05$) where $t < -2.000$ or $t > 2.000$.

clumps that exist in our study areas are very old (Wallace and Romney 1972), so these cycling and redistribution processes probably have been underway for many centuries at any given site. Some effects of specific shrub species on the redistribution of mineral nutrients in zones near roots are illustrated in the data of Table 6.

An estimate of the annual reservoir of nitrogen and mineral elements in new leaf material available for litter deposition from study site No. 5 is given in Table 7. If all the litter remained on site, this reservoir could contribute nitrogen, 3.64 kg/ha; phosphorus, 0.312 kg/ha; sodium 0.577 kg/ha; potassium 5.20 kg/ha; calcium 4.95 kg/ha; and iron and manganese 31.82 and 4.30 g/ha, respectively. These values were calculated from new leaf production in 1968 (Table 3) and from chemical analysis in 1969 (Table 4). They probably represent about one-third of the total nitrogen and mineral nutrients involved in the annual turnover for the area during a normal year. The remaining contribution of nutrients for cycling would be supplied by litter-fall from the standing dead wood and from the litter of annual plant species. These estimates are based upon a normal production year for this ecosystem. However, two growth seasons have occurred during the past decade (1969 and 1973) in which the new photosynthetic production of many perennial species was from three to five times greater than in the other years (unpubl. data). Conversely, years have also occurred in which new production was less than one-half that of 1968. Beatley

TABLE 6. Soil properties underneath shrub and bare areas at different locations illustrating some effects of specific shrub species on redistribution of mineral nutrients in zones near roots.

	A. canescens		*A. confertifolia*		*G. spinosa*		*L. tridentata*		*L. andersonii*	
Soil properties*	Shrub	Bare	Shrub	Bare	Shrub	Bare	Shrub	Bare	Shrub	Bare
Moisture, -0.3 bar	13.1	12.1	13.4	14.9	8.8	10.4	18.9	17.1	19.4	15.9
pH (paste)	8.5	8.6	8.6	8.9	8.4	8.7	8.4	8.6	8.4	8.6
EC_{25}° mmhos/cm	3.19	0.34	2.98	0.68	1.36	0.38	2.57	0.64	3.20	0.46
Saturation extract soluble cations and anions:										
Na, meq/l	7.20	0.55	27.95	4.23	1.03	0.41	2.93	0.23	3.82	0.63
K, meq/l	15.17	1.05	3.98	1.59	13.57	0.72	4.23	1.50	6.58	0.71
Ca, meq/l	32.31	2.42	6.79	1.34	9.68	3.63	30.18	6.09	28.75	3.55
Mg, meq/l	25.54	1.05	4.80	1.22	9.94	1.86	10.99	2.31	12.80	0.43
Cl, meq/l	10.87	0.27	12.66	0.82	4.68	2.42	4.29	0.16	10.12	0.53
NO_3, meq/l	13.75	0.33	0.68	0.02	—	—	36.29	0.05	—	—
SO_4, meq/l	1.52	0.07	0.59	0.13	0.12	0.02	1.19	0.09	0.95	0.02
Exchangeable cations (NH_4OAc-extractable):										
Na, meq/100 g	0.72	0.48	3.84	1.91	0.41	0.53	0.41	0.30	0.39	0.31
K, meq/100 g	10.83	6.43	7.75	9.22	5.16	2.64	2.63	2.30	3.59	1.69
Ca + Mg meq/ 100 g	6.99	9.20	5.69	8.11	7.44	7.45	12.55	4.66	10.44	7.32
C.E.C., meq/ 100 g	18.6	16.1	17.3	19.3	13.0	10.6	15.6	13.5	14.5	9.3
Lime, % < 2 mm	5.0	3.0	7.8	7.3	1.0	1.6	13.9	15.1	17.3	25.9
Organic C, %	0.63	0.11	0.40	0.21	0.97	0.12	1.54	0.55	1.18	0.34
Organic N, × 10^{-1}%	0.84	0.12	0.37	0.22	0.90	0.14	1.31	0.63	1.19	0.31
P ($NaHCO_3$-ext.), ug/g	2.3	0.1	1.2	0.4	5.8	1.2	1.6	0.8	1.1	0.2
DTPA-extractable micronutrients:										
Fe, ug/g	0.3	0.2	0.1	0.1	0.6	0.4	0.5	0.4	0.5	0.4
Zn, ug/g	0.57	0.36	0.70	0.38	0.45	0.40	0.70	0.93	0.84	2.21
Cu, ug/g	0.28	0.27	0.17	0.26	0.15	0.10	0.26	0.25	0.13	0.15
Mn, ug/g	1.87	0.49	2.99	2.19	3.83	1.44	3.07	2.68	2.29	1.672

*Values per cm normalized to 30 cm depth under shrub clump and bare areas.

TABLE 7. Annual reservoir of nitrogen and mineral elements in new leaves of perennial vegetation available for litter deposition and mineralization at study site no. 5.

Plant species	N	P	Na	K	Ca	Mg
			kg/ha*			
Acamptopappus shockleyi	0.11	0.009	0.006	0.19	0.06	0.02
Ambrosia dumosa	1.29	0.115	0.035	1.70	0.93	0.17
Atriplex confertifolia	0.28	0.037	0.424	0.66	0.38	0.06
Ephedra nevadensis	0.02	0.002	0.001	0.02	0.01	0.01
Ceratoides lanata	0.15	0.009	0.002	0.16	0.06	0.02
Grayia spinosa	0.05	0.002	0.004	0.21	0.09	0.04
Krameria parvifolia	0.59	0.087	0.088	0.60	0.34	0.10
Larrea tridentata	0.34	0.021	0.014	0.28	0.20	0.03
Lycium andersonii	0.81	0.030	0.003	1.38	2.88	0.36
Total	3.64	0.312	0.577	5.20	4.95	0.81

*Calculations based on biomass estimates for 1968 and chemical analyses for 1969; sum of total elements is 15.76 kg/ha.

(1969b) reported enormous yearly variations in winter annual production in this ecosystem. The nitrogen values in these estimates fall within the range of values for shrubs of a low-fertility desert area reported by Garcia-Moya and McKell (1970) and for a saltbrush community reported by Charley and Cowling (1968). These mineral element estimates are in the same range of some values for desert zones reported by Rodin and Bazilevich (1965).

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Table 7 continued.

Si	Zn	Cu	Fe	Mn	B	Sr	Ba
			g/ha*				
0.017	0.08	0.03	0.58	0.18	0.16	0.10	0.01
0.047	0.87	0.22	7.94	0.71	3.10	1.73	0.27
0.016	0.09	0.05	3.47	0.30	0.70	1.24	0.48
0.001	0.01	0.01	0.06	0.01	0.01	0.03	0.01
0.002	0.09	0.02	0.46	0.27	0.17	0.18	0.02
0.001	0.08	0.01	0.31	0.28	0.13	0.06	0.01
0.050	0.47	0.17	7.29	1.20	1.09	2.76	0.47
0.059	0.34	0.03	7.70	0.54	1.16	0.58	0.14
0.012	1.02	0.10	4.01	0.81	1.61	16.04	0.44
0.205	3.05	0.64	31.82	4.30	8.13	22.72	1.85

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ECOTONAL DISTRIBUTION OF SALT-TOLERANT SHRUBS IN THE NORTHERN MOJAVE DESERT

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Abstract.— Ecotonal distribution of salt-tolerant shrubs was investigated under different kinds of edaphic conditions common to open and closed drainage basins in the northern Mojave Desert. Contributing causal factors involved changes in soil salinity, texture, and moisture stress. Varying degrees of halophytism occurred, ranging from plant species that are facultative in their adaptation to salinity to those that require comparatively high salt concentrations in soil for normal growth and development.

The main thrust of recent research on salt sensitivity has centered around osmotic and toxic effects of salts and the interaction between the various salts and ions adversely affecting plants (Strogonov 1962, Boyko 1966, Ranwell 1972, Waisel 1972, Reimold and Queen 1974, Poljakoff-Mayber and Gale 1975). Biological adaptation of the halophytes to salinity has occurred in different ways. Some halophytes absorb comparatively small amounts of salts as the result of unique biological properties. Others accumulate considerable amounts of salts in different plant parts that aid in the regulation of internal osmotic pressure. Some halophytes are capable of regulating their salt balance by mechanisms such as excretion of excess salts through special glands or abscission of leaves containing high levels of salt. Due to special biological features, halophytes can overcome the high osmotic pressure of the soil solution by decreasing their own osmotic potential. In such cases, rates of photosynthesis and transpiration are little influenced by high salt levels (Kleinkopf and Wallace 1974, Gale 1975). In certain plants this osmotic potential develops mainly from an accumulation of organic substances (Wallace and Kleinkopf 1974). In others it develops due to mineral salts absorbed from the saline soil substrate.

Environmental studies conducted in conjunction with nuclear weapons testing programs at the Nevada Test Site provided an opportunity to investigate some ecological characteristics of salt-tolerant shrubs in both open and closed drainage basins in the northern Mojave Desert (Wallace and Romney 1972, Romney et al. 1973, Wallace et al. 1973a, 1973b, 1974, Kleinkopf et al. 1975). The bajadas draining into playas of open and closed basins in southern Nevada often have prominent ecotonal demarcation lines below which certain plant species do not grow. Various hypotheses have been presented to explain ecotonal transition zones, including the influence of such factors as low temperature (Beatley 1974), salinity (Shreve 1940, Shantz and Piemeisel 1940), fine-textured soil (Gardner 1951, Branson et al. 1967), and excess of water (Fosberg 1940, Shreve and Wiggins 1964). These environmental factors were monitored as part of our environmental studies program and are evaluated in conjunction with the findings reported herein.

Methods

Readers are referred to earlier reports by Wallace and Romney (1972) and Romney et al. (1973) and those of Beatley (1969, 1974, 1976) for greater details concerning the description of study areas and the results obtained from extensive investigations of soil and vegetation in the northern Mojave Desert areas of the Nevada Test Site. We shall present data in this report from three of

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several different ecotonal transition zones involved in this study.

The first ecotonal study site is located in an open drainage basin (Rock Valley) on the east slope of the Amargosa River watershed. The area sampled is approximately 0.5 km^2 in extent with a downslope length of 500 m. The elevation is about 1050 m, and the slope is to the northwest with a gradient varying from 1 to 3 percent. The dominant and codominant shrub species in this particular ecotonal transition area were separated into three generally homogeneous vegetation zones that were oriented in parallel bands of about the same width, perpendicular to the slope. From 25 to 30 quadrats, 2 × 25 m, were sampled in each zone at coordinate locations generated by a computer program to insure random dispersion. All shrubs were identified by nondestructive dimensional measurements (Romney et al. 1973) from which calculations were made to estimate the spatial distribution. Taxonomy of the area was worked out by Beatley (1969, 1976).

The second ecotonal transect is located across a sharp *Larrea-Atriplex* demarcation line above the playa on the north side of the Frenchman Flat closed drainage basin. Elevation is about 950 m and the slope is to the south at about 2 percent. A 15 × 500 m transect across the ecotonal zone was divided into 50 m sections within which all shrubs were measured.

The third ecotonal transition area studied involved a transect extending down the west-facing bajada onto the Frenchman Lake playa. Five sampling stations were established along the transect, about 1 km apart, at which shrub measurements were made in 2 × 50 m quadrats. Elevation changed from 1040 to 940 m, with the slope varying from 1 to 3 percent at the three sampling sites on the bajada.

Soil sampling pits along each of these transects were dug either by hand or by back-hoe to permit an examination and sampling of the soil profile underneath both shrub and bare areas. The depth of each pit was to the caliche hardpan or, if no restricting layer existed, to a depth well into the C horizon. Profile horizons were described and samples were collected for physical and chemical analysis by the methods of the USDA Salinity Laboratory (1954).

Vegetation samples were collected from each of the sampling sites for subsequent chemical analysis by methods previously described (Romney et al. 1973).

RESULTS AND DISCUSSION

Distribution of shrubs within the three vegetation zones investigated in the Rock Valley open drainage basin is listed in Table 1. The zones are numbered 1, 2, and 3, representing upper, intermediate, and lower positions downslope along the transect, respectively.

Edaphic conditions within this ecotonal transition area are typical of the open-drained bajadas we have investigated in southern Nevada. The soil is derived from heterogeneous, highly calcareous alluvium, composed primarily of Cambrian limestones with some tuff and basalt. The surface is a well-developed desert pavement with a massive and strongly cemented caliche layer at depths ranging from 30 to 70 cm. The soil profile horizons are young and often poorly developed. Salt concentrations in the upper profile are relatively low and consist mainly of calcium and magnesium salts. Sodium salts

TABLE 1. Distribution of shrubs in ecotonal zone segments in an open-drainage area of Rock Valley. (Direction of slope →)

Species	Number of plants per hectare		
	Zone 1	Zone 2	Zone 3
Acamptopappus shockleyi Gray	46	0	28
Ambrosia dumosa (Gray) Payne	1844	2474	2504
Atriplex confertifolia (Torr. & Frem.) Wats.	0	0	276
Ephedra nevadensis Wats.	849	845	275
Ceratoides lanata (Pursh) J. T. Howell	155	951	443
Grayia spinosa (Hook) Moq.	203	702	2202
Krameria parvifolia Benth.	1957	951	773
Larrea tridentata (Sesse & Moc. ex DC.) Cov.	1122	907	1004
Lycium andersonii A. Gray	1136	452	83
Lycium pallidum Miers	88	706	815
Total	7400	7988	8403

tend to accumulate at lower depths in the soil profile, especially in local areas where terrain features have restricted drainage. In the case of this particular study area, the main difference in edaphic features was an increase in the silt content of the soil profile, accompanied by an accumulation of sodium salts at depths below 30 cm, proceeding downslope along the transect.

Each of the shrub species present in this transition zone exhibit some degree of facultative adaptation for salt tolerance, but none is known to have obligate requirements (Wallace and Romney 1972, Wallace et al. 1973a, 1973b, 1974). Those species which increase in density in zones progressing downslope are the ones that commonly are more salt tolerant in nature. Notably so are *Ambrosia dumosa* (A. Gray) Payne, *Atriplex confertifolia* (Torr. & Frem.) Wats., *Grayia spinosa* (Hook) Moq., and *Lycium pallidum* Miers. There also was an interaction with soil texture in this area. *Ambrosia dumosa*, *Ceratoides lanata* (Pursh) J. T. Howell, and *L. pallidum* are better adapted to finer textured soils than *Larrea tridentata* (Sesse & Moc. ex DC.) Cov. or *Lycium andersonii* A. Gray, and these species responded accordingly at this study site.

The second transect is across a sharp ecotonal demarcation line between *L. tridentata* and *Atriplex canescens* (Pursh.) Nutt. communities situated between the bajada and playa of the Frenchman Flat closed drainage basin. Plant distribution along the transect is shown in Table 2. The analyses disclosed an ecotonal demarcation zone among several other species at this study site that is not so apparent from visual observations. The transition across the ecotone was equally sharp among several plant species. The distribution patterns for *A. dumosa*, *C. lanata* and *L. tridentata* were much more alike than under the situation given in Table 1. Different edaphic factors, therefore, could be involved. Since *C. lanata* distribution paralleled *L. tridentata*, one might conclude that soil salinity is not a simple causal factor at this particular ecotone, inasmuch as *C. lanata* can grow in moderately saline soil (Vest 1962) but *L. tridentata* does not. An alternative explanation could be that ecotypes are differentially sensitive to salt. We hasten to point out, therefore, that the distribution of *C. lanata* extended well beyond the *Larrea* demarcation line onto the playa at some of the other transects investigated elsewhere around the ecotone.

It should be taken into account that sensitivity of seeds and young seedlings to soil salinity and to pH could be limiting causal factors at this ecotone, either at the present time or earlier when the population initially became established. The soil profiles along this transect showed surface pH values ranging from 8.0 to 9.0. The soluble salts at the surface were moderate (EC_{25} varied from 2.07 to 3.06 mmhos/cm). Salt accumulations, including soluble boron and nitrate, generally increased at greater depths in the soil profile within the playa. In some earlier work, Barbour (1968) observed that *L. tridentata* seed germination was not affected by high soil pH but that subsequent seedling development was markedly decreased, especially above pH 8.0. The lack of any young seedlings in the ecotonal area suggests that seedling survival is a rare event that may be partially regulated by the high soil pH levels now present. Size stratification occurs within the shrub population, however, which indicates that favorable moisture conditions for seedling sur-

TABLE 2. Distribution of plant species along a 500 m transect across the *Larrea-Atriplex* ecotone line in north Frenchman Flat. (Direction of slope →)

Species	Number of plants in 15 × 50 m segments									
Ambrosia dumosa (Gray) Payne	263	168	96	16	47	29	23	14	0	0
Atriplex canescens (Pursh.) Nutt.	54	47	74	100	149	246	183	192	240	202
Ceratoides lanata (Pursh) J. T. Howell	99	84	52	10	25	6	4	2	1	1
Larrea tridentata (Sesse & Moc. ex DC.) Cov.	55	75	40	54	28	3	0	1	0	0
Lycium andersonii A. Gray	2	5	3	1	0	0	1	0	0	0
Salsola iberica Sennen & Pau	1	0	0	0	18	54	42	56	44	56
Sphaeralcea ambigua Gray	37	61	50	106	49	121	126	129	256	203

vival have occurred periodically, presumably many decades apart.

Another factor thought to be involved in regulating shrub distribution at this ecotone is periodic flooding of the basin floor beyond the boundaries of the dry lake bed. Shrubs that are sensitive to poor root aeration or standing water on foliage can be damaged when inundated with flood water. A case in point was observed recently near Baker, California (Wallace and Romney 1972). *Larrea tridentata* is known to require good aeration of the root zone and well-drained soils (Shreve and Wiggins 1964). Complete inundation need not be effected to keep *L. tridentata* from populating a site; a higher than normal water table could be just as detrimental to some sensitive species.

Monitoring of soil and air temperatures from May 1967 to January 1973 gave very little indication that a temperature differential across this ecotone was an important causal factor compared to the edaphic features.

The mineral element composition of shrubs did not differ significantly across the ecotonal transition zone. Data in Table 3 for shrubs sampled near the middle of the transect are representative of those sampled elsewhere along the ecotone. The uniformity of mineral composition (i.e., cation and anion balance) in these salt-tolerant shrubs, irrespective of location and edaphic conditions (Romney et al. 1973), attests to their adaptive capacity to regulate their own salt balance.

The distribution of shrub species along the 5 km ecotonal transect across the bajada and playa in east Frenchman Flat is shown in Table 4. Species diversity became less complex progressing downslope onto the bajada. These data are a good example of how the more sensitive species give way to the more salt-tolerant ones under changing edaphic conditions. It would not be prudent in this instance, however, to assume that increasing salinity was the only causal factor of community or species distribution. Factors of moisture stress and soil texture also must be taken

TABLE 3. Mineral composition of leaves of shrubs from the north Frenchman Flat ecotonal zone.

Species	N	Cl	S	P	Na	K	Ca	Mg	B
	Percent of dry weight								ug/g
A. dumosa	3.68	0.85	0.71	0.44	0.08	5.63	2.28	0.53	130
A. canescens	2.44	1.65	1.80	0.15	1.05	8.02	3.80	1.14	60
C. lanata	2.79	0.41	0.34	0.19	0.10	3.38	1.67	0.43	49
L. tridentata	2.37	0.68	0.12	0.29	0.03	2.53	1.64	0.19	76
L. andersonii	2.32	1.00	0.85	0.24	0.03	6.30	9.92	0.91	75
S. ambigua	2.12	0.31	0.26	0.72	0.13	3.35	2.98	0.53	160

TABLE 4. Shrub distribution across a 5 km ecotonal transect in east Frenchman Flat. (Increasing salt gradient →)

Species	Percent frequency at sampling sites*				
	1	2	3	4	5
Acamptopappus shockleyi Gray	2.1	9.2	–	–	–
Ambrosia dumosa (Gray) Payne	2.4	59.2	13.5	–	–
Atriplex canescens (Pursh) Nutt.	–	–	5.0	90.2	–
Atriplex confertifolia (Torr. & Frem.) Wats.	6.4	–	43.2	9.8	100
Psorothamnus fremontii (Torr.) Barneby	19.1	–	–	–	–
Ephedra nevadensis Wats.	4.3	–	–	–	–
Ceratoides lanata (Pursh) J.T. Howell	6.5	6.6	5.4	–	–
Hymenoclea salsola T & G.	4.3	–	5.4	–	–
Krameria parvifolia Benth.	8.5	1.3	–	–	–
Larrea tridentata Ses	40.4	13.2	24.3	–	–
Sphaeralcea ambigua Gray	2.1	–	2.7	–	–
Thamnosma montana Torr. & Frem.	2.1	–	–	–	–
Yucca brevifolia Engelm. in Wats.	2.1	6.6	–	–	–

*Shrubs contributing less than 1 percent are unlisted.

into account because marked changes occurred, progressing downslope onto the playa.

Some soil properties at the different sampling sites across the East Frenchman Flat transect are listed in Table 5. Increased soil salinity occurred, especially at the two sites along the playa where only the two *Atriplex* species grew in abundance. Calcium dominated the soluble cation pattern in the upland area of the transect, and sodium became more dominant on the playa, as one might expect in a closed drainage basin. Chloride and nitrate concentrations increased in the soil profile of the dry lake playa.

The east Frenchman Flat transect is a good example relating salinity to community or species distribution. On the other hand, this relationship was not so clear-cut at several other transects across the ecotonal zone, surrounding the Frenchman Dry Lake playa (Romney et al. 1973), where better correlation occurred with the edaphic features of soil moisture stress and texture. This has been the experience of other investigators where attempts to relate salinity alone to community or species distribution gave inconsistent results (Gates et al. 1956, Branson et al. 1967). Branson et al. (1970) speculate that upland halophytes dominate certain areas because of tolerance to high osmotic stress or high physical moisture stress, or a combination of both. We find indications of this occurring at our study areas in southern Nevada. We also see much evidence, as expressed by Unger (1966), "that the most salt-tolerant species have the widest salinity tolerance and can survive under low as well as high salinities. The less tolerant species are limited in their distribution to low and nonsaline areas."

A summary of the bibliography of the vegetation and soils of Nevada was compiled by Tueller et al. (1971).

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TABLE 5. Soil properties (30 cm depth) across the 5 km transect in east Frenchman Flat. (Direction of slope →)

Soil properties	Site 1	Site 2	Site 3	Site 4	Site 5
pH, sat. extract	8.7	8.7	8.8	8.8	8.9
EC_{25}, mmhos/cm	2.15	1.89	1.00	2.40	2.98
Saturation extract ions					
Na (meq./liter)	3.57	1.37	2.47	15.45	27.95
K (meq./liter)	6.13	4.48	2.48	5.25	3.98
Ca (meq./liter)	22.69	17.39	6.93	11.78	6.79
Mg (meq./liter)	8.97	5.85	3.65	12.43	4.80
Cl (meq./liter)	1.26	1.40	2.28	6.37	12.66
NO_3 (meq./liter)	6.62	6.16	5.00	17.50	23.10
SO_4 (meq./liter)	0.52	0.41	0.40	0.54	0.59
Exch. Na, percent	2.0	2.2	2.9	6.2	22.1

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PARENT MATERIAL WHICH PRODUCES SALINE OUTCROPS AS A FACTOR IN DIFFERENTIAL DISTRIBUTION OF PERENNIAL PLANTS IN THE NORTHERN MOJAVE DESERT

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ABSTRACT.— An area of 0.46 km² divided into six zones in the northern Mojave Desert transitional with the Great Basin Desert has been studied. Diversity is high among the perennial plant species within the 0.46 km² area. Common species for the two deserts that are present in the area studied are *Atriplex confertifolia* (Torr. & Frem.) S. Wats., *Ceratoides lanata* (Pursh) J. T. Howell, *Grayia spinosa* (Hook.) Moq., *Ephedra nevadensis* S. Wats. Some other species present include *Lycium andersonii* A. Gray, *Lycium pallidum* Miers, *Ambrosia dumosa* (A. Gray) Payne., *Larrea tridentata* (Sesse & Moc. ex DC) Cov., *Acamptopappus shockleyi* A. Gray, and *Krameria parvifolia*, Benth. Some of the species are relatively salt tolerant and some are relatively salt sensitive. A total of 4282 individual plants were measured. There was considerable variation in distribution of the 10 dominant species present, apparently due to zonal variations of salinity dispersed within the study area. Correlation coefficients among pairs of the species for different zones illustrate interrelationships among the salt-tolerant and salt-sensitive species. Observations on an adjacent hillside with rock outcroppings indicate that the saline differences in this area are partly due to outcroppings of parent volcanic rock materials that yield Na salts upon weathering.

A vegetational map of a 0.46 km² area in Rock Valley of the northern Mojave Desert was presented elsewhere (El-Ghonemy et al. 1980, this volume). This is the Rock Valley Desert Biome validation site used in the International Biological Program (Turner 1973, 1975, 1976, Turner and McBrayer, 1974). The purpose of this report is to further explore the differences in plant species distribution on that site as influenced by zonal variations in salinity. The information involved also has relationships with the ecotonal lines studied elsewhere at the Nevada Test Site (Romney and Wallace 1980, this volume).

MATERIALS AND METHODS

Data collected for the IBP validation site (Turner 1973, 1975, 1976, Turner and McBrayer 1974) and used in the development of a vegetational map and other findings (El-Ghonemy et al. 1980a and 1980b, this volume) were also used in this report. Sampling and data calculation procedures were described in those reports.

An additional 4 × 100m belt transect was established on a hillside further upslope from the main study plot. It was selected because of rock outcroppings that gave vegetational patterns somewhat similar to the differences observed within the large study plot. All plants were identified, counted, and measured by dimension analysis (Wallace and Romney 1972), and leaf tissue samples were taken for chemical analysis. Soil samples were taken at 10 m intervals along the transect. They were subjected to determination of EC and pH. For convenience of presenting results, the transect was divided into four plots each 25 m long. The rock outcrop was near the top of the transect.

Mineral element contents of plants were determined by emission spectrography; nitrogen was determined by Kjeldahl analysis; Cl was determined by titration.

RESULTS AND DISCUSSION

The number of plants per hectare in various zones of the 0.46 km² plot are shown in Table 1. The zone numbers were designated in earlier IBP reports (Turner 1973, 1976, Turner and McBrayer 1974). Results serve to illustrate the differential distribution encoun-

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tered because of the soil differences. Zones 24 and 25 were the only ones having *Atriplex confertifolia* (Torr. & Frem.) S. Wats. This species is highly tolerant of salt (Wallace et al. 1973a). *Grayia spinosa* (Hook.) Moq. was present in Zones 20 and 21 in small numbers only, but was very prominent in Zones 23, 24, and 25. *Lycium andersonii* A. Gray was present in exactly the opposite manner, whereas, *Lycium pallidum* was distributed as was *G. spinosa*. *Lycium pallidum* Miers is much more tolerant of salt than is *L. andersonii* (Ashcroft and Wallace 1976, Wallace et al. 1973b, Beatley 1976).

Correlation coefficients were calculated for the species pairs for the data in Table 1 to further show relationships between the species according to differences in the soil involved (Table 2). *Atriplex confertifolia* was not included in these correlations because of its absence in four of the zones. Of salt-tolerant plants, *Lycium pallidum* and *G. spinosa* were positively correlated. Of salt-nontolerant species, *L. tridentata*, *Krameria par-*

TABLE 1. Number of plants per hectare in the 0.46 km^2 study plot.

	Zone					
Species	20	21	22	23	24	25
Acamptopappus shockleyi A. Gray	46	—	28	45	28	101
Atriplex confertifolia (Torr. & Frem.) S. Wats	—	—		—	276	192
Ephedra nevadensis S. Wats	849	845	1177	1438	275	785
Ceratoides lanata (Pursh) J. T. Howell	155	951	122	2179	443	773
Ambrosia dumosa (A. Gray) Payne	1844	2474	2998	3877	2504	3402
Grayia spinosa (Hook.) Moq.	203	702	252	1830	2202	3388
Krameria parvifolia Benth.	1957	951	2103	1394	773	1166
Larrea tridentata (Sesse & Moc ex DC.) Cov.	1122	907	1205	1046	1004	1043
Lycium andersonii A. Gray	1136	452	981	713	83	314
Lycium pallidum Miers	88	706	224	697	815	1020
Total	7400	7988	9090	13219	8403	12184

TABLE 2. Correlation coefficients between number of plants/ha for the various species among zones in Rock Valley (± 0.700 needed for P = 0.05).

	Ephedra nevadensis	*Ceratoides lanata*	*Ambrosia dumosa*	*Grayia spinosa*	*Krameria parvifolia*	*Larrea tridentata*	*Lycium andersonii*	*Lycium pallidum*
Ephedra nevadensis S. Wats.	—	+0.534	+0.570	-0.287	+0.571	+0.373	+0.633	-0.303
Ceratoides lanata (Pursh) J.T. Howell	+0.534	—	+0.724	+0.352	-0.332	-0.415	-0.179	-0.470
Ambrosia dumosa (A. Gray) Payne	+0.570	+0.724	—	-0.555	-0.105	+0.033	-0.197	+0.517
Grayia spinosa (Hook.) Moq.	-0.287	+0.352	-0.555	—	-0.623	-0.338	-0.748	+0.888
Krameria parvifolia Benth	+0.571	-0.332	-0.105	-0.623	—	+0.890	+0.941	-0.858
Larrea tridentata (Sesse Moc. ex DC.) Cov.	+0.373	-0.415	+0.033	-0.338	+0.890	—	+0.700	-0.674
Lycium andersonii A. Gray	+0.633	-0.179	-0.197	-0.748	+0.941	+0.700	—	-0.900
Lycium pallidum Miers	-0.303	+0.470	+0.517	+0.888	-0.858	-0.674	-0.900	—

vifolia Benth., and *L. andersonii* were positively correlated. The individuals of the two groups were highly negatively correlated with one other.

Mineral analyses of leaves of plants from the various zones (Table 3) indicate little difference that can explain the results. The Cl concentration in leaves may be slightly higher from Zones 24 and 25.

The frequency of plant species in the four sections of the hillside transect (Table 4) showed characteristics similar to the large plot. Visual study of the transect area indicated that the salt-tolerant shrubs were more prevalent on sites containing outcrops of parent material. The average pH of the soil (0–15 cm) at the four intervals along the transect from bottom to top was 8.78, 8.90, 8.85, and 9.09. There were few differences except that the soil around the parent rock outcrop was slightly more alkaline. The EC (mmho/cm) values of the four soil samples beginning at the bottom were 2.43, 2.53, 2.07, and 2.75. None were really excessively

TABLE 3. Mineral element composition of leaf samples from the various zones. Samples taken in May 1973.

Zone	N	Cl	P	K	Ca	Mg	Na	B
			Percent of dry weight				ug/g	
			Grayia spinosa (Hook.) Moq.					
20	3.48	0.90	0.24	3.01	1.82	–	1,635	52
20E	3.65	1.10	0.24	2.67	2.20	1.41	1,261	48
21	1.56	0.57	0.14	3.45	2.20	1.07	99	58
23	2.38	0.42	0.24	3.50	2.69	1.35	352	58
24	1.73	1.19	0.14	2.92	2.63	1.37	341	69
25	2.27	1.04	0.17	2.99	2.38	1.18	719	66
			Lycium andersonii A. Gray					
20	3.17	3.29	0.16	2.03	4.90	0.76	2,133	28
20E	3.33	4.18	0.17	1.65	5.06	0.88	2,739	35
21	3.21	4.93	0.15	2.09	5.71	0.88	3,000	30
22	3.15	4.57	0.19	1.83	4.90	0.87	2,453	33
23	3.14	4.14	0.22	2.14	5.96	0.97	3,268	37
24	2.86	4.95	0.14	2.34	6.73	0.89	3,276	35
25	3.24	6.46	0.18	1.54	5.21	0.68	2,228	31
			Lycium pallidum Miers					
20	4.19	1.98	0.29	2.15	3.74	1.08	12,600	56
21	4.08	3.47	0.20	1.68	3.96	1.18	10,600	20
22	2.85	2.61	0.18	1.49	3.35	1.15	2,100	34
23	3.26	2.59	0.16	2.11	3.84	1.26	2,700	40
24	3.18	3.83	0.17	1.28	4.81	1.34	2,200	47
25	3.26	4.02	0.15	3.04	5.54	1.22	3,000	20
			Larrea tridentata (Sesse & Moc. ex DC.) Cov.					
20	2.18	0.30	0.18	1.53	1.20	0.13	279	56
20E	2.18	0.24	0.21	1.90	0.90	0.21	328	48
21	2.37	0.16	0.26	2.06	1.34	0.18	343	72
22	1.97	0.12	0.27	1.72	1.67	0.26	377	56
23	1.95	0.17	0.34	1.68	1.45	0.23	811	67
24	2.12	0.30	0.24	2.40	1.08	0.18	473	74
25	2.04	0.33	0.21	1.74	1.31	0.20	867	77
			Atriplex confertifolia (Torr. & Frem.) S. Wats					
21	3.73	4.58	0.33	2.65	1.79	0.61	3.04	35
24	3.98	5.29	0.28	2.07	2.52	0.56	2.58	36
			Coleogyne ramosissima Torr.					
20	1.79	0.07	0.22	1.47	3.83	0.49	180	25
20E	2.06	0.01						
21	2.34	0.02	0.25	2.03	1.53	0.27	210	33
25	2.10	0.01	0.27	1.17	2.92	0.41	76	21

Table 3 continued.

Zone	N	Cl	P	K	Ca	Mg	Na	B
			Percent of dry weight				ug/g	
			Ceratoides lanata (Pursh) J.T. Howell					
21	3.55	0.16	0.29	2.66	0.93	0.34	194	20
23	3.73	0.37	0.32	2.45	1.55	0.54	103	35
24	3.40	0.24	0.29	2.61	1.53	0.39	90	27
25	3.07	0.32	0.29	2.58	1.19	0.33	74	26
			Ephedra nevadensis S. Wats.					
20	3.90	0.39	0.40	3.31	0.75	0.22	66	32
20E	4.05	0.34	0.90	5.43	2.39	0.66	228	57
21	4.00	0.40	0.41	3.05	0.73	0.19	68	33
24	3.52	0.35	0.36	3.20	0.57	0.18	135	26
25	4.24	0.51	0.37	3.55	0.70	0.18	96	27
			Ambrosia dumosa (A. Gray) Payne					
20	4.56	0.88	0.31	2.70	3.05	0.43	241	43
20E	4.18	0.72	0.37	2.94	1.47	0.42	237	88
22	4.57	1.03	0.39	2.83	1.93	0.52	483	59
24	4.28	1.23	0.32	2.70	3.11	0.48	261	89
25	4.25	1.33	0.32	3.94	2.75	0.46	563	82

saline within the first 15 cm of the soil profile. Nevertheless, the outcrops of exposed rock were high in sodium salts. The salt resulting from the weathering processes in the rock probably leaches away rapidly because of the slope.

Table 5 shows some other vegetational characteristics of this hillside transect. More detailed studies of these sites should elucidate some of the subtle ways that soil properties can determine the nature of vegetation in this desert.

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TABLE 4. Frequency of plant species in the four sections of the hillside transect (top is the rock outcrop with saline characteristics).

Species	Transect on saline outcrop			
	Base ¼	¼	¼	Top ¼
		Percent frequency		
Atriplex confertifolia (Torr. & Frem.) S. Wats	0.0	0.0	1.7	16.3
Psorothamnus fremontii (Torr.) Barneby	0.0	0.0	8.5	4.1
Ceratoides lanata (Pursh) J.T. Howell	9.7	9.7	20.3	6.1
Grayia spinosa (Hook.) Moq.	0.0	0.0	5.1	0.0
Lycium pallidum Miers	29.0	19.4	3.4	20.4
Larrea tridentata (Sesse Moc. ex DC.) Cov.	12.9	6.5	1.7	0.0
Lycium andersonii A. Gray	9.7	9.7	11.9	6.1
Ambrosia dumosa (A. Gray) Payne	3.2	9.7	13.6	18.4
Krameria parvifolia Benth	29.0	25.8	5.1	8.2
Machaeranthera tortifolia (A. Gray) Cronq. & Keck	0.0	6.5	3.4	12.2
Ephedra nevadensis S. Wats.	3.2	9.7	15.3	4.1
Lepidium fremontii S. Wats.	0.0	0.0	6.8	0.0
Sphaeralcea ambigua A. Gray	3.2	0.0	3.4	0.0
Oryzopsis hymenoides (Roem. & Schult.) Ricker	0.0	3.2	0.0	0.0
Encelia virginensis A. Nels.	0.0	0.0	0.0	4.1

TABLE 5. Vegetation characteristics of the hillside transect (divided into one-quarter segments for comparisons).

Species	Cover percent	Plant Rel.Dom. percent	Plant area m^2/ha	Plant volume m^3/ha	Plant biomass kg/ha
		Basal ¼ segment			
Ephedra nevadensis		1.4	22.1	9.3	13.4
Ceratoides lanata		1.7	26.7	15.6	47.1
Ambrosia dumosa		8.4	130.6	74.5	165.7
Krameria parvifolia		16.2	253.1	58.8	127.2
Larrea tridentata		19.1	297.6	192.5	304.6
Lycium andersonii		17.7	176.5	168.5	309.1
Lycium pallidum		35.2	548.7	336.1	274.4
Sphaeralcea ambigua		0.1	3.1	0.9	0.4
	15.58		Total	856.2	1242.0
		Lower ¼ segment			
Ephedra nevadensis		1.0	13.4	4.3	6.3
Ceratoides lanata		2.4	30.8	12.5	37.7
Ambrosia dumosa		4.6	60.2	19.4	43.2
Krameria parvifolia		21.1	275.8	62.7	135.5
Larrea tridentata		18.4	241.7	228.8	250.3
Lycium andersonii		22.1	289.8	203.1	342.1
Lycium pallidum		29.1	380.6	229.9	176.2
Oryzopsis hymenoides		0.1	0.8	0.1	0.9
Machaeranthera tortifolia		1.3	16.7	3.3	5.3
	13.10		Total	764.1	997.5
		Upper ¼ segment			
Atriplex confertifolia		1.7	23.7	10.7	54.8
Psorothamnus fremontii		14.6	199.8	76.7	189.5
Ephedra nevadensis		20.9	188.7	134.3	195.1
Ambrosia dumosa		11.1	152.3	58.8	176.9
Ceratoides lanata		11.6	158.4	51.1	113.7
Grayia spinosa		6.8	93.6	45.4	90.5
Krameria parvifolia		5.3	72.0	13.9	30.1
Larrea tridentata		0.9	12.6	3.8	22.7
Lycium andersonii		20.6	281.6	158.2	361.0
Lycium pallidum		4.8	65.3	31.1	40.7
Sphaeralcea ambigua		0.2	2.6	0.2	0.1
Lepidium fremontii		0.5	7.1	1.1	3.4
Machaeranthera tortifolia		1.0	13.3		
	13.69		Total	589.2	1284.9
		Top ¼ segment (rock outcrops)			
Atriplex confertifolia		17.5	144.4	59.6	305.8
Psorothamnus fremontii		3.1	25.5	7.1	17.6
Ephedra nevadensis		0.8	6.3	1.1	1.6
Ceratoides lanata		0.8	6.9	1.4	4.1
Ambrosia dumosa		23.9	196.5	56.2	125.2
Krameria parvifolia		16.9	139.0	27.8	60.1
Lycium andersonii		3.6	29.6	8.2	43.2
Lycium pallidum		27.8	229.2	85.0	135.5
Encelia virginensis		1.5	12.6	3.1	0.0
Machaeranthera tortifolia		4.1	33.6	8.2	13.2
	8.24		Total	257.7	706.4

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FREQUENCY DISTRIBUTION AND CORRELATION AMONG MINERAL ELEMENTS IN *LYCIUM ANDERSONII* FROM THE NORTHERN MOJAVE DESERT

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ABSTRACT.— Two hundred samples of leaves of *Lycium andersonii* A. Gray, each representing one plant and divided among six different locations, were assayed by emission spectrography. Information for 12 different elements is reported in terms of concentrations, frequency distribution, correlations, and some soil characteristics. The objective was to ascertain the nature of variability for mineral elements within a species. Composition varied significantly for all 12 elements among locations, all within about 20 km. At least part of the variation was due to soil characteristics. Samples from Rock Valley were highest in K, Na, and Li, which effect is associated with volcanic outcrop. Samples from Mercury Valley were highest in P, Mg, Ba, and B. At least Mg is related to the soil composition. Correlation coefficients between element pairs were often very different for all 200 samples versus those obtained for individual locations. Some of the values for all 200 samples together proved to be artifacts. The highest correlation was for Ca × Sr (positive) and next was Ca × Mg (also positive). Most correlations were slightly or strongly positive (24 of 32). Only P × Ca, Ca × Na, Ca × B, and Sr × P seemed to be significantly negative of the 32 correlations examined. Frequency distribution patterns where common populations were grouped were often normally distributed. Li, as previously reported, and Na, Cu, Mn, and B and Ba at some locations were not normally distributed. Wide variations in the concentrations of individual elements in leaves of these species were encountered.

Mineral composition of the plants in any ecosystem is one of its distinguishing characteristics. The essential nature of at least 13 mineral elements for plants, with their abundance in soil, in many cases helps to determine the nature of the vegetational pattern. The same also can be said for some nonessential elements. In fact, excesses of both essential and nonessential elements largely determine vegetational characteristics under many conditions, and this occurrence is very common in desert ecosystems where young, poorly leached soils are usually involved (Fuller 1975, Romney et al. 1973).

The purpose of this report is to explain in some detail the mineral compositon of leaves of one plant species occurring with fair abundance in the northern Mojave Desert. The species, *Lycium andersonii* A. Gray, accumulates relatively high levels of Ca and Li and characteristically avoids salinity (Romney et al. 1973, Wallace et al. 1973, Ashcroft and Wallace 1976). Such data also would help to indicate the presence of ecotypes. Data for Li in these plants were reported previously (Romney et al. 1977).

MATERIALS AND METHODS

Lycium andersonii samples were collected in May 1976 from six different areas in the southern portion of the Nevada Test Site (northern Mojave Desert). The areas were Mercury Valley, west Mercury Valley, Rock Valley, base of Skull Mountain in Rock Valley (near 410 road), Frenchman Flat, and southwest Frenchman Flat. Each sample consisted of about 2 g of dry leaves that involved about 2000 individual leaves for each sample. There were 33 or 34 samples from each location and 200 total samples for all the locations. Each sample represented a single plant. Samples were collected just after a series of rains and otherwise were not washed (Al and Ti analysis indicated minimum contamination by soil). The samples were dried, weighed, ground in a plastic mill, and otherwise prepared for analysis by emission spectrography.

The soils characteristics from these areas are detailed in the report of Romney et al. (1973).

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RESULTS AND DISCUSSION

The mineral composition of leaves from all six locations differed for all 12 elements included in this report (Table 1). The samples from Mercury Valley were highest in P, Mg, B, and Ba. Rock Valley, which is partly overlain with volcanic material and igneous outcrops (Beatley 1976) had leaves with the highest Na, K, and Li.

The Rock Valley samples were also lowest in P, Fe, and Mn, and the southwest Frenchman Flat location was lowest in Cu, Sr, Ba, and Li.

The variability in composition from location to location was largely due to variations

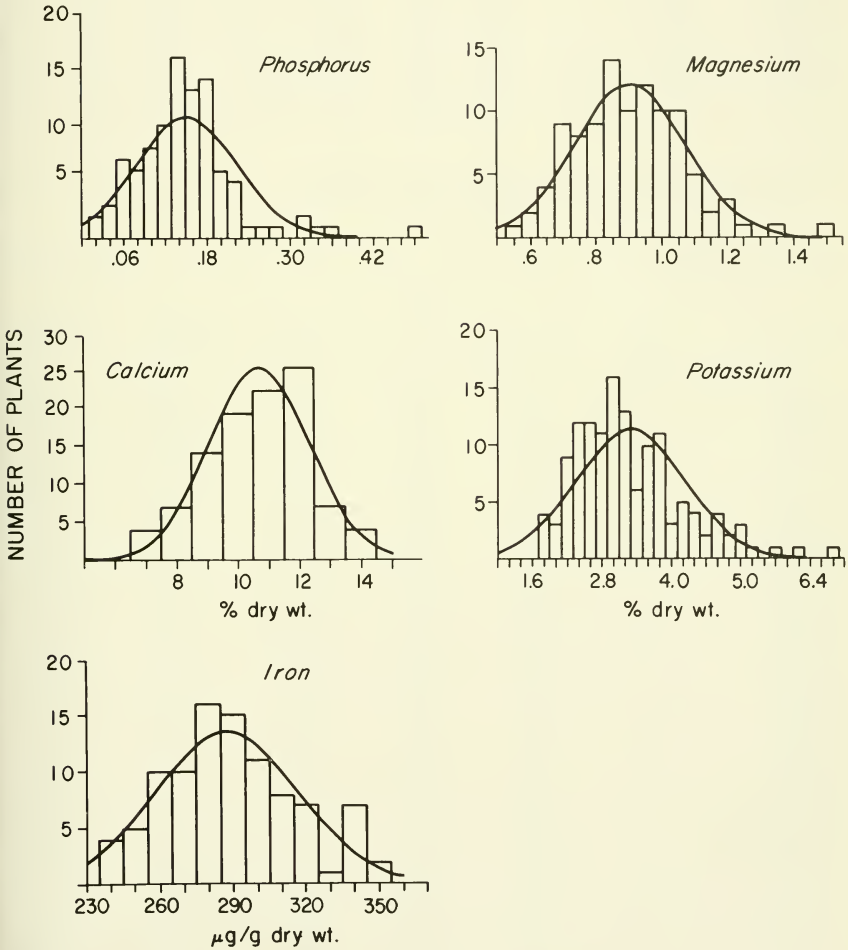

Fig. 1. Frequency distribution of K, Ca, P, Mg, and Fe in indicated groupings of locations for *L. andersonii* leaves in which groupings are not statistically different according to analysis of variance. (K = WM, F, M, 410; Ca = WM, SWF, 410; P = F, SWF, 410; Mg = WM, SWF, 410; Fe = RV, WM, M). See Table 1 for meanings of locations.

TABLE 1. Mineral composition of May 1976 leaves of *Lycium andersonii* from six different locations in the northern Mojave Desert.

	Mercury		Frenchman		SW Frenchman		W. Mercury	
	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
P, μg/g	2030a	884	1385b	795	1579b	897	1015c	372
Na, %	0.044	0.070	0.024b	0.016	0.025b	0.004	0.148b	0.177
K, %	3.42ab	0.972	3.32b	0.751	2.70c	0.900	2.98bc	0.893
Ca, %	6.72d	1.83	9.47b	1.43	10.74a	1.64	10.51a	1.77
Mg, %	1.78a	0.24	1.06b	0.18	0.94c	0.12	0.88v	0.34
Cu, μg/g	2.58c	1.11	2.97bc	1.28	1.85d	0.84	4.38a	2.34
Fe, μg/g	292cd	23	313b	42	364a	31	287d	38
Mn, μg/g	47b	27	128a	50	87a	27	47b	28
B, μg/g	41.5a	18.5	28.4c	5.8	36.5ab	7.6	35.9ab	10.2
Sr, μg/g	628b	106	550c	101	429d	70	737a	137
Ba, μg/g	56a	17.9	40bc	20.7	34d	4.6	34c	7.0
Li, μg/g	38.5ab	31.0	22.3cd	20.4	14.6d	14.3	44.8abc	36.5
Cation sum me/100 g	574		647		686		682	

*Values for each element followed by a common letter are not statistically different at the 0.05 level.

TABLE 2. Correlation coefficients for pairs of elements of *Lycium andersonii* leaves from different locations in the northern Mojave Desert.

Pairs	All locations	Mean for 6 locations	Mercury	Frenchman	SW Frenchman
n	194–200	194–200	33	33	34
P × Ca	–0.28	–0.29	–0.40	–0.12	–0.51
P × Cu	+0.16	0.40	0.11	0.68	0.77
P × B	+0.23	0.21	0.04	0.06	0.38
P × Fe	+0.14	0.00	–0.06	+0.48	–0.03
K × Na	0.30	0.22	0.22	–0.04	0.65
K × Ca	–0.20	–0.07	0.17	–0.27	–0.19
K × Sr	0.25	0.08	–0.13	–0.15	0.09
K × Ba	0.15	0.01	–0.08	0.05	0.10
K × Li	0.29	0.20	0.37	0.29	0.06
Ca × Na	–0.26	0.16	0.05	–0.29	–0.43
Ca × Mg	–0.37	0.46	0.04	0.60	0.57
Ca × Fe	0.34	0.22	0.16	0.22	0.17
Ca × Mn	0.21	0.17	–0.01	0.32	0.21
Ca × B	–0.13	–0.17	–0.19	–0.26	–0.10
Ca × Sr	0.09	+0.50	0.58	0.47	0.60
Ca × Ba	–0.25	0.23	0.46	–0.26	0.01
Ca × Li	–0.08	0.05	–0.11	0.27	–0.11
Na × P	–0.25	0.13	0.01	–0.09	0.64
Na × Sr	0.33	–0.04	0.20	0.04	–0.22
Na × Li	0.32	0.14	0.15	–0.26	0.33
Mg × Sr	0.14	+0.32	0.20	0.48	0.24
Mg × Ba	0.48	0.07	0.04	0.11	0.01
Mg × Li	0.12	0.32	0.18	0.71	0.17
Fe × Mg	–0.09	0.32	0.20	0.48	0.24
Fe × Mn	0.37	0.19	0.07	0.33	0.36
Fe × Sr	–0.20	0.42	0.61	0.39	0.13
Fe × Ba	–0.11	0.31	0.26	0.31	0.13
Fe × Li	–0.15	0.11	0.11	0.33	–0.01
Sr × Ba	0.27	0.21	0.20	–0.12	0.41
Sr × P	–0.26	–0.18	–0.38	0.14	–0.36
Sr × Li	0.19	0.02	–0.19	0.28	–0.06
Ba × Li	0.10	0.11	–0.01	–0.02	0.36

*r = 0.14 sig at 0.05 for all locations; 0.33 for individual locations.

Table 1 continued.

Rock Valley Mean	S.D.	Highway 410 Mean	S.D.	F ratio	Prob F extended	Mean of all	S.D. of all	C.V. of all	LSD 0.05
957c	407	1525b	463	11.1	0.0000	1423	761	53.5	327
0.951a	0.525	0.033b	0.039	87.1	0.0000	0.198	0.399	201.5	0.108
3.91a	1.356	3.45ab	1.107	5.6	0.0001	329	1.07	32.5	0.49
7.63c	1.73	10.77a	1.54	36.3	0.0000	9.34	2.29	24.5	0.80
1.13b	0.20	0.90c	0.13	105.8	0.0000	1.19	0.36	30.3	0.09
2.72bc	0.99	3.37b	1.04	13.1	0.0000	2.98	1.56	52.3	0.66
282d	26	305bc	36	27.1	0.0000	307	43	40.2	16.1
41b	16	46b	19	44.8	0.0000	66	43	34.6	14.4
32.5bc	11.3	38.8ab	12.6	5.21	0.0002	35.6	12.3	34.6	5.63
756a	109	655b	160	36.2	0.0000	625	161	25.8	56.7
39bc	7.2	41b	10.6	29.2	0.0000	39	15.1	38.7	5.6
54.5a	45.4	30.9bcd	32.8	4.9	0.0004	36.3	35.3	97.2	16.1
617		703		105.8					

Table 2 continued.

West Mercury 32	Rock Valley 34	Hwy 410 34	Location +	Location –	No. loc. sig. at 0.05	Sig. of all loc.
–0.28	–0.32	–0.08	0	6	2	0.01
0.37	0.37	0.10	6	0	4	0.05
0.10	0.20	0.48	6	0	2	0.01
+0.09	–0.28	–0.18	2	4	1	0.05
0.23	0.30	–0.05	4	2	1	0.01
0.16	0.01	0.03	3	3	0	0.01
0.01	0.17	0.47	4	2	1	0.01
–0.21	0.14	0.05	4	2	0	0.05
–0.04	0.54	–0.01	4	2	2	0.01
–0.15	0.03	–0.16	2	4	1	0.01
0.56	0.55	0.44	6	0	5	0.01
0.05	0.33	0.39	6	0	2	0.01
0.21	0.16	0.13	5	1	0	0.01
0.19	–0.63	0.04	2	4	1	0.10
0.38	0.55	0.44	6	0	6	NS
0.22	0.60	0.37	5	1	3	0.01
–0.24	0.27	0.21	3	3	0	NS
0.00	0.04	0.20	4	1	1	0.01
–0.16	–0.05	–0.07	2	4	0	0.01
0.57	0.15	–0.10	4	2	2	0.01
0.11	0.58	0.33	6	0	3	0.05
–0.11	0.36	0.01	5	1	1	0.01
0.16	0.31	0.41	6	0	2	NS
0.11	0.58	0.33	6	0	3	NS
0.12	0.13	0.12	6	0	2	0.01
0.50	0.54	0.32	6	0	4	0.01
0.23	0.52	0.41	6	0	2	NS
–0.08	–0.02	0.31	3	3	1	0.01
0.40	0.57	0.18	5	1	3	0.01
–0.08	–0.41	0.03	2	4	3	0.01
–0.19	0.27	–0.21	2	4	0	0.01
0.03	0.16	0.16	4	2	1	NS

in the edaphic characteristics (Romney et al. 1973). The area with high Mg in leaves (and low Ca) had high available Mg in soil (Romney et al. 1973).

The relationship between Ca and Mg was not always simple. For each of the locations except one, the correlation coefficient obtained when Ca and Mg were correlated was strongly positive (Table 2). The one not significant was at the location having highest Mg and the lowest Ca (r = +0.04), so even then the relationship was not inverse. When all 200 samples were included in a common correlation, however, the r was –0.37 compared with a mean of +0.46 for the six locations determined individually. The overall r then must be considered as an artifact and indicates possible erroneous conclusions that can be made when correlation coefficients are obtained for large variable populations.

Most of the 32 correlation coefficients in Table 2 were positive (24 of them as the average of the 6 locations). This generally conforms to the report of Garten (1976) for data elsewhere. Consistent and important negative correlations were obtained for P × Ca, Ca × Na, Ca × B, and Sr × P. There are known physiological bases for some of these. In addition to Ca × Mg, other strong positive correlations existed between P and Cu (r = +0.40), Ca × Sr (r = +0.50), Mg × Sr (r = +0.32), and Fe × Sr (r = +0.42).

Frequency distribution patterns of the elements were obtained for groups of locations where analysis of variance data indicated that no differences existed between or among the particular locations. This permitted the use of as many as all samples (200) and, at least, about one-half of them in a frequency distribution determination. Where normal distribution was not apparent, data were also plotted as logarithm-normal. The histograms (Fig. 1) for Ca, Mg, P, K, and Fe with n of around 90 showed normal distribution (Table 3). Manganese did not show a normal distribution (Fig. 2), but it did on the ln normal basis (Fig. 2 and Table 3). Two of three B groupings gave a normal distribution (Fig. 3 and Table 3); a third grouping gave a ln normal distribution (Fig. 3, Table 3).

The Cu concentrations of these *L. andersonii* plants were low in comparison to most plant species. The values were lower than those found for *L. andersonii* collected over a wider area (Wallace and Romney 1972). The Cu values were not normally distributed (Fig. 4) but skewed toward the smaller values (Table 3). When all six sites were combined, a ln normal distribution was obtained even though there were four distinct populations (Table 1). Part of this Cu variation in distribution could be analytical.

Two Ba groupings gave a normal distribution and one did not (Fig. 5, Table 3). Again the ln normal gave a distribution which could not be rejected as normal (Fig. 5, Table 3). Two Sr groupings gave normal distribution (Fig. 6, Table 3).

In the former study of Li where distribution was neither normal nor ln normal (Romney et al. 1977), differential distribution of Li in soil was given as an explanation. In one of the present data groupings, however, Li did give a ln normal distribution (Fig. 7, Table 3). It would appear that this species tends toward a normal distribution of metals, but that soil variation shifts to other types of distribution.

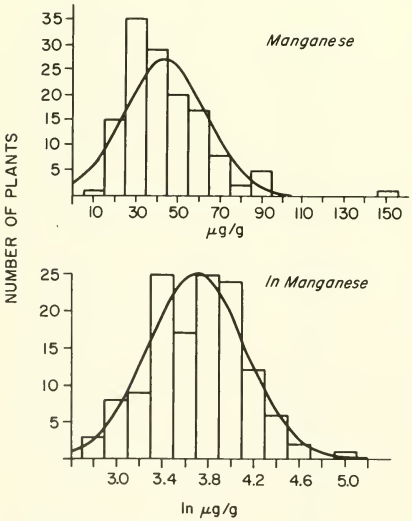

Fig. 2. Frequency distribution of Mn in *L. andersonii* leaves (RV, 410, M, and WM for arithmetic and the same grouping for ln of Mn concentration). See Figure 1 for further explanation.

TABLE 3. Evaluation(1) of normality of frequency distribution histograms (Figs. 1–7)

Element	Mean percent	Locations	n	Chi^2 goodness of fit Test of normality	Skewness	Kurtosis(2)
P	0.150	FR,SWF,410	98	Cannot reject	1.2407**	0.7023**
Na	0.0550	All except RV	168	Reject	4.2458**	Not tested
K	3.291	WM,F,M,410	134	Cannot reject	0.9592	0.8031
Ca	10.673	WM,SWF,410	102	Cannot reject	–0.2688	0.8214
Mg	0.903	WM,SWF,410	102	Cannot reject	0.5005**	0.7933
	ug/g					
Cu_1	2.8	M,RV,FM	98	Reject	0.7430**	0.7932
Cu_2	3.0	410,RV,FM	99	Reject	0.5837**	0.8135
Cu_3	2.9	410,RV,FM,M	132	Reject	0.5866**	0.8178
Cu_4	3.0	ALL	199	Reject	1.4078**	0.7494**
Fe	287	RV,WM,M	99	Cannot reject	–0.1201	0.7719
Mn	44.2	RV,WM,M,410	133	Reject	1.5509**	0.7475**
B_1	36.0	RV,WM,410,SWF	134	Cannot reject	1.6832**	0.7069**
B_2	37.5	WM,M,410,SWF	134	Reject	1.8032**	0.7008**
B_3	36.5	WM,RV,M,410,SWF	166	Cannot reject	1.5353**	0.8875**
Sr_1	637	M,410	67	Cannot reject	0.9195**	0.7754
Sr_2	746	WM,RV	66	Cannot reject	–0.2714	0.8198
Ba_1	364	WM,RV,F	99	Reject	0.2980	0.8069
Ba_2	38.8	RV,F,410	99	Cannot reject	0.5407**	0.7726
Ba_3	37.7	WM,RV,F,410	133	Cannot reject	0.5526	0.7837
Li_1	23.9	F,410,SWF	71	Reject	2.3171**	0.7028**
Li_2	31.6	F,410,M	78	Reject	1.5474**	0.7631
Li_3	37.9	WM,M,410	90	Reject	1.1725**	0.7918
Li_4	46.4	RV,WM,M	88	Reject	0.9633**	0.8054
$\ln Li_4$	3.391	RV,WM,M	88	Cannot reject	–0.6095**	0.8127

(1) Statistical significance level for all tests is 5 percent.
**Indicates significance
(2) Alternate kurtosis index proposed for $N < 200$ by R. C. Geary. See Snedecor & Cochran *Statistical Methods*, 6th ed., 88; and R. C. Geary, *Biometrika* 28, 295 (1936) (Index is about 0.80, depending on sample size. Table of probability points is in reference).

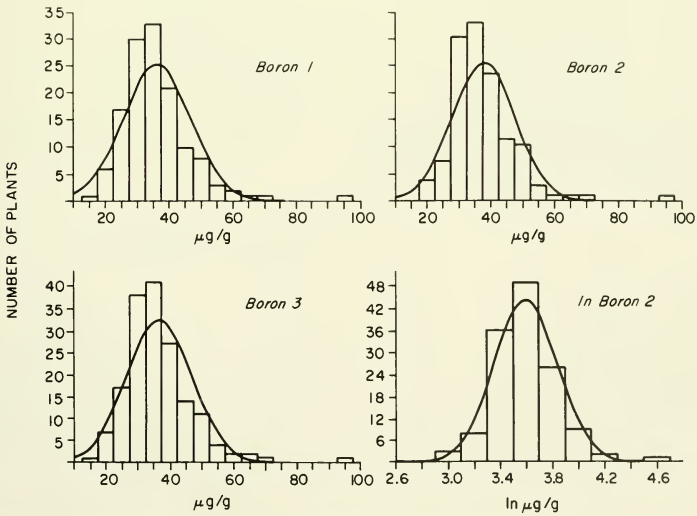

Fig. 3. Frequency distribution of B in leaves of *L. andersonii* (Boron 1 = RV, WM, SWF, 410; Boron 2 = WM, SWF, 410, M; Boron 3 = RV, WM, SWF, 410, M). See Figure 1 for further explanation.

A cluster tree for 21 elements in all samples of *L. andersonii* leaves is shown in Figure 8. Calcium, the dominant mineral element in *L. andersonii* leaves, clusters with Cr. These in turn cluster closely with the so-called dust elements Fe, Ti, Al, Si, and in this case also Mn. The trace metal Li that is prominent in *L. andersonii* (the species is an accumulator of Li) clusters with another monovalent metal, Na, which also is in *L. andersonii* in trace quantities only. These two elements are joined by the monovalent K, which is present in leaves of this species at levels of from about 2 to 5 percent. These three elements later join with Cu, V, and Sr. Mg and Ba are clustered and these join with

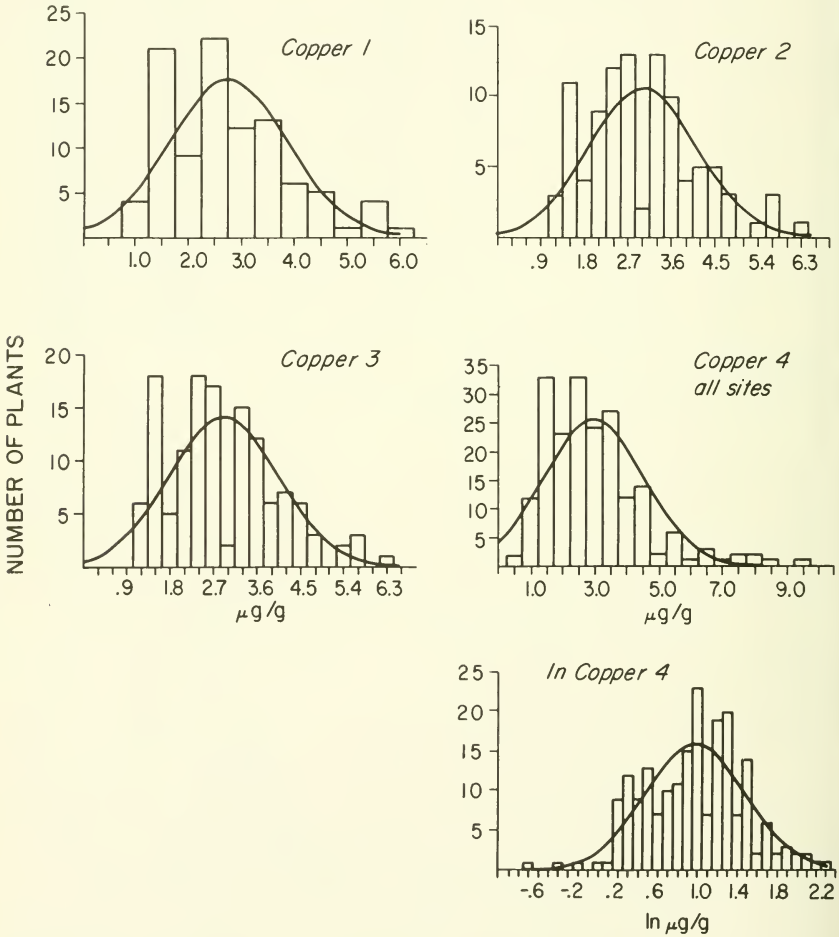

Fig. 4. Frequency distribution of Cu in leaves of *L. andersonii* (Copper 1 = M, RV, F; Copper 2 = RV, F, 410; Copper 3 = M, RV, F, 410; Copper 4 is all six sites combined). See Figure 1 for further explanation.

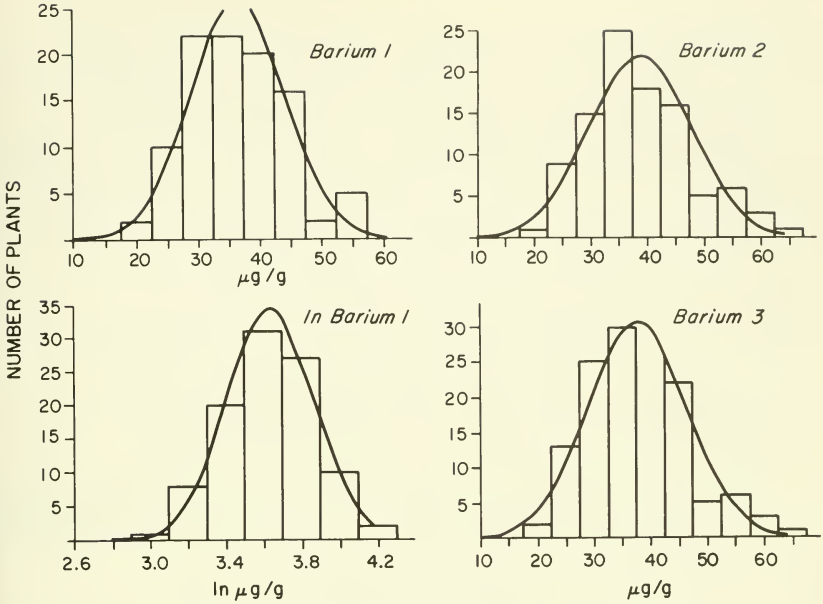

Fig. 5. Frequency distribution of Ba in leaves of *L. andersonii* (Ba 1 = WM, RV, F; Ba 2 = RV, F, 410; Ba 3 = WM, RV, F, 410). See Figure 1 for further explanation.

P. These interactions as yet have not been used to explain behavior of this species in the northern Mojave Desert, but opportunities are present.

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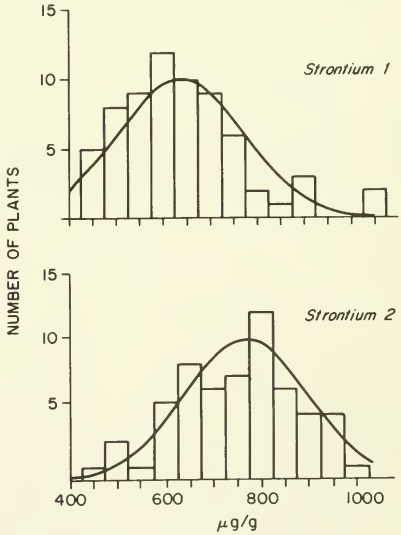

Fig. 6. Frequency distribution of Sr in leaves of *L. andersonii* (Sr_1 = M, 410; Sr_2 = WM, RV). See Figure 1 for further explanation.

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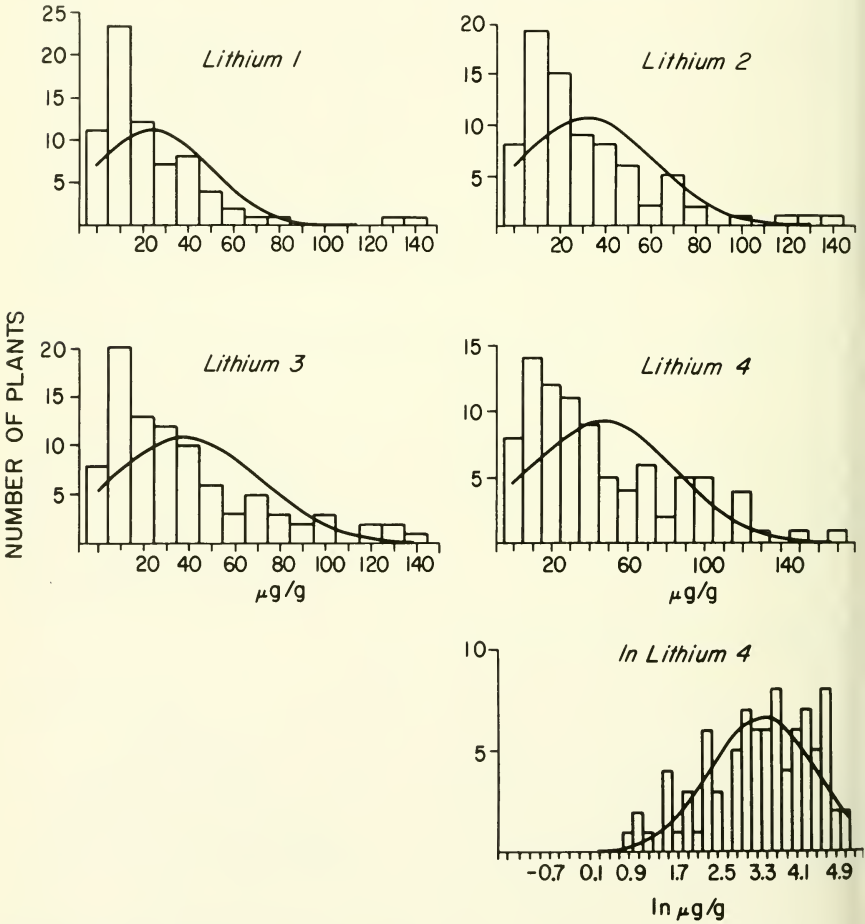

Fig. 7. Frequency distribution of Li in leaves of *L. andersonii* (Li 1 = SWF, F, 410; Li 2 = F, 410, M; Li 3 = 410, M, WM; Li 4 = M, WM, RV). See Figure 1 for further explanation.

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TREE PRINTED OVER CORRELATION MATRIX (SCALED 0-100).
CLUSTERING BY AVERAGE DISTANCE METHOD.
   VARIABLE
NAME      NO.
          ------------------------------------------------------------/
P       (  2) 61 61/40 50 55 56 63 35/61 54 57/49/49/36 48 55 58 58 55 51/
                /                    /        /  /  /                    /
          ----/                    /        /  /  /                    /
MG      (  6) 77/49 55 56 42 49 57/54 42 51/49/49/34 46 47 41 36 37 46/
                /                  /        /  /  /                  /
               /                  /        /  /  /                  /
BA      ( 19)/51 59 57 58 65 68/52 43 50/49/49/39 44 44 40 40 43 40/
                                /        /  /  /                  /
          ----------------/        /  /  /                  /
NA      (  3) 68/64/50 53 65/45 45 48/49/49/38 38 39 47 38 39 37/
                /  /        /        /  /  /                  /
               /  /        /        /  /  /                  /
LI      ( 20)/63/55 63 62/50 50 48/49/49/45 46 42 46 43 43 36/
                /        /        /  /  /                  /
               /        /        /  /  /                  /
K       (  4)/48 56 61/54 60 53/49/49/42 42 42 45 42 44 44/
                /        /  /  /                  /
          -------/        /  /  /                  /
CU      (  7) 68/60/48 46 48/49/49/53 57 46 48 50 49 44/
                /  /        /  /  /                  /
               /  /        /  /  /                  /
V       ( 14)/66/46 56 50/49/49/58 60 45 46 52 53 43/
                /        /  /  /                  /
               /        /  /  /                  /
SR      ( 18)/51 58 48/49/49/57 54 43 40 40 43 36/
                        /  /  /                  /
          -------/  /  /                  /
B       ( 10) 63/50/49/49/44 44 53 53 53 54 42/
                /  /  /  /                  /
               /  /  /  /                  /
MO      ( 16)/53/49/49/57 47 53 51 57 60 50/
                /  /  /                  /
               /  /  /                  /
PB      ( 22)/49/49/46 46 46 48 48 48 47/
                /  /                  /
               /  /                  /
SN      ( 21)/49/49 49 49 49 49 49 49/
                /                  /
               /                  /
NI      ( 15)/49 49 49 49 49 49 49/
                                  /
          -------------------/
CA      (  5) 79/66 56 69 66 59/
                /                  /
               /                  /
CR      ( 17)/67 59 65 62 64/
                                  /
          -------------/
FE      (  8) 87/88 86/68/
                /        /  /
               /        /  /
TI      ( 13)/85 83/62/
                    /  /
          ----/  /
AL      ( 11) 97/65/
                /  /
               /  /
SI      ( 12)/64/
                /
               /
MN      (  9)/
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Fig. 8. Cluster tree derived from correlation matrix of mineral element composition of *L. andersonii* leaves. The values in this tree have been scaled 0 to 100 according to the following: Value above 0, correlation –1.000; value above 5, correlation –0.900; value above 10, correlation –0.800; value above 15, correlation –0.700; value above 20, correlation –0.600; value above 25, correlation –0.500; value above 30, correlation –0.500; value above 35, correlation –0.300; value above 40, correlation –0.200; value above 45, correlation –0.100; value above 50, correlation 0.000; value above 55, correlation 0.100; value above 60, correlation 0.200; value above 65, correlation 0.300; value above 70, correlation 0.400; value above 75, correlation 0.500; value above 80, correlation 0.600; value above 85, correlation 0.700; value above 90, correlation 0.800; value above 95, correlation 0.900.

MINERAL COMPOSITION OF *ATRIPLEX HYMENELYTRA* GROWING IN THE NORTHERN MOJAVE DESERT

A. Wallace[1], E. M. Romney[1], R. B. Hunter[1], J. E. Kinnear[1], and G. V. Alexander[1]

ABSTRACT.— Fifty samples of *Atriplex hymenelytra* (Torr.) S. Wats. were collected from several different locations in southern Nevada and California to test variability in mineral composition. Only Na, V, P, Ca, Mg, Mn, and Sr in the samples appeared to represent a uniform population resulting in normal curves for frequency distribution. Even so, about 40 percent of the variance for these elements was due to location. All elements differed enough with location so that no element really represented a uniform population. The coefficient of variation for most elements was over 40 percent and one was over 100 percent. The proportion of variance due to analytical variation averaged 16.2 ± 13.1 percent (standard deviation), that due to location was 43.0 ± 13.4 percent, and that due to variation of plants within location was 40.7 ± 13.0 percent.

Atriplex hymenelytra (Torr.) S. Wats. (desert holly) is a halophyte that accumulates NaCl in leaves (Wallace and Romney 1972, Romney et al. 1973, Wallace et al. 1973a, 1973b). Many *Atriplex* species, including *A. hymenelytra,* have salt glands in leaves (Jones and Hodgkinson (1970).

Atriplex hymenelytra generally grows in the mountain passes in southern Nevada, and it is common along roadways where soil has been disturbed. It is very common in Death Valley (Hunt 1966). The objective of this work was to study mineral composition of leaves of this plant species collected from a relatively wide area of the northern Mojave Desert. A somewhat similar study was made of another species (*Lycium andersonii*) collected from a relatively narrow range (within 20 km) of the same desert (Wallace et al. 1980, this volume).

TABLE 1. Statistical information for the mineral composition of *A. hymenelytra.*

		Mean	S.D.	C.V.	Lowest	Highest
P	ug/g	3434	1554	0.45	307	6739
Na	%	8.791	2.201	0.25	3.12	15.84
K	%	5.435	2.172	0.40	2.04	13.59
Ca	%	1.409	0.735	0.52	0.31	5.08
Mg	ug/g	4547	1868	0.41	2057	11717
Zn	ug/g	24.5	20.6	0.84	Near 0	82
Cu	ug/g	5.3	3.9	0.74	0.9	23
Fe	ug/g	305	137	0.45	161	828
Mn	ug/g	146	116	0.79	27	673
B	ug/g	83.3	70.3	0.84	18	250
Al	ug/g	346	208	0.60	46	1101
Si	ug/g	1587	1348	0.85	241	8892
Ti	ug/g	41.1	26.2	0.64	7.9	124
V	ug/g	4.7	1.0	0.22	2.7	8.0
Mo	ug/g	2.8	2.4	0.86	0.5	11.0
Sr	ug/g	288	187	0.65	27	953
Ba	ug/g	10.5	7.0	0.67	2.6	41
Li	ug/g	11.2	12.1	1.08	0.0	89
Pb	ug/g	9.8	8.9	0.91	0.0	36

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MATERIALS AND METHODS

Fifty samples of *Atriplex hymenelytra* (Torr.) S. Wats. were collected in southern Nevada and adjacent areas in California in early 1976. Some were from the Nevada Test Site and others were from along a highway between Baker, California, and Mercury, Nevada. A range of about 150 km between sample sites occurred. Usually 4 or 5 samples were taken from a location and each sample represented one individual plant, as in the *Lycium andersonii* collection (Wallace et al. 1980, this volume). Samples were not washed and were prepared for analysis by emission spectrography. Each sample was assayed in triplicate.

The sample sites were east and south of the city Shoshone, near Tacoma, near Pahrump, on Highway 95, and in Rock Valley of the Nevada Test Site.

RESULTS AND DISCUSSION

Only 134 of the 150 replicate analyses were used in the statistical evaluation because of various failures in analysis of some of the elements. The means, standard deviations, coefficients of variation (C.V.), and proportion of variance due to analytical error are given in Table 1. As a generality, the C.V. values are much larger than the corresponding values for *L. andersonii* (Wallace et al. 1980, this volume). The proportion of the variance due to analytical error was relatively low, however (Table 1). Except for K, V, and Li it was 20 percent or less, sometimes much less. There was no relationship between these values and the C.V. ($r = -0.21$) shown in Table 1.

Frequency distribution of metal concentrations for 19 different elements are presented in Figures 1 to 5. A statistical evaluation of

Table 1 continued.

Variance ratio			Chi^2 goodness of fit test of normality	Skewness at 0.05?	Substitute kurtosis coeff. significant?
Analytical error	Within location	Between location			
0.14	0.32	0.54	Cannot rej.	No	No
0.20	0.40	0.41	Cannot rej.	No	No
0.40	0.41	0.19	Reject	Yes	No
0.11	0.46	0.43	Cannot rej.	Yes	Yes
0.07	0.40	0.53	Cannot rej.	Yes	No
0.13	0.41	0.45	Reject	Yes	No
0.02	0.58	0.40	Reject	Yes	Yes
0.18	0.33	0.49	Reject	Yes	Yes
0.15	0.49	0.36	Cannot rej.	Yes	Yes
0.02	0.18	0.79	Reject	Yes	No
0.10	0.51	0.39	Reject	Yes	Yes
0.07	0.71	0.22	Reject	Yes	Yes
0.15	0.45	0.39	Reject	Yes	No
0.43	0.17	0.40	Cannot rej.	No	No
0.04	0.44	0.53	Reject	Yes	Yes
0.05	0.51	0.45	Cannot rej.	Yes	No
0.18	0.38	0.44	Cannot rej.	Yes	No
0.45	0.30	0.24	Reject	Yes	Yes
0.18	0.28	0.53	Reject	No	Yes

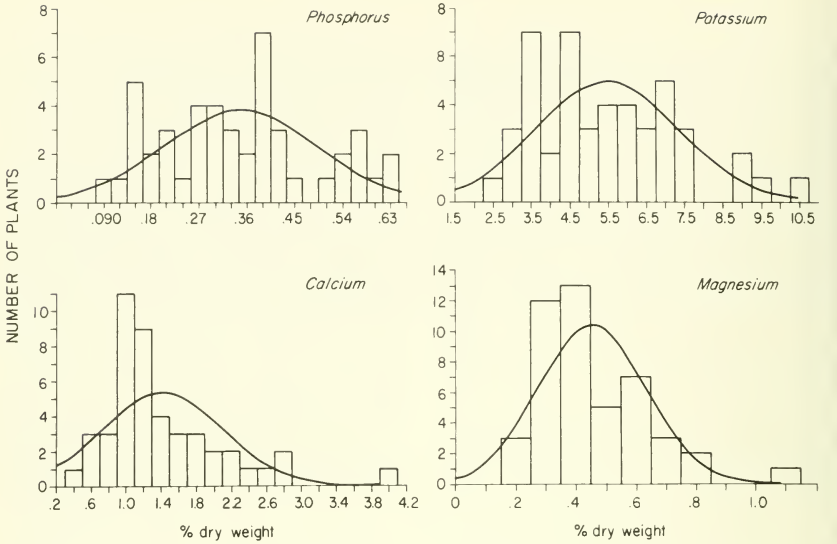

Fig. 1. Frequency distribution of P, K, Ca, and Mg in 50 samples of *Atriplex hymenelytra* leaves.

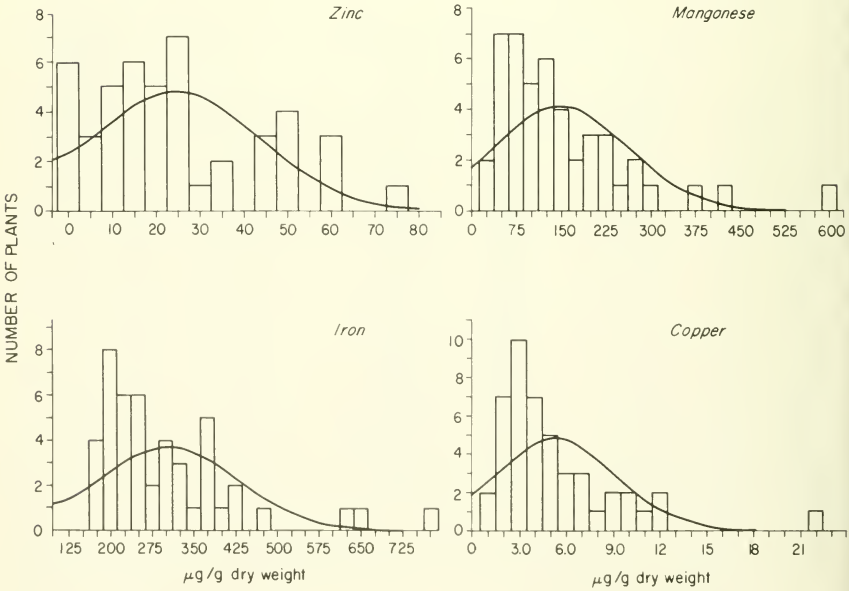

Fig. 2. Frequency distribution of Zn, Mn, Fe, and Cu in 50 samples of *Atriplex hymenelytra* leaves.

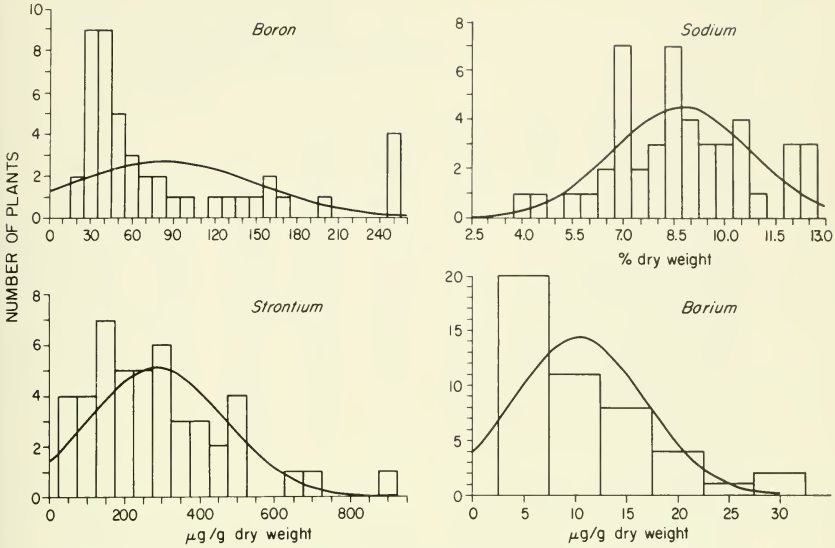

Fig. 3. Frequency distribution of B, Na, Sr, and Ba in 50 samples of *Atriplex hymenelytra* leaves.

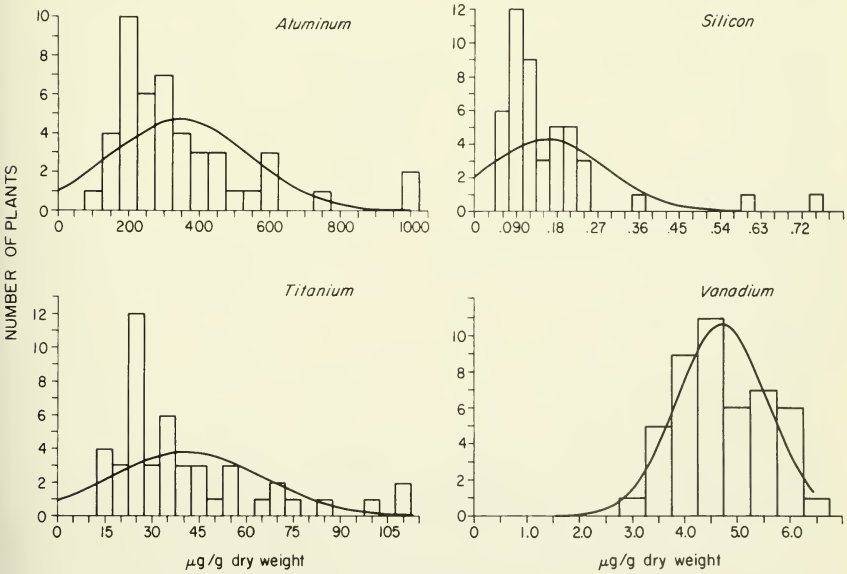

Fig. 4. Frequency distribution of Al, Si, Ti, and V in 50 samples of *Atriplex hymenelytra* leaves.

TABLE 2. Correlation matrix for the pairs of elements indicated in the analysis of *Atriplex hymenelytra**.

	P	Na	K	Ca	Mg	Zn	Cu	Fe	Mn	B
Na	–0.188									
K	–0.049	0.175								
Ca	–0.376	–0.361	0.172							
Mg	–0.326	–0.163	0.175	0.492						
Zn	0.417	0.039	0.206	–0.042	–0.372					
Cu	0.521	–0.092	0.289	–0.058	–0.228	0.462				
Fe	0.155	–0.075	–0.153	–0.081	0.257	–0.147	0.002			
Mn	0.423	–0.153	0.083	–0.125	–0.074	0.214	0.473	–0.126		
B	0.120	–0.127	–0.378	–0.131	–0.110	–0.192	–0.303	0.405	–0.232	
Al	0.168	–0.104	–0.202	–0.017	0.294	–0.161	–0.020	0.920	–0.118	0.391
Si	0.260	–0.133	–0.204	–0.131	0.209	–0.148	0.060	0.862	–0.102	0.361
Ti	0.122	0.038	–0.124	–0.135	0.228	0.212	–0.065	0.861	–0.180	0.376
V	–0.398	0.415	0.218	0.263	0.293	–0.295	–0.278	–0.033	–0.287	–0.119
Mo	0.3807	0.077	0.338	–0.091	0.078	0.075	0.577	–0.177	0.487	–0.418
Sr	–0.255	–0.126	–0.111	0.185	0.213	–0.277	–0.225	0.056	–0.103	–0.100
Ba	0.061	0.040	–0.074	–0.114	0.408	–0.256	0.013	0.719	0.135	0.138
Li	0.076	–0.064	–0.040	–0.079	–0.146	–0.168	–0.205	–0.294	0.330	0.108
Pb	0.073	0.412	0.165	–0.287	–0.012	0.163	0.180	0.068	–0.026	–0.128

	Al	Si	Ti	V	Mo	Sr	Ba	Li
Si	0.920							
Ti	0.861	0.805						
V	–0.007	–0.124	0.051					
Mo	–0.240	–0.198	–0.161	–0.128				
Sr	0.070	–0.037	0.118	0.206	0.129			
Ba	0.718	0.696	0.677	0.062	0.033	0.118		
Li	–0.277	–0.195	–0.249	0.002	0.022	–0.245	–0.306	
Pb	0.024	0.062	0.044	0.194	–0.007	–0.142	0.177	–0.061

*A value of ± 0.168 needed for significance at the 0.05 level.

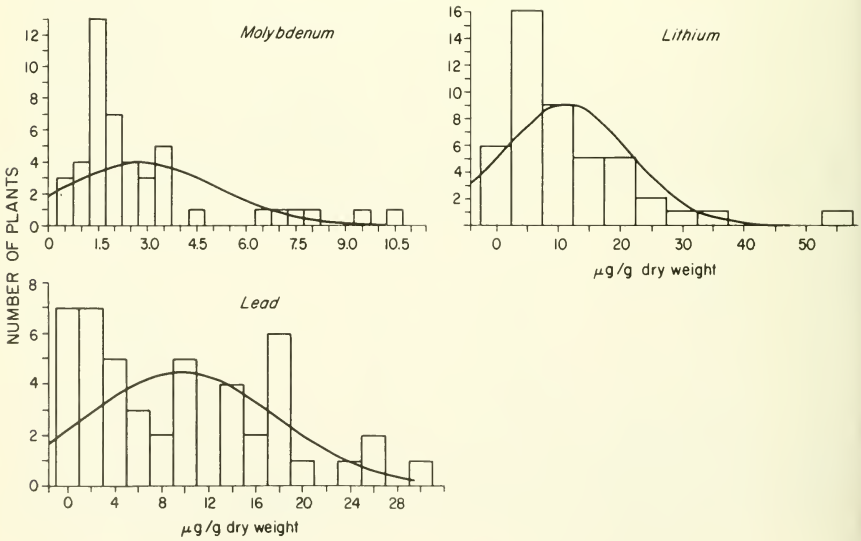

Fig. 5. Frequency distribution of Mo, Li, and Pb in 50 samples of *Atriplex hymenelytra* leaves.

```
TREE PRINTED OVER CORRELATION MATRIX (SCALED 0-100).
CLUSTERING BY AVERAGE DISTANCE METHOD.
   VARIABLE
NAME      NO.
                 -----------------------------------------------------/
P         (  2) 76 68 71/70/53/40 30 53 47/31 33 37 57 58 63 56 53 56/
                              /  /  /           /                    /
                 -------/  /  /                 /                    /
CU        (  8) 78/73/73/39/45 36 58 64/47 38 38 50 49 53 46 50 34/
                 /  /  /  /                 /                       /
                /  /  /  /                 /                       /
MO        ( 16)/74/53/51/46 43 49 66/45 53 56 41 37 40 41 51 29/
                /  /  /                 /                          /
               /  /  /                 /                          /
MN        ( 10)/60/66/42 35 48 54/43 46 44 43 44 44 41 43 38/
                /  /                 /                             /
               /  /                 /                             /
ZN        (  7)/41/52 35 58 60/47 31 36 42 41 42 39 37 40/
                /                 /                                /
               /                 /                                /
LI        ( 19)/46 50 46 43/46 42 37 35 36 40 37 34 55/
                            /                                     /
                 ----------/                                     /
NA        (  3) 70/70/58/31 41 43 46 44 43 51 52 43/
                 /  /  /                                        /
                /  /  /                                        /
V         ( 15)/59/60/63 64 60 48 49 43 52 53 44/
                /  /                                           /
               /  /                                           /
PB        ( 20)/58/35 49 42 46 51 53 52 58 43/
                /                                              /
               /                                              /
K         (  4)/58 58 44 42 39 39 43 46 31/
                                                              /
                 -------------------------/
CA        (  5) 74/59/45 49 43 43 44 43/
                 /  /                 /
                /  /                 /
MG        (  6)/60/62 64 60 61 70 44/
                /                   /
               /                   /
SR        ( 17)/52 53 48 55 55 45/
                                 /
                 ----------------/
FE        (  9) 95 93/93/85/70/
                        /  /  /  /
                 ----/  /  /  /
AL        ( 12) 95/93/85/69/
                 /  /  /  /
                /  /  /  /
SI        ( 13)/90/84/68/
                /  /  /
               /  /  /
TI        ( 14)/83/68/
                /  /
               /  /
BA        ( 18)/56/
                /
               /
B         ( 11)/
```

Fig. 6. Cluster analyses tree described from the correlation matrix. The values in this tree have been scaled 0 to 100 according to the following: Value above 0, correlation –1.000; value above 5, correlation –0.900; value above 10, correlation –0.800; value above 15, correlation –0.700; value above 20, correlation –0.600; value above 25, correlation –0.500; value above 30, correlation –0.400; value above 35, correlation –0.300; value above 40, correlation –0.200; value above 45, correlation –0.100; value above 50, correlation 0.000; value above 55, correlation 0.100; value above 60, correlation 0.200; value above 65, correlation 0.300; value above 70, correlation 0.400; value above 75, correlation 0.500; value above 80, correlation 0.600; value above 85, correlation 0.700; value above 90, correlation 0.800; value above 95, correlation 0.900.

the normality of each of the histograms is presented in Table 1. Even though the samples were collected over a range of about 150 km, normality could not be rejected for several of the elements. Included were P, Ca, and Mg (Fig. 1), Zn and Mn (Fig. 2), Na, Sr, and Ba (Fig. 3), and V (Fig. 4).

The mean Na concentration was 8.79 percent. The C.V. of this value was 24.6 percent, which was, except for V, lowest of the elements. Only 20 percent of this 24.6 percent was due to analytical variance. The frequency distribution for Na gave a normal curve (Fig. 3). It is of interest that all the samples from the collection covering about 150 km resulted in a uniform population for Na. It must be recognized that part of the Na would be on the leaf surface due to salt glands (Jones and Hodgkinson 1970).

The cluster analysis (Fig. 6) showed a marked relationship among the "dust" elements Fe, Al, Si, and Ti. An explanation of the variable clustering process as shown in the diagram (Fig. 6) follows: the process begins with the cluster consisting of variable Cu (8), the second variable listed in the diagram. This cluster joins with the cluster below it consisting of the variable Mo (16). The new cluster is indicated on the figure by the intersection of the dashes beginning above variable Cu (8), with the slashes starting next to the variable Mo (16).

This cluster joins with the cluster below it consisting of the variable Mn (10). The new cluster is indicated on the tree by the intersection of the dashes beginning above variable Cu (8), with the slashes starting next to variable Mn (10).

This cluster joins with the cluster above it consisting of the variable P (2). The new cluster is indicated on the tree by the intersection of the dashes beginning above variable P (2) with the slashes starting next to variable Mn (10). This cluster joins with the cluster below it consisting of the variable Zn (7). The new cluster is indicated on the tree by the intersection of the dashes beginning above variable P (2), with the slashes starting next to variable Li (19).

This cluster joins with the cluster below it consisting of the variables Na (3) down to K (4). The new cluster is indicated on the tree by the intersection of the dashes beginning above variable P (2), with the slashes starting next to variable K (4). The process continues until each variable is joined to at least one other variable.

Twenty-seven significant negative correlation coefficients were observed among pairs of elements (Table 2). This is a greater proportion than observed by Gartner (1976) for East Coast vegetation.

ACKNOWLEDGMENTS

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FIELD STUDIES OF MINERAL NUTRITION OF *LARREA TRIDENTATA*: IMPORTANCE OF N, pH, AND Fe

R. B. Hunter[1], A. Wallace[1], and E. M. Romney[1]

ABSTRACT.— Multivariate analysis of soil and plant data from the northern Mojave Desert was used to investigate aspects of the mineral nutrition of *Larrea tridentata* (Sesse & Moc. ex DC.) Cov. *Larrea tridentata* biomass was significantly correlated with soil NO_3^- and pH and leaf Fe content. Leaf cation accumulation was negatively correlated with leaf Fe concentration.

There are several hypotheses for the often strikingly discontinuous distribution of *Larrea tridentata* (Sesse & Moc ex DC.) Cov. in southwestern U.S. deserts. Beatley (1974) suggested that absence of *L. tridentata* from playas of the Nevada Test Site in the northern Mojave Desert is due to limiting cold during winter temperature inversions. Elimination from playas by occasional flooding (Wallace and Romney 1972) would be related to root oxygen deprivation, which has been studied by Lunt et al. (1973). Hallmark and Allen (1975) studied 11 west Texas soil variables and found weak correlations of *L. tridentata* distribution with lime and gravel content. Barbour (1970) found no significant effects of pH and salinity changes across *L. tridentata* ecotone lines, although germination of *L. tridentata* was related to salinity.

Romney et al. (1973) published a volume of soil, plant, and meteorological data exhaustively describing 78 sites in the Mojave Desert and Mojave-Great Basin transition zones of the Nevada Test Site. Fifty of these sites support a *L. tridentata* population. For this study we used these data to investigate edaphological factors involved in *L. tridentata* mineral nutrition and plant size.

METHODS

Programs for multivariate statistical analyses-correlation matrices, multiple linear regression, and principal component analysis were prepared by Dixon (1971). The analyses were run for 49 of the 50 sites, because one site that lacked biomass data for *L. tridentata* was deleted.

Sum of cations and cations minus N were the sums in me/100 g of leaf K, Na, Mg, and Ca, with me N/100 g subtracted in the latter case.

"Dust" contamination of several elements was calculated using a simple linear regression line of leaf concentration of the element versus either Si or Al, whichever correlated most strongly. The residual of the equation was assumed to represent "metabolic" content (abbreviated "meta"), and the slope times the Si or Al concentration was considered contamination. (The terms *dust* and *metabolic* express one of several possible interpretations of these factors.)

Soil depth was considered either the deepest point recorded or the depth to a caliche hardpan.

RESULTS

Table 1 lists means and standard deviations of the variables on 49 *L. tridentata*-inhabited sites used in the subsequent analyses. The soils are very gravelly, high in lime, and in some cases underlain by a caliche hardpan. The pH fluctuates narrowly near 8.3. Aboveground biomass ranged from 932 to 3726 kg/ha, and *L. tridentata* biomass ranged from 9 to 1664 kg/ha. Leaf sum of cations averaged 158 me/100 g, and cations minus N averaged −10 me/100 g, indicating approx-

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TABLE 1. Averages for variables analyzed in this study. Measurements were made at 49 sites in the northern Mojave Desert.

Variable	Avg ± sd	Unit	Variable	Avg ± sd	Unit
Community parameters			*Soil variables*[a]		
Total biomass	1859 ± 770	kg/ha	Clay	4 ± 3	%
Total density	10 ± 5	thousands/ha	Silt	7 ± 4	%
Larrea biomass	714 ± 349	kg/ha	Organic C	0.3 ± 0.2	%
Larrea size	757 ± 300	g/plant	Organic	0.04 ± 0.02	%
Larrea leaf minerals			*Saturation extract*		
N	169 ± 20	me/100 g	pH A_1	8.4 ± 0.4	
P	0.21 ± 0.06	%	pH C_1	8.6 ± 0.3	
Na	0.05 ± 0.03	%	EC25	1.0 ± 0.9	mmho/cm
Si	0.3 ± 0.1	%			
K	56 ± 18	me/100 g	CEC	12 ± 4	me/100 g
Ca	80 ± 21	me/100 g	Na	3 ± 4	me/l
Mg	19 ± 6	me/100 g	K	3 ± 2	me/l
Sum of cations	158 ± 34	me/100 g	Ca	7 ± 9	me/l
Dust corrected sum of cations	152 ± 34	me/100 g	$SO_4^=$	1 ± 2	me/l
Cations – N	-10 ± 34	me/100	NO_3 – N	13 ± 32	ug/g
Dust Mg	4 ± 2	ug/g			
Dust Na	1.1 ±	me/100 g			
Zn	25 ± 7	ug/g	Highest Na	14 ± 20	ug/g
Cu	3.2 ± 1.9	ug/g			
Fe	384 ± 171	ug/g	Highest NO_3	67 ± 88	ug/g
Meta Fe	183 ± 125	ug/g	Highest NO_3 below A_1	50 ± 91	ug/g
Dust Fe	204 ± 98	ug/g			
Mn	40 ± 11	ug/g	*DTPA extract*		
B	79 ± 20	ug/g	Cu	0.13 ± 0.06	ug/g
Al	537 ± 261	ug/g	Fe	0.22 ± 0.17	ug/g
			$NaHCO_3$ extract		
			P	1 ± 1	ug/g

[a]All soil variables are for the C_1 horizon except pH A and those "highest" values from which the greatest value measured at the site was used.

imate equality between nitrogen and cation milliequivalents.

Variables correlating significantly ($p = <0.05$) with *L. tridentata* biomass and sum of cations are presented in Table 2. These independent variables "explain" generally less than 20 percent of the variability in biomass. Total leaf Fe, meta Fe, and leaf P and Zn correlated unusually strongly with the sum of cations. Of the three soil variables studied (Table 2), $C_1NO_3^-$ correlated most strongly with plant size. The C_1 refers to soil horizon.

Table 3 shows variables that correlated significantly ($p = <0.05$) with leaf Fe fractions. Of the soil variables, only depth and silt content correlated significantly with meta Fe, clay with dust Fe, and soil depth with overall leaf Fe. Soil Fe, as extracted by DTPA, did not correlate significantly with any leaf Fe variable.

Table 4 presents the results of multiple linear regression of independent variables versus *L. tridentata* biomass per plant and sum of cations. The analyses were run in such a way that no variable had an F-to-enter ≤ 4.0. With three variables entered, 44 percent of the plant size variability is explained, and metabolic Fe variations explained 36 percent of the sum of cations.

The first 2 of 20 principal components of

TABLE 2. Correlation coefficients (r) of selected variables correlating significantly ($p = <0.05$) with *L. tridentata* biomass and leaf cations.

Variables	*L. tridentata* Biomass/plant	Leaf Sum of cations
C_1pH	-0.30	0.29
C_1NO_3 μg/g	0.45	ns
Soil EC25°	0.39	ns
C_1 Ca	0.43	ns
Soil depth cm	0.39	ns
C_1 Zn	-0.36	ns
Leaf Fe	-0.36	-0.40
Meta Fe	-0.37	-0.56
Leaf P	ns	0.47
Leaf Zn	ns	0.50

TABLE 3. Correlation coefficients of variables significantly ($p = <0.05$) correlated with leaf Fe fractions and DTPA extractable soil Fe.

	Leaf Fe	Dust Fe	Meta Fe	Soil Fe
		r		
Sum of leaf cations	–0.40	ns	–0.56	ns
Leaf Na	0.39	0.54	ns	ns
Leaf K	–0.50	ns	–0.56	ns
Leaf Ca	–0.31	ns	–0.47	ns
Leaf Si	0.70	0.87	ns	ns
Leaf Al	0.70	1.00	ns	ns
Leaf Mn	0.48	0.59	ns	ns
Leaf P	ns	ns	–0.43	ns
Leaf Zn	ns	ns	–0.46	ns
Dust Fe	0.70	1.00	ns	ns
Meta Fe	0.82	ns	1.00	ns
Larrea-Biomass/plant	–0.36	ns	–0.37	ns
Overall Biomass/ha	–0.30	ns	–0.32	ns
Depth	–0.32	ns	–0.35	ns
C_1 Clay	ns	0.31	ns	0.40
C_1 Silt	ns	ns	0.30	0.47
Organic C	ns	ns	ns	0.55
Organic N	ns	ns	ns	0.53
Water holding capacity	0.29	ns	ns	0.47

L. tridentata leaf mineral composition accounted for 46 percent of the total variance. Variables scoring highest on the first component were leaf Fe and sum of cations. Those scoring highest on the second component were cations minus N and leaf Al. Analyses of community and soil variables showed a diffuse distribution of variance among the factors studied.

Soil pH correlated significantly with percent clay ($r = +0.30$) and saturation extract Mg ($r = -0.40$), besides the correlations with *L. tridentata* size and sum of cations (Table 2). Both saturation extract and paste pH were measured. Paste pH did not correlate significantly with sum of cations and was not considered for the bulk of this study.

DISCUSSION

There are a multitude of variables affecting size of *L. tridentata* plants in the field. Several important factors not considered here include rainfall, plant age, incidence of grazing, and competition with neighboring shrubs. Because these data are from the field, no variable was controlled. We thus feel justified in imputing significance to variables that can explain just 10 to 20 percent of the variability in plant size.

Of the three factors correlating strongest with plant size, only the first, $C_1NO_3^-$ concentration, is easily explained. The correlation implies that NO_3^- levels, measured at single points, limit plant growth, and that they are

TABLE 4. Multiple linear regressions of independent variables affecting *Larrea tridentata* biomass* per plant and leaf sum of cations.**

Step	Variable added	Coefficient	Multiple r^2	Constant
A. Biomass per plant (g) = 3.47 (C_1NO_3) – 1.13 (Meta Fe) – 376.8 (pH) ÷ 4139				
1.	C_1NO_3	3.47	0.20	688
2.	Meta Fe	–1.13	0.33	865
3.	C_1pH	–376.8	0.44	4139
B. Sum of leaf cations, me/100 g = 181.5 – 0.16 (Meta Fe)				
1.	Meta Fe	–0.16	0.36	181.5

No other independent variables had significant F value to enter.

Larrea tridentata biomass per hectare was deleted.
**Deleted variables were cation-N, leaf K, leaf Ca, and leaf Mg.

representative of those over the whole 100 m^2 transect used to determine plant size. The data are also consistent with the distribution of shrub roots that are primarily in the Band C horizons.

It is somewhat surprising that the small variations in pH should correlate with *L. tridentata* size. The hydrogen ion concentration ranges from 10^{-8} to 10^{-9} *M*, though other cations are present at 10^{-3} *M* (Table 1). Because the correlation was negative, it is possible the higher soil pH values tend to inhibit *L. tridentata* growth.

No attempt was made to measure rhizosphere pH, though data of Turner (1972) suggest that in desert soils rhizosphere pH is reduced even in these heavily calcareous soils. Smiley (1974) found that lime buffered soil against pH changes caused by nitrogen uptake, but Stark (1973) and Hanawalt and Whittaker (1977) found that an acid soil extract represented plant-available nutrients better than neutral extracts.

Van Egmond and Aktas (1977) reported that Fe-efficient soybeans excrete more H^+ into the medium than do Fe-inefficient varieties. However, we found no correlation between soil pH and leaf Fe variables.

Larrea tridentata should certainly be considered an Fe-efficient species. The negative correlation between leaf Fe and plant size may be explained in several ways, but it is not consistent with suggestions of Fe deficiency affecting size. Indeed, the correlation reflected a cause-effect relationship, and Fe toxicity would be indicated.

Iron uptake, translocation, and physiology have been extensively studied, but may still be characterized as poorly understood (Thorne and Wallace 1944, Brown 1956, Khadr and Wallace 1964, Brown and Ambler 1974, Jones 1976). A frequent observation has been an association of Fe with K uptake (Thorne and Wallace 1944, Brown 1956, Hernando and Sanfuentes 1976). In this study we found correlation of leaf Fe variables with both leaf K and *L. tridentata* biomass, but not between biomass and leaf K. The strong negative association of meta Fe with both leaf K and sum of cations are consistent with the hypothesis that lime-induced chlorosis is related to cation-anion balance and internal leaf pH (Wallace et al. 1976). The positive correlation of leaf Zn with sum of cations ($r = +0.50$), and the negative correlation of meta Fe ($r = -0.56$) suggest an Fe-Zn interaction.

One implication of these findings is that the Fe nutrition of *L. tridentata* growing on calcareous soils is similar to, but different in degree from, that of species exhibiting lime-induced chlorosis.

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RETRANSLOCATION OF TAGGED CARBON IN *AMBROSIA DUMOSA*

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ABSTRACT.— *Ambrosia dumosa* (A. Gray) Payne cuttings grown in solution culture were exposed to $^{14}CO_2$ to measure the distribution of labeled photosynthate among leaves, stems, and roots after 4, 24, and 48 h. For all sampling periods, the highest levels of ^{14}C were found in leaves and the lowest in roots; however, considerable ^{14}C had moved to roots in 48 h. In a 12-week study of *A. dumosa* in solution culture, plants increased in size more than 17 times and flowered and produced seeds. The plants had received $^{14}CO_2$ in photosynthesis at the start. The gradual loss of ^{14}C from the plants in the 12 weeks averaged 3.5 percent per week (coefficient of variation = 58 percent). This represents an average respiration rate of 0.21 mg C g dry weight^{-1} h^{-1}. This compares favorably with other means for determining respiration rate. The percentage of ^{14}C in the root portion of the plant varied little over 6 sampling periods, indicating that essentially none of the initially fixed ^{14}C left the roots during the 12 weeks of test. The ^{14}C entering fruits and seeds came from leaves only. The biomass of fruit parts resulted more from new photosynthate than from retranslocation from leaves. In a study in which *A. dumosa* plants were defoliated, little ^{14}C moved from roots to new shoot growth.

The United States International Biological Program Desert Biome has concentrated considerable research effort in studies of the carbon cycle. Certain questions could not be answered easily by conventional procedures, but tagging of plants with ^{14}C in photosynthesis was one means of obtaining answers for some questions (Wallace et al. 1979, Vollmer et al. 1975, 1976). Among the questions of concern were the following: Does carbon move from leaves to roots continuously, or as a pulse from that which has been newly fixed? Does carbon in roots contribute to new shoot growth? Does carbon in leaves or stems and/or roots contribute to fruit growth? What is the rate of carbon loss due to respiration? These questions could be approached with the ^{14}C technique under controlled conditions.

MATERIALS AND METHODS

Ambrosia dumosa (A. Gray) Payne cuttings were grown for 30 days in solution culture in a glasshouse, at which time the shoots were about 15 cm tall. The shoots were then exposed to $^{14}CO_2$ (about 5 uCi/plant) in plastic bags for 2 h. Two plants each were separated into leaves, stems, and roots after 4, 24, and 48 h. The methods generally were like those previously used (Bamberg et al. 1975).

Two-month-old *A. dumosa* cuttings growing in 3700 ml nutrient solutions in a glasshouse were exposed to $^{14}CO_2$ by the general procedures described above. Three plants were separated into plant parts for ^{14}C determination after 24 h, 1 week, 2 weeks, 4 weeks, 8 weeks, and 12 weeks to determine changes in distribution with time.

To ascertain movement of previously fixed ^{14}C from crown and root materials to shoots, an experiment was conducted in which four *A. dumosa* plants, each growing in 1600 g soil, were exposed to $^{14}CO_2$ as above. Leaves of the plants were sampled at 2 h and 24 h. After 48 h the shoots of the plants were cut off. The shoots were allowed to regrow and at 78 days the plants were removed from the soil and separated into parts, including fine roots separated by salt-flotation with $MgSO_4$. All plant parts were counted for ^{14}C by Q-gas counting.

RESULTS AND DISCUSSION

Table 1 shows the distribution of ^{14}C in leaves, stems, and roots of *A. dumosa* plants at 4, 24, and 48 h after labeling. Most of the

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label was confined to the leaves and stems, with only 4.7–7.4 percent going to the roots, even though they comprised 15–19 percent of the biomass. Changes with time in the percentage of ^{14}C in the different plant parts were not readily apparent, although the proportion of root ^{14}C might have increased slightly. As the experiment progressed, the amount of ^{14}C per unit weight decreased due to both dilution by new growth and respiratory loss. Roots maintained a relatively constant ^{14}C:weight ratio, but that of leaves and stems dropped sharply. This seems to indicate that most of the gains and losses of carbon during this 48-hour period occurred in the latter two structures or that dilution was involved.

Redistribution or reallocation of carbon in *A. dumosa* was studied over a 12-week period in a solution culture experiment (Table 2). Changes were followed over six different sampling times. The plants flowered and fruited during the test, which permitted a measure of mobility of the carbon from the initially fixed ^{14}C. Three plants were harvested at each time period for the measurement.

The plants increased in size over 17 times during the course of the 12-week experiment. The respiratory loss of the ^{14}C was relatively small. The estimates were about 9 percent at one week, 4 percent for 2 weeks, 14 percent for 4 weeks, 33 percent for 8 weeks, and 22 percent for 12 weeks. The irregularity of the values indicate variability. A normalized value for all five values results in 3.5 percent loss per week as an average. The standard deviation for the 3.5 percent value is 2.07 percent, with a coefficient of variation of 58 percent.

If this value (3.5 percent per week) represents a respiration rate, it would be 2.1×10^{-4} mg C mg dry weight^{-1}h^{-1} or 0.21 mg C g dry weight^{-1}h^{-1} at any point in the history of these plants. This compares fairly well for actual respiration measurements. It represents the respiration rate for the active growing stages and not for dormancy for this species (Vollmer et al. 1976).

The percentage of ^{14}C in the root portion

TABLE 1. Distribution of ^{14}C in *Ambrosia dumosa* grown in solution culture after tagging with $^{14}CO_2$ in photosynthesis.

Hours after labeling	Leaf	Stem	Root	Whole plant
		Dry weight, mg		
4	642	409	252	1303
24	1025	429	254	1708
48	1215	616	376	2207
		Percent plant parts by weight		
4	49.3	31.4	19.3	100
24	60.0	25.1	14.9	100
48	55.1	27.9	17.0	100
		cpm/plant part (× 1000)		
4	424	159	25.2	608
24	437	145	35.3	617
48	366	147	51.0	554
		Percent of ^{14}C in plant parts		
4	69.7	26.2	4.1	100
24	70.8	23.5	5.7	100
48	66.1	26.5	7.4	100
		cpm/g (× 1000)		
4	660	389	100	467
24	427	339	139	362
48	301	240	109	251

of the plants varied little for the six sampling periods, even when seeds were produced. It was about the same at 24 h (5.1 percent) as at 12 weeks (5.8 percent). We may conclude, therefore, that the ^{14}C moved to roots only on the day of fixation. None left the roots thereafter during the 12 weeks of test. More dry matter than ^{14}C was moved to the fruiting parts and seeds, implying that most of the photosynthate used for fruiting was new. The ^{14}C that was translocated to seeds seemed to come from leaves only.

Redistribution of carbon in *A. dumosa* was further studied with plants grown in soil. Four plants exposed to $^{14}CO_2$ were defoliated after 2 days, and a portion of the stem was also removed. Any ^{14}C thereafter found in leaves and new stems had to be translocated from old parts. After 78 days following defoliation 8 percent of the ^{14}C was in the leaves, and 0.5 percent was in new stems with more than 57 percent in roots (Table 3). This indicates as in the other tests that ^{14}C is not readily moved from roots after initial fixation. The small amount of ^{14}C that did move to the leaves probably was mobilized when the leaves were initiated. At 78 days, 24 percent of the plant biomass was leaves with 8 percent of the ^{14}C. Thirty percent of the plant biomass was roots with 57.5 percent of the ^{14}C.

TABLE 2. Dry weight and distribution of dry weight and ^{14}C in plant parts at different times following exposure of *Ambrosia dumosa* to $^{14}CO_2$.

Plant part	2 h	1 week	2 weeks	4 weeks	8 weeks	12 weeks
			Dry weight, mg/plant			
Leaf	992	1,191	3,350	3,520	7,655	18,361
Stem	700	1,454	1,758	3,226	6,752	10,150
Transition	58	94	133	212	224	1,078
Root	190	397	576	890	2,304	2,555
Seed	—	—	—	2,023	2,673	1,816
Total	1,940	3,856	5,817	9,871	19,608	33,960
			cpm/g			
Leaf	553,267	274,933	163,347	109,760	41,950	18,990
Stem	338,980	124,540	109,673	61,447	20,240	17,910
Transition	72,695	62,120	91,013	34,860	26,020	16,780
Root	222,033	112,987	78,693	54,513	17,630	14,830
Seed	—	—	—	38,920	18,910	36,360
			cpm/plant			
Leaf	548,841	525,395	547,212	386,355	321,127	348,675
Stem	237,286	181,081	192,806	198,228	136,660	181,787
Transition	4,216	5,839	12,105	7,390	5,828	18,089
Root	42,186	44,856	45,327	48,516	40,620	37,891
Seed	—	—	—	78,735	50,546	66,030
			Dry weight/total plant weight (percent)			
Leaf	51.1	49.6	57.6	35.7	39.0	54.0
Stem	36.1	37.7	30.2	32.7	34.5	29.9
Root	9.8	10.3	9.9	9.0	11.8	7.5
Transition	3.0	2.4	2.3	2.1	1.1	3.2
Seed	0.0	0.0	0.0	20.5	13.6	5.4
Total	100.0	100.0	100.0	100.0	100.0	100.0
			cpm/plant (percent)			
Leaf	65.9	69.4	68.6	53.7	57.9	53.4
Stem	28.5	23.9	24.2	27.6	24.6	27.9
Transition	0.5	0.8	1.5	1.0	1.1	2.8
Root	5.1	5.9	5.7	6.8	7.3	5.8
Seed	0.0	0.0	0.0	10.9	9.1	10.1
Total	100.0	100.0	100.0	100.0	100.0	100.0

TABLE 3. Distribution of ^{14}C in *A. dumosa* plants 78 days after exposure of the shoots to $^{14}CO_2$ and 76 days after removal of all the leaves and the stems from the plants.*

Plant part	Dry wt g/plant	cpm/g	cpm/ plant	Percent dist.	SD of percent dist.	CV of percent dist, percent.
Leaves	2.02	610	1232	8.0	2.50	31
New stems	0.53	135	72	0.5	0.07	13
Old stems	2.53	1520	3846	24.9	7.31	29
Crown	0.82	1725	1415	9.1	6.03	66
Big root	0.37	2580	955	6.2	3.18	51
Small root	0.33	3525	1163	7.5	1.47	20
Fine root	1.82	3730	6789	43.8	11.78	27
Totals or means	8.42	1838	15472	100.0	—	—

*Leaf concentration of ^{14}C at 2, 24, and 48 h from exposure to $^{14}CO_2$ were 82,135, 39,670, and 37,230 cpm/g dry weight, respectively.

Leaf concentrations of ^{14}C at 2 h, 24 h, and 48 h from exposure to $^{14}CO_2$ (82,135, 39,630, and 37,230 cpm/g) indicated that either there was considerable loss due to dark respiration in this C-3 plant or that this period was the time in which translocation to roots primarily occurred.

It can be argued that these experiments under partially controlled conditions may not represent field conditions adequately. In the companion study with *Larrea tridentata* (Sesse & Moc ex DC.) Cov. in the field (Wallace et al. 1980), ^{14}C persisted in plants, especially in the roots, for more than three years after time of fixation.

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PERSISTENCE OF ^{14}C LABELED CARBON IN *LARREA TRIDENTATA* UP TO 40 MONTHS AFTER PHOTOSYNTHETIC FIXATION IN THE NORTHERN MOJAVE DESERT

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ABSTRACT.— *Larrea tridentata* (Sesse Moc. ex DC) Cov. exposed to $^{14}CO_2$ retained about 20 percent of its ^{14}C after 16 and also after 26 months. In leaves, however, a lower specific activity was present at 26 months than at 16 months, and a smaller percentage of ^{14}C in the plant occurred in leaves at 26 months than at 16 months (3 percent vs 10 percent). This indicates some, but little, reuse of carbon from the structural components of the plants. The strong tendency of the species to retain this carbon may be related to a survival mechanism. After 40 months the results were more erratic, with 11 percent of the ^{14}C remaining in plants and only 2 percent of the total remaining in the leaves. The specific activity of ^{14}C in the organic debris fraction obtained with saturated salt flotation of roots after small and fine roots had been physically removed indicated that from 27 to 35 percent of the organic debris had the same specific activity as roots and probably could be considered as roots. This compares with the 45 percent value determined previously by a different technique. The below-ground to aboveground ratio for biomass of these plants was about 2.5:1. The below-ground to above-ground ratio for the ^{14}C was about 0.5 at 16 months, 1.3 at 26 months, and 2.5 at 40 months. The estimates obtained in this study were used to correct our previous data for below-ground biomass. Accordingly, somewhere between 3000 and 5000 kg/ha roots are present in the Rock Valley area. An increase with time of the below-ground to aboveground ^{14}C ratio probably indicates loss of ^{14}C from above-ground parts rather than additional transport to roots.

One difficult aspect of plant studies in deserts is that of estimating below-ground biomass. Our previous studies have emphasized the magnitude of this problem (Bamberg et al. 1973, 1974, Vollmer et al. 1975, 1976, and Wallace, Bamberg, and Cha 1974), and it is further emphasized by the wide differences in below-ground biomass reported for the same area by different workers within our own group using different techniques of measurement.

Some approximations for root:shoot ratios in our studies for the northern Mojave Desert are near 1:1, but others approach 4:1. In the Great Basin Desert root:shoot ratios were reported that varied from around 8:1 to more than 12:1 (Caldwell and Camp 1974, Caldwell et al. 1974, Caldwell et al. 1976). The purpose of this study was to determine the persistence of ^{14}C labeled carbon in *Larrea tridentata* (Sesse & Moc. ex DC) Cov. and to further assess the problem of root biomass of this desert species.

MATERIALS AND METHODS

Plants in Mercury Valley, Nevada, were exposed to $^{14}CO_2$ with techniques previously used (Bamberg et al. 1973, 1974, Wallace et al. 1974). Six naturally growing *L. tridentata* were exposed to $^{14}CO_2$ for 2 h on the morning of 14 May 1974. Each plant was exposed to 125 uCi $^{14}CO_2$. Twigs were sampled at the end of this 2-h period for use in estimating the total $^{14}CO_2$ fixed by the plants. Two of these plants were excavated 16 months later on 17 September 1975 (Vollmer et al. 1975). Samples of all parts were then counted for ^{14}C by Q-gas technique and corrected for self absorption by methods reported previously (Bamberg et al. 1973). Two other plants were excavated on 16 July 1976, and the last two plants were excavated for analysis on 21 September 1977.

Soil from within a radius of 2.5 times the radius of the plant canopy was sampled for use in fine root biomass determinations. Soil

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samples (1 liter) were added to a saturated NaCl solution. Soil organic matter was separated by flotation and hand-sorted to obtain fine roots. The organic debris which could not be identified as roots was also separated. These samples were prepared and counted for ^{14}C. The roots were dried and ashed and found to contain 60–75 percent noncombustible ash. The high ash content was due to soil and salt contaminants adhering to roots. Root weights were normalized to 25 percent ash. The amount of roots in the soil surrounding the plants was estimated by extrapolating from small soil samples to the total volume of soils within a radius of 2.5 times the radius of the plant canopy to a depth of 30 cm. This method is similar to that employed by Bamberg et al. (1974) and Vollmer et al. (1975).

RESULTS AND DISCUSSION

Larrea tridentata that had been exposed to $^{14}CO_2$ 16 months previously at the Nevada Test Site retained about 20 percent of the ^{14}C that was originally fixed (Table 1). This amount was essentially unchanged at 26 months (Table 2). At 26 months, however, a lower specific activity was found in leaves than at 16 months, and a smaller percentage of the remaining ^{14}C was in the leaves at 26 months (3 percent) compared with 16 months (about 10 percent). This is indicative of low respiratory turnover and low remobilization of carbon from the structural components of this desert shrub.

Even though *L. tridentata* is evergreen, it does have turnover of leaves close to annually (Wallace and Romney 1972), so there would be a regular loss of ^{14}C in an experiment such as this. The loss would not be as great as the ^{14}C content of leaves, however, because of the retranslocation of around 50 percent of the carbon from the leaves to the shrub before leaf abscission. Except for leaves, we were unable to distinguish between the ^{14}C contents of the two sets of plants collected at 16 months and at 26 months. Because three annual phenological cycles are involved for the pair of plants harvested at 26 months and because somewhere around 20 percent of the original fixed ^{14}C was still in the plants similar to that at 16 months, a survival mechanism may be in-

TABLE 1. Plant biomass and ^{14}C content within a radius of 2.5 times the canopy radius on 17 September 1975 for two previously tagged (16 months) *Larrea tridentata*.

	Plant No. 1		Plant No. 4	
	Biomass (dry weight)			
	Grams	Percent	Grams	Percent
Leaves	30.3	8	38.2	8
Stems	118.5	20	90.9	19
Small roots (<1 mm)	52.1	—	80.1	—
Medium roots (1 to 3 mm)	109.0	—	164.0	—
Other roots	43.4	—	52.4	—
Total roots	204.5	52	296.5	61
Total roots*	245.4	62	355.8	73
Total	394.2	100	434.9	100

	Plant No. 1			Plant No. 4		
	^{14}C Content					
	cpm	Percent	cpm/g dry wt	cpm	Percent	cpm/g dry wt
May 1974	1,583,000	—	—	3,200,000	—	—
September 1976, total plant	283,300	100	751	481,700	100	1054
Leaves	23,100	8	762	72,100	15	1887
Stems	150,500	53	1270	211,400	44	2326
Roots	91,500	32	447	165,100	34	557
Total roots corrected for organic debris*	109,700	39	447	198,200	41	557

*Organic debris corrected to specific activity of roots. See Table 2.

volved. A high degree of conservation of carbon occurred.

The third pair of plants originally exposed to $^{14}CO_2$ in May of 1974 was sampled at approximately 40 months. Data are in Table 3. About 2 percent of the remaining ^{14}C was in leaves at this date. About 11 percent of the original ^{14}C fixed remained in the plants.

The information in Tables 1 to 3 has bearing on the below-ground to aboveground ratio of biomass and the below-ground annual productivity of shrubs. Workers from the Great Basin desert have found larger proportions of roots than we have for the Mojave Desert (Caldwell and Camp 1974, Caldwell et al. 1974, Caldwell et al. 1976). Our original estimate of below-ground to aboveground ratios were low (around 1) (Wallace, Bamberg, and Cha 1974). More recent estimates for the Mojave Desert were around 2 or 3 (Vollmer et al. 1976, Bamberg et al. 1974).

The biomass root/stem ratios for the two plants in Table 2 were 4.9 and 3.1; for ^{14}C the ratios were 1.9 and 1.1, respectively. The same values for the plant in Table 1 (16 months after labeling) were 2.1 and 3.9 for biomass and 0.7 and 0.9 for ^{14}C. The biomass root/stem ratios for the two plants sampled at 40 months were 6.0 and 7.6, and the ^{14}C ratios were 1.6 and 5.1. It appeared that the biomass ratio was slightly higher at 26 or 40 months than at 16 months and that the ^{14}C ratio generally increased as time passed by. Part of the difference, however, could be due to technique, and part may be due to loss of ^{14}C from aboveground parts with age.

The data in Table 2 further resolve the problem of whether or not organic debris floated from the soil samples with saturated solutions of salts should be considered as roots. Three factors relate to the problem. Such material is very high in ash because of the saturated salt and the soil contamination. Correction values are necessary. Not all sub-

TABLE 2. Plant biomass and ^{14}C content within a radius of 2.5 times the canopy radius on 16 July 1976 of two *Larrea tridentata* plants exposed to $^{14}CO_2$ 26 months previously at Mercury, Nevada (roots normalized to 25 percent ash).

	Plant No. 2		Plant No. 6	
	Biomass (dry weight)			
	Grams	Percent	Grams	Percent
Flowers	5.5	1.0	5.1	0.8
Leaves	37.7	6.7	49.8	8.0
Stems	88.1	15.7	138.8	22.2
Roots	333.3	59.4	320.1	51.1
Organic debris*	355.8	–	275.9	–
Corrected value of O.D.**	96.7	17.2	111.8	17.9
Total roots	430.0	76.6	431.9	69.0
Total	561.3	100.0	625.6	100

	Plant No. 2			Plant No. 6		
	^{14}C Content					
	cpm	Percent	cpm/g dry wt	cpm	Percent	cpm/g dry wt
14 May 1974	2,793,000	–	–	3,775,000	–	–
16 July 1976, total plant	595,200	100.0	120	701,500	100.0	1,121
Flowers	665	0.1	110	510	0.1	100
Leaves	15,000	2.5	398	22,900	3.3	460
Stems	201,500	33.9	2,287	325,300	46.3	2,344
Roots	293,000	49.2	879	261,500	37.3	817
Organic debris*	85,000	–	239	91,300	–	331
Corrected value of O.D.**	85,000	14.3	879	91,300	13.0	817
Total roots	378,000	63.5	879	352,800	563	817

*Organic material floated from soil with concentrated NaCl + normalized to 25 percent ash. Some of it may be a very fine fraction of roots.
**Organic debris corrected to specific activity of roots.

samples from soil about the ^{14}C-treated plants had ^{14}C in the organic debris floated from the soil samples, and such probably should not be considered as root material. In about 90 percent of the cases the fine roots contained ^{14}C, but only 10 percent of the organic debris samples contained the isotope. The specific activity of the ^{14}C in the organic debris is lower than that for roots (see Tables 1 and 2). Nonroot material then is involved to the extent of correction of weights to a constant specific activity as was done in Tables 1, 2, and 3. This, of course, could be erroneous because the ^{14}C could arise from dead, partially decayed roots. The proportion of the organic debris not considered as roots then was 73 percent and 60 percent for the two shrubs in Table 2. Vollmer et al. (1975) had determined that 45 percent of the organic debris was roots and the results of the two studies do not differ greatly.

The ratio of weight of roots to aboveground parts in Tables 2 and 3 varied from about 1.6 to over 3 with the corrected values for roots. The average of all 4 cases was 2.5. The ratio of the root-shoot distribution of ^{14}C in the plants after the 26 months is also interesting (Table 1). The average ratio for the corrected root ^{14}C ratio was about 1.4. Neither the 2.5 nor the 1.4 ratio approach those found for Great Basin shrubs (Caldwell and Camp 1974). They do, however, indicate the presence of greater biomass below-ground than aboveground.

The root/stem ratio of 1.4 for ^{14}C from Table 2 is of further interest. After 26 months, more of the ^{14}C in the plants was below ground than above ground, which corresponds with the root weights. In our earlier studies (Wallace and Romney 1980, this volume) the ^{14}C ratio for root/stem was around 0.2 for the relatively short-time basis. The shift may be related to loss of ^{14}C-containing materials from shoots rather than to transport of more of it below ground. This would indicate that, over a period of years, there is a greater loss of aboveground parts than below-ground parts.

TABLE 3. Plant biomass and ^{14}C content within a radius of 2.5 times the canopy radius on 21 September 1976 of two *Larrea tridentata* plants exposed to $^{14}CO_2$ 40 months previously at Mercury, Nevada (roots normalized to 25 percent ash).

	Plant No. 3		Plant No. 5	
	Biomass (dry weight)			
	Grams	Percent	Grams	Percent
Leaves	59.3	9.0	52.1	11.6
Stems	86.2	13.1	46.1	10.0
Roots	247.3	37.4	206.3	45.9
Organic debris*	864.7***	–	428.2	–
Corrected value of O.D.**	267.0	40.5	145.2	32.3
Total root	514.3***	77.9	351.5	78.2
Total	659.8	100.0	449.7	100.0

	Plant No. 3			Plant No. 5		
	^{14}C Content					
	cpm	Percent	cpm/g dry wt	cpm	Percent	cpm/g dry wt
14 May 1974	3,049,000	–	–	5,985,000	–	–
21 Sept. 1977, total plant	220,300	100.0	333.9	825,600	100.0	
Leaves	6,000	2.7	100.2	13,600	1.7	261.0
Stems	82,000	37.2	951.3	133,600	16.2	2898.0
Roots	63,600	28.9	257.5	506,600	61.4	2455.6
Organic debris*	68,700	–	79.5	171,800	–	832.7
Corrected value of O.D.**	68,700	31.2	257.5	171,800	20.8	2455.6
Total roots	132,300	60.1	257.5	678,400	82.2	2455.6

*Organic material floated from soil with concentrated NaCl + normalized to 25 percent ash. Some of it may be a very fine fraction of roots.
**Organic debris corrected to specific activity of roots.
***Value is abnormally high because of a broken irrigation sprinkler nearby which resulted in much grass in the area.

In 1974, we made some estimates of root biomass for the northern Mojave Desert (Table 2 of Wallace et al. 1974). It would appear from the data reported here that the root values of the earlier study probably should be further corrected to include the root portion in the organic debris portion. An estimated correction factor is the corrected versus the uncorrected values in Table 1. These are 1.29 (430/333) and 1.35 (432–320) for weights of the two plants, and the values in Table 2 of Wallace et al. (1974) should be corrected by that amount (mean = 1.32). An interspace correction should also be made in that the 1974 samples were extended into the interspace soil only as far as we found roots. The development of a correction factor of 1.23 for interspace is given elsewhere, and the values for the earlier data are calculated in Table 4.

The twice-corrected values for root/stem in Table 4 is 1.73 and for root/root + stem is 0.63. These values are, of course, subject to errors, but they are still lower than comparable data from the Great Basin desert.

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TABLE 4. Estimates of standing stem and root weights for plot at Rock Valley (from a 0.46 km^2 plot). (Revised from Wallace et al. 1974.)

Species	No. of plants/ha	Calc. stem dry wt g/plant	Standard deviation of stem wt g/plant	Stem kg/ha	Root kg/ha	Root corrected for debris (1.32) kg/ha	Root corrected for interspace (1.23) kg/ha
Acamptopappus shockleyi	47	68.3	82.8	3.2	1.8	2.4	2.9
Atriplex confertifolia	75	33.7	32.8	2.5	1.1	1.5	1.8
Ephedra nevadensis	783	119.1	202.9	93.3	77.9	102.8	126.5
Eurotia lanata	478	62.7	96.9	30.0	27.0	35.0	43.8
Ambrosia dumosa	2394	108.7	111.0	260.2	301.0	397.3	488.7
Grayia spinosa	1196	74.3	85.8	88.9	64.0	84.5	103.9
Krameria parvifolia	1482	136.4	96.9	202.1	159.4	210.4	258.8
Larrea tridentata	1046	437.9	454.1	458.0	566.7	748.0	920.1
Larrea andersonii	710	171.2	244.3	263.7	220.1	290.5	357.4
Lycium pallidum	459	264.4	216.4	121.3	199.7	263.6	324.3
Total	8670	—	—	1523.3	1618.7	2136.6	2628.2

^{14}C DISTRIBUTION IN ROOTS FOLLOWING PHOTOSYNTHESIS OF THE LABEL IN PERENNIAL PLANTS IN THE NORTHERN MOJAVE DESERT

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Abstract.— In April and May of 1973, 24 individual plants were exposed to $^{14}CO_2$ with techniques used in our other studies in the field. Seven to 8 months later, part of the plants were excavated and counted by plant part for ^{14}C. The remainder of the plants were excavated at 13 months. The results indicated that from 3 to 20 percent of the carbon for leaves in the next year came from stems and roots of *Grayia spinosa* (Hook) Moq., *Ceratoides lanata* (Pursh) J. T. Howell, *Atriplex confertifolia* (Torr. & Frem.) S. Wats., *Lycium pallidum* Miers, *Ambrosia dumosa* (A. Gray) Payne, and *Acamptopappus shockleyi* A. Gray. Nearly all of the root segments were labeled at sampling time; however, some of the roots were labeled at higher amounts than others. Some roots had very little ^{14}C, and these are assumed to be very new roots rather than dead roots because of their small size. The roots with high levels of ^{14}C are assumed to be formed near the time of labeling, and those with low levels to be formed after the time of labeling. From 17 to 65 percent of the ^{14}C fixed was recovered after 7 to 13 months.

Introduction

^{14}C techniques have been used in studies of carbon allocation in desert plants and of root growth and distribution (Caldwell et al. 1974, 1975, 1976, Bamberg et al. 1973, 1974). One of the questions which arose in those studies is the nature of root labeling when a single labeled pulse is fixed in photosynthesis. Much can be deduced from the nature of carbon allocation according to the manner in which a single pulse of ^{14}C is distributed within the plant. The major purpose of this study was to determine the distribution of ^{14}C in individual roots and in segments of those roots following a single exposure to $^{14}CO_2$ of the shoots of plants growing in the desert. Another purpose was to ascertain the proportion of new growth in the springtime that arises from retranslocation from old parts of winter deciduous plants. The specific activity of ^{14}C in the new shoot growth compared with that in the old parts could result in an estimate of the portion of the new growth that is parasitic on the old parts versus the fraction which comes from new photosynthesis. It is recognized that this approach could only indicate a minimum of the fraction coming from old parts. The ^{14}C then would underestimate because it is not uniformly mixed with all the labile pool carbon. Another purpose in this study was to ascertain if new roots could be identified by absence in them of labeled ^{14}C in the year after its application.

Materials and Methods

In May 1973, 24 perennial plants in Rock Valley and Mercury Valley, Nevada, were exposed to $^{14}CO_2$ with the technique previously used in these studies (Bamberg et al. 1973, 1974, Wallace et al. 1974). Briefly, at about 0900, four *Ambrosia dumosa* (A. Gray) Payne plants were covered with transparent plastic bags of 2 mil thickness, and 125 uCi $^{14}CO_2$ were released into each bag. Considerable water vapor condensed on the inside of the bags. Two hours later the bags were removed, and leaf and stem samples were taken from each plant for determination by Q-gas counting of the amount of ^{14}C fixed, using the technique of Hendler (1959). All values were corrected to sample size of 50 mg. Counting efficiency with the procedure is of the order of 10 percent. Counting accuracy was made to a confidence level of 95 percent. The subsamples of leaves and twigs represented between 5 percent and 10 percent of all those on the plant, but for each subsample a precise number of leaves was collected and an accurate estimate of those remaining on the

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plant was made so that a reasonably accurate assessment of the total ^{14}C fixed by the plant could be determined. Part of these plants (approximately half) were removed from the soil and separated into individual roots, stems, and leaves in December 1973 and January 1974 (during the dormant season). The rest of the plants were removed in June 1974 and treated similarly. This sampling was after the spring new growth period. Activity of ^{14}C and weights of plant parts were obtained for all plants.

TABLE 1. ^{14}C status of plants from Mercury Valley, exposed to $^{14}CO_2$ in May 1973.

Species	Initial total ^{14}C fixed $\times 10^3$ cpm	% of ^{14}C remaining			
		Roots	Stems	Leaves	Total
Larrea tridentata	2529	10.3	14.7	12.8	37.8
Atriplex confertifolia	3340	3.0	18.9	18.4	40.3
Ambrosia dumosa	2095	5.2	7.1	4.3	16.6
Krameria parvifolia	622	14.1	51.7	0.0	65.8
Atriplex confertifolia	2051	2.9	21.8	11.2	35.9
Ambrosia dumosa	1621	9.7	53.9	0.7	64.3
Acamptopappus shockleyi	1343	7.6	45.8	0.0	53.4
Larrea tridentata	2690	11.8	16.1	8.3	36.2
Means	–	8.1	28.8	5.8	44.9
Larrea tridentata	835	7.3	7.6	4.9	19.8
Atriplex confertifolia	2600	3.5	20.5	5.7°	29.7
Ambrosia dumosa	914	5.2	41.8	8.9°	55.8
Ambrosia dumosa	2039	8.7	25.6	3.4°	37.7
Ambrosia dumosa	2022	ND	46.2	8.0°	ND
Acamptopappus shockleyi	1277	3.9	23.7	6.5°	34.0
Means	–	5.7	27.6	6.7°	35.3

°These values represent retranslocation from old stems and roots to new growth.
ND is not determined.
+ leaves were dead.

TABLE 2. ^{14}C status of plants from Rock Valley, Nevada, exposed to $^{14}CO_2$ in April 1973.

Species	Initial total ^{14}C x 10^3 cpm	% ^{14}C fixed remaining			
		Roots	Stems	Leaves	Total
L. andersonii	960	40.4	31.9	–	72.3
G. spinosa	999	26.9	34.2	–	61.1
C. lanata	2397	10.5	21.5	3.1	35.1
A. confertifolia	2092	7.9	12.7	10.7	42.3
L. pallidum	909	29.4	28.3	–	57.7
Mean	–	23.0	27.9	–	53.7
L. andersonii	988	26.9	29.5	1.3°	57.7
G. spinosa	1226	13.3	39.4	7.3°	60.0
C. lanata	1959	13.6	44.6	4.9°	63.1
A. confertifolia	2193	4.6	12.8	2.9°	20.3
L. pallidum	792	19.8	16.4	1.0°	37.2
Mean	–	15.6	28.5	4.0°	47.7

°These values represent retranslocation from old stems and roots to new growth following dormancy.

RESULTS AND DISCUSSION

The amount of $^{14}CO_2$ fixed in the 14 perennial plants exposed to $^{14}CO_2$ in Mercury Valley in May 1973 and the 10 in Rock Valley in April 1973, together with the distribution among plant parts in either December 1973 or May or June 1974, are in Tables 1 and 2. From 17 to 65 percent of the ^{14}C remained in the plants at sampling time, depending on time and location. This was the range for both 7 and 13 months at each of

Table 1 continued.

% relative distribution of ^{14}C			Dry wt g/plant			Root	g new leaves that could have come from roots or stems
Roots	Stems	Leaves	Roots	Stems	Leaves	root + stem %	
Excavated in December 1973							
27.2	38.9	33.9	21.0	21.2	8.8	49.8	—
7.4	46.9	45.7	20.2	44.2	45.4	31.4	—
31.3	42.8	25.9	45.9	69.9	10.0+	39.6	—
21.4	78.6	0.0	120.4	95.5	0.0	55.8	—
8.1	60.7	31.2	12.1	26.0	12.1	31.8	—
15.1	83.8	1.1	29.2	26.0	4.3	52.9	—
14.2	85.8	0.0	15.6	28.0	0.0	35.8	—
32.6	44.6	22.8	85.0	92.0	16.0	41.0	—
19.7	60.3	20.0	—	—	—	46.6	—
Excavated in June 1974							
36.9	38.4	24.7	128.8	122.7	62.0	51.2	15.3
11.7	69.0	19.2°	87.6	137.0	123.0	39.0	23.6°
9.3	74.9	15.9°	47.0	65.1	16.1	41.7	2.6°
23.1	67.9	9.0°	75.6	76.0	43.0	49.9	3.9°
ND	ND	ND	ND	70.0	37.9	ND	ND
11.5	69.7	19.1°	25.1	35.2	22.2	41.7	4.2°
18.5	64.0	17.5°	—	—	—	44.7	—

Table 2 continued.

% relative distribution of ^{14}C			Dry wt g/plant			Root	g new leaves that could have come from roots or stems
Roots	Stems	Leaves	Roots	Stems	Leaves	root + stem %	
Excavated in December 1973							
55.9	44.1	—	108.9	77.1	—	57.4	—
44.0	56.0	—	76.4	58.5	—	56.6	—
29.9	61.3	8.8	20.6	17.0	14.9	54.3	—
18.7	56.0	25.3	26.1	56.0	20.0	31.8	—
51.0	49.0	—	59.9	18.6	—	76.3	—
39.9	53.3	6.8	—	—	—	55.4	—
Excavated in May 1974							
46.6	51.1	2.3°	87.9	99.4	15.7	46.9	0.4°
22.2	65.0	12.2°	51.2	77.1	23.5	39.9	2.9°
21.6	70.7	7.8°	112.2	114.3	21.8	49.6	1.7
21.7	63.1	14.3°	40.4	58.7	25.3	40.8	3.6°
53.2	44.1	2.7°	147.6	36.3	5.7	80.3	0.2°
33.3	58.8	7.9°	—	—	—	51.5	—

the areas studied. These values are of interest. In a companion study with *Larrea tridentata* (Sesse & Moc. ex DC.) Cov., about 10 percent of the ^{14}C label remained in the plants 40 months after labeling. Losses each year would come through respiration, abscised leaves, and fruit production.

Small quantities (3 to 20 percent) of the ^{14}C remaining in the plants were present in the spring leaves of deciduous plants that had become defoliated in the fall and winter. This means that from 3 to 20 percent at least of the new leaf growth was derived from C coming from old stems and roots. The remainder came from new CO_2 fixation. Be-

TABLE 3. Distribution of ^{14}C in roots of plants from Mercury Valley, Nevada, excavated seven months following exposure of leaves to $^{14}CO_2$.

Larrea tridentata—Mercury Valley—December 1973 (2,690,000 cpm ^{14}C fixed)

Root	Depth from surface cm	Length of root, cm 0–10	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	90–100	100–110	Dry weight of roots g
		cpm/g dry weight											
Main	–	4580	8280	2740	2480	2080	1960						18.16
A	2	2640	2480	3220	3760	3800	3840	4080	5620				2.99
B	3	2500	2420	2740	2860	4300	4020	3780					4.61
C	2	760	920	1320	1300	1300							0.33
D	6	2720	2860	3140	3220	3340	3020	2840	2920				3.12
E	7	4000	3820	3780	3920	4600							0.54
F	2	2760	2460	2080	2100	2180	2020	1840					1.62
G	10	2220	2180	2120	2300	3040	2520	1960					4.11
H	3	3940	6050	8020	9040								1.65
I	8	2980	2900	3120	3300	3240	3080	3680	3840	3740	3600	3540	8.01
J	11	2280	2080	2240									2.09
K	9	6160	6380	6200	6680								1.97
L	3	4660	4520	2220	4040	4260	3640	3600	3500	3360			12.88
M	5	6680	6960	6560	6220	5520	5180						3.13
N	6	5340	4540	4420	4460	4280	4120	4180	4280				0.82

Miscellaneous and fine roots 1140 cpm/g dry wt (7.8 g); litter 4640 (23.4 g); leaves 13,920 (16.0 g); stems 4720 (92.0 g).

Atriplex confertifolia—Mercury Valley—December 1973 (3,340,000 cpm ^{14}C fixed)

Root	Depth from surface cm	Length of root, cm 0–10	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	Dry weight of roots g
		cpm/g dry weight									
Main	–	3440	2440	2460	2920	3880	4060				10.77
A	4	2400	2200								0.31
B	8	11020	13280	12100	13000	12560	13280	12980	12020	12050	0.19
C	8	6980	7000	8200	10580	10360	10220	11060	10200		0.15
D	6	22820	16800	14200	15420	16200	17000	15210	15280	19200	1.03
E	4	3080	3000	2980							0.30
F	22	1100	1220								0.27
G	20	5980	5820	5700	5600	5460					0.33
H	30	2100	2160	2170	2220						0.24
I	off D	720	780	720	340	220					0.34
J	27	2340	2200	2080	2610	2740					2.11
K	29	2040	1760	1780							0.11

Fine roots 4820 cpm/g dry wt (0.2 g); crown pieces 2100 (3.9 g); dead stump 200 (14.9g); miscellaneous roots 3000 (1.3 g); litter 9540 (30 g); leaves 13520 (45.4 g); stem 15420 (40.3 g).

Table 3 continued.

Ambrosia dumosa—Mercury Valley—December 1973 (1,621,000 cpm ^{14}C fixed)

Root	Depth from surface	Length of root, cm 0–10	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	90–100	Dry weight of roots
	cm	cpm/g dry weight										g
Main	–	5320	6340	6500	7820	4920						10.70
A	9	5840	6080	6160								0.19
B	9	8780	8080	7700	7280	5500	4820					0.99
C	9	5640	6800	5500	5580	6000	6440	5200	4860	6050	7640	4.51
D	11	4520	4960	5520	5500	5660	4320	4860	5620			2.56
E	18	5860	5960	5780	6200	6520						1.13
F	16	3820	4200	4620								0.71
G	19	1216										0.19
H	25	7140	7500	8460	5940							9.80

Miscellaneous and fine roots 2020 (3.6 g); litter 16540 (4.9 g); no leaves; stem 33600 (26.0 g).

Atriplex confertifolia—Mercury Valley—December 1973 (2,051,000 cpm ^{14}C fixed)

Root	Depth from surface	Length of root, cm 0–10	10–20	20–30	30–40	40–50	Dry weight of roots
	cm	cpm/g dry weight					g
Main	0	6720	4500	4960	5100	3900	6.91
A	4	8540	9480	17800			0.11
B	9	4240	6020	7433	7680	9000	0.33
C	11	4180	4020	3800	3720		0.87
D	25	3960	4020	4160			0.30

Miscellaneous and fine roots 2700 cpm/g dry wt (1.9 g); litter 13,680 (10.3 g); leaves 19,000 (12.1 g); stems 17,100 (26.0 g).

Ambrosia dumosa—Mercury Valley—December 1973 (2,095,000 cpm ^{14}C fixed)

Root	Depth from surface	Length of root, cm 0–10	10–20	20–30	30–40	Dry weight of roots
	cm	cpm/g dry weight				g
Main	–	1120	840	1220	720	25.28
A	6	2460				0.04
B	10	640	760	660		2.11
C	10	940	1080	1200		1.26
D	10	1800	1600	1580		0.78
E	10	1760	1800	2720		0.63
F	11	1140	1220	1300	760	0.60
G	13	1740	2440	2020		0.85
H	10	1640	1760	2020		0.99
I	15	3100	3840	4940		1.09
J	15	1900	1680	2220		0.58
K	17	860				0.13
L	20	200	120	100	20	1.24
M	20	1680	1960	1800	1860	0.81
N	25	100	20			0.24
O	25	160	100			0.20
P	27	500	398			0.47

Crown 1260 cpm/g dry wt (7.4 g); shoots 2880 (79.9 g); fine roots 1180 (2.3 g)

Table 3 continued.

Larrea tridentata—Mercury Valley—December 1973 (2,529,000 cpm ^{14}C fixed)

Root	Depth from surface cm	Length of root, cm 0–10	10–20	20–30	30–40	40–50	50–60	60–70
		cpm/g dry weight						
Main	—	14600	9900	3580				
A	1/2	67380	6360	2440				
A_1	1/10	9360	500		2020			
A_2	1/10	5940	740					
B	2/10	13540	6900	5240				
C	1/2	3660	2100					
D	1	21040	20620	22320	15280			
E	1/2	—	—	(not counted)				
F	3	500						
G	3	27660	23940	25120	23500	22580	23360	21560
H	13	8620	8020	9120	9000	10400		
I	20	9560	9240	9860	10720	9000	8420	

Root	Depth from surface cm	Length of root, cm 70–80	80–90	90–100	100–110	110–120	120–130	Dry weight of roots g
		cpm/g dry weight						
Main	—							7.16
A	1/10							0.67
A_1	1/10							0.10
A_2	1/2							0.17
B	2/10							0.26
C	1/2							0.16
D	1							0.72
E	1/2							0.36
F	3							0.09
G	3	21000	20280	21020	21600	21780	21760	3.50
H	13							0.72
I	20							1.87

Crown cpm/g dry wt 10,000 (2.3 g); leaf 36,860 (8.8 g); stem 18640 (21.2 g); fine roots 2740 (2.5 g).

Acamptopappus shockleyi—Mercury Valley—December 1973 (1,343,000 cpm ^{14}C fixed)

Root	Depth from surface cm	Length of root, cm 0–10	10–20	20–30	30–40	40–50	Dry weight of roots g
		cpm/g dry weight					
Main	—	4200	8660	3660			5.21
A	3	—	—	—	(not counted)		0.03
B	3	—	—	—	(not counted)		0.04
C	3	—	—	—	(not counted)		0.04
D	2	—	—	—	(not counted)		0.02
E	3	—			(not counted)		0.05
F	5	—	—	—	(not counted)		0.06
G	8	6220	5620	5420	5880	5600	1.37
H	7	14520	15220	18760			0.37
I	10	6660	8040	10060			0.73
J	10	6500	10900	8800			0.97
K	11	1560	1040	300			0.45
L	13	7880	8940				0.80
M	16	6660	9880	9860	23360		0.65
N	15	4600					0.25

Miscellaneous and fine roots 6540 (2.0 g); Litter 5760 (2.3 g); no leaves; stem 21980 (28.0 g).

Table 3 continued.

Krameria parvifolia—Mercury Valley—December 1973 (622,000 cpm ^{14}C fixed)

Root	Depth from surface	Length of root, cm 0–10	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	90–100
	cm	cpm/g dry weight									
Main	–	320	540	1360							
A	7	260	220	160	160	160	300	240	80	80	100
B	4	8280	8000								
C	3	12640									
D	10	980	820	680	780	1540	2010	3560	5920		
E	13	1100	620	400	340	120	40				
F	6	500	480	460	500	540	720	780			
G	14	1320	980	760	920	880	1080				
H	4	2560	2000	1460	1400	1480					
I	12	360	340	380	340	660	620	520	400	320	280
J	9	1260	1300	1720	1610	880	780	720	780	760	1160
K	12	700	620	540	600	700	760	900	2020		
L	10	740	740	780	700	720	680	720	960	1040	1020
M	7	340	280		420	680		220		300	180

Root	Depth from surface	Length of root, cm 100–110	110–120	120–130	130–140	160–170	170–180	180–190	200–250	250–300	Dry weight of roots g
	cm	cpm/g dry weight									
Main	–										56.76
A	7										3.98
B	4										0.32
C	3										0.19
D	10										2.15
E	13										1.31
F	6										1.96
G	14										1.40
H	4										0.53
I	12										6.72
J	9	1160	1160								17.13
K	12										2.54
L	10	960									4.80
M	7		220	200	180	240	360	500	300	380	32.25

Litter 7060 cpm/g dry weight (18.8 g); miscellaneous and fine roots 660 (1.0 g); no leaves; stem 5980 (95.5 g).

tween December and May and June there seemed to be greater loss of the ^{14}C from roots than from leaves, but this may not be related to the transfer to the new leaves.

The distribution of the ^{14}C in segments of individual roots at sampling time, 7 to 13 months after exposure to $^{14}CO_2$, is in Tables 3 to 6. Although most roots were reasonably uniformly labeled for a given plant, some roots had higher activities than the majority and others were less labeled. The high specific activity of roots may represent roots being formed at the time of labeling, and the low specific activity roots may be those formed after the time of labeling. Usually, each root was uniformly labeled along its length with little indication of a pulse point.

It seems that old roots were labeled to some degree or other. Our expectation of finding new unlabeled roots was not fulfilled. New roots, like new leaves, seemed to have a fraction of their carbon coming from old plant parts so that they were labeled also. Old carbon then is at least in part labile in both stems and roots among the winter deciduous perennials. It may be less so in the evergreen *L. tridentata*, which seems to conserve carbon and use very little of it in new

TABLE 4. Distribution of ^{14}C in roots of plants from Mercury Valley, Nevada, excavated one year after exposure of leaves to $^{14}CO_2$.

Larrea tridentata No. 4—Mercury Valley—June 1974 (835,000 cpm ^{14}C fixed)

Root	Depth from surface	Length of root, cm 0–10	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90
	cm	cpm/g dry weight								
Main	–	340	160	280	260	200	160	180		
A	8	920	920	920	920	920	1000	1120	1320	1000
B	10	440	440	500	660	620	940	680	1160	1200
C	30	500	520	420	440					
D	30	240	200	160						
E	33	160	160							
F	33	200	200	320	480	500	640	700	720	680
F	39	560	520	360	140					

Root	Depth from surface	Length of root, cm 90–100	100–110	110–120	120–130	120–140	140–150	150–160	170–180	Dry weight of roots
	cm	cpm/g dry weight								g
Main	–									56.48
A	8	700	860	1040	920	800	940			28.03
B	10	1160	1100	1040	1000	860	800	800	680	7.00
C	30									1.14
D	30									0.97
E	33									0.39
F	33	640	500	280						13.00
F	39									0.45

Miscellaneous roots cpm/g dry wt 260 (5.0 g); leaves 660 (62.0 g); small stem 1000 (26.7 g); large stem 380 (96.0 g).

Atriplex confertifolia—Mercury Valley—June 1974 (2,600,000 cpm ^{14}C fixed)

Root	Depth from surface	Length of root, cm 0–10	10–20	20–30	30–40	40–50	50–60	60–70	Dry weight of roots
	cm	cpm/g dry weight							g
Main	–	1220	1980	1620	680	740	700		30.09
A	6	100	120						0.05
B	7	200							0.06
C	14	1760	1260	1520	1340				3.78
D	16	3080	2460	2900	2300	2400			0.40
E	16	680	500	510	120				0.55
F	18	1000	1780	1040	880	920			4.17
G	22	3800	3400	4200	3000				2.50
H	24	1200	860						0.42
I	22	1200	440						0.06
J	27	720	4450						0.09
K	27	1100	1940	1340	1120				0.32
L	21	1440	1140	1140	1020	1060	920	940	2.02
M	29	1100	1325						0.15
N	19	1200	800	660	720				2.15

Miscellaneous roots 1980 (3.9 g); leaves 1200 (123.0 g); stem 3520 (90.0 g); stem crown 20 (37.0 g); litter 2620 (83.0 g).

Ambrosia dumosa—Mercury Valley—June 1974 (2,039,000 cpm ^{14}C fixed)

Root	Depth from surface	Length of root, cm 0–10	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	Dry weight of roots
	cm	cpm/g dry weight									g

Table 4 continued.

Main	–	2300	2360	2700	1840	1440	1460	1160			32.57
A	8	5520	6080	7320							1.11
B	9	3280	4340	4960	5040						0.74
C	10	3400	4160								0.26
D	8	2500	2120	1180	2180	1400					4.14
E	12	2340	2240	2400	3600						1.69
F	12	4160	3900	2680	4700	4380	4700	4380			3.81
G	14	2380	2760	2820	2640	2320	2120	2460	3300		5.59
H	12	5380	5320	4980	4580	5300	4860	4540	5240	4460	3.35
I	13	680	520	540	700						1.77
J	14	1920	1540								0.45
K	18	2640	3000	3360	3340	3700	3200	2100			5.42
L	20	3520	2260	3160							1.41
M	25	1100	1240	1240	1060	1140					1.16
N	26	1480	1120	700	680	720	1360	1278			2.52

Miscellaneous roots cpm/g dry wt 1180 (1.0 g); leaves 1600 (43.0 g); small stem 9680 (27.6 g); large stem 5120 (48.4 g); litter 800 (5.3 g).

Acamptopappus shockleyi—Mercury Valley—June 1974 (1,277,000 cpm ^{14}C fixed)

Root	Depth from surface cm	Length of root, cm 0–10	10–20	20–30	30–40	40–50	50–60	60–70	Dry weight of roots g
		cpm/g dry weight							
Main	0	2020	1820	1720	2120	2340	2360		14.94
A	3	3930	3750	2000					0.05
B	4	2560	21000						0.04
C	5	980							0.08
D	6	1380	4000						0.07
E	5	4420							0.08
F	9	2520							0.04
G	20	1360	1300	1860	2780				0.70
H	20	2460	2680	3520					0.48
I	20	1000	960						0.30
J	20	1860	1640	2060	2320	3700	5720	5300	0.81
K	23	2120	2400	2400					0.42
L	26	2120	2740	2540	2820	3500			1.02

Miscellaneous roots cpm/g dry wt 2360 (1.7 g); miscellaneous roots 446 (0.7 g); leaves 3740 (22.2 g); small stems 9940 (15.0 g); large stems 7580 (20.1 g).

Ambrosia dumosa—Mercury Valley No. 7—June 1974 (914,000 cpm ^{14}C fixed)

Root	Depth from surface cm	Length of root, cm 0–10	10–20	20–30	30–40	40–50	50–60	60–70	Dry weight of roots g
		cpm/g dry weight							
Main	–	1420	1500	600	1020				16.68
A	10	480	880	900					1.36
B	9	1840	2060	2020					0.75
C	12	120	42						0.21
D	10	6091							0.08
E	13	1640	700	540					0.54
F	17	0	0	0	0				1.52
G	16	0	0	0	0				2.42
H	16	780	1000	760	420	240			4.45
I	18	860	900	800	560	720	660		2.65
J	16	1540	1480	1480	1120				2.65
K	16	1440	1300	1220	1220	1400	1500	2260	2.66
L	20	1260	1120	800	960	1780			0.24

Leaves 5040 cpm/g dry wt (16.1 g); small stems 22000 (15.9 g); large stems 4360 (49.2 g).

TABLE 5. Distribution of ^{14}C in roots of plants from Rock Valley, Nevada, excavated eight months following exposure to $^{14}CO_2$.

Ceratoides lanata—Rock Valley—December 1973 (2,397,000 cpm ^{14}C fixed)

Root	Depth from surface	Length of roots, cm 0–10	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	Dry weight of roots
	cm	cpm/g dry weight									g
Main	–	14280	12300	10940	7920	7960	10800	12320	5260	5200	8.08
A	3	30100	26400	27200	25800						0.09
B	5	17960	17200	18800							0.12
C	9	15820	17600	18200	20740	16800					0.23
D	10	19020	19600	18100	15210	15300					1.19
E	9	16980	18900	23100	27600	22800					0.26
F	11	10180	14600	14100	33800	30000					0.11
G	14	11040	11460	10980	12100	10160					0.82
H	15	12280	11160	10060	9920	8060	7600	7480	7300		1.85

Miscellaneous and fine roots 11000 cpm/g dry wt (5.2 g); stems 30380 (17.0 g); leaves 22420 (14.9 g); litter 4220 (14.9 g).

Atriplex confertifolia—Rock Valley—December 1973 (2,092,000 cpm ^{14}C fixed)

Root	Depth from surface	Length of root, cm 0–10	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	Dry weight of roots
	cm	cpm/g dry weight									g
Main	–	8200	4740								10.13
A	9	3660	3620	4260	4320						0.42
B	5	15260	9820	4860	4700	4720					0.38
C	13	1180	1300	1100	1200						0.17
D	17	2060	2125	1820	1700						0.46
E	18	40	20								0.11
F	20	6720	6000								0.35
G	18	8980	7210	6620	6240	6000	5920				1.09
H	18	4480	4162	3200	2080	3602	3200	4060	3980	5620	2.46
I	14	2760	3000	3700	3280	3620	2810	2300	2500		3.35

Litter 12720 cpm/g dry wt (13.3 g); miscellaneous and fine roots 4240 (3.8 g); stem 8860 (56.0 g); leaves 11220 (20.0 g).

Lycium pallidum—Rock Valley—December 1973 (909,000 cpm ^{14}C fixed)

Root	Depth from surface	Length of root, cm 0–10	10–20	20–30	30–40	40–50	50–60	60–70
	cm	cpm/g dry weight						
Main	–	3460	3780	4016	3910	3880	4520	4620
A	3	1660	1580					
B	6	1400	1400					
C	8	4120	2620	2420	1700	1680	1640	
D	8	2740	2700	1720	1700	420	302	
E	10	2810	2740					
F	12	6860	6600					
G	18	4440	4000	4300	4820	5060	4340	2800
H	33	1360	1400	1800				
I	40	4920	5420	7860	6040	3540	4040	4200
J	45	5560	4980					
K	55	5420	5210	5200	5000	4880		
L	36	7860	7520	7660	7840	7900	9500	9400

Table 5 continued. *Lycium pallidum* continued.

Root	Depth from surface cm	Length of root, cm 70–80	80–90	90–100	100–110	110–120	Dry weight of roots g
		cpm/g dry weight					
Main	–	5120	5000	4500	3020		28.50
A	3						0.09
B	6						0.23
C	8						0.65
D	8						0.45
E	10						0.08
F	12						0.12
G	18	2700					2.61
H	33						0.57
I	40	4460	4700	4640	3820	3700	7.63
J	45						0.17
K	55						1.19
L	36	9020	8300				1.56

Dead crown material 20 (68.4 g); live crown material 5400 (5.1 g); live roots 2800 (0.4 g); stems 4280 (13.5 g); litter 6180 (4.7 g); miscellaneous roots 2560 (7.9 g).

Grayia spinosa—Rock Valley—December 1973 (999,000 cpm ^{14}C fixed)

Root	Depth from surface cm	Length of root, cm 0–10	10–20	20–30	30–40	40–50	50–60	60–70	70–80	Dry weight of roots g
		cpm/g dry weight								
Main	–	4240	5140	3640	2560	2660				17.99
A	5	960	40							0.13
B	5	5120	3620	3500	3460	3480	3420	3460	3410	5.03
C	4	12280	11680	12100	11920	13400	16320			0.84
D	5	9840	8120	6600	5580	4440	4310	4014		3.86
E	13	9260	9410	9600	9980	9620	8240	9210	10460	2.26
F	5	23140	22160	21000	19800	19820				0.76
G	10	2660	2600	2560	2300	2160	3000	3500		0.41
H	15	60	60	0	0					0.20
I	19	5400	5480	5180	6900	7800				1.75
J	30	2720	2600	2580	2260	2020				1.41
K	40	2080	1960							0.25
L	38	2580								0.25
M	35	2280	2200	2420	2580	2620				3.17

Miscellaneous and fine roots cpm/g dry wt 1040 (2.8 g); litter 9580 (12.9 g); stem 5780 (55.8 g).

Lycium andersonii—Rock Valley—December 1973 (960,000 cpm ^{14}C fixed)

Root	Depth from surface cm	Length of root, cm 0–10	10–20	20–30	30–40	40–50	50–60	60–70	70–80
		cpm/g dry weight							
Main	–	1020	900	720	700	700	880	750	600
A	6	11320	11000	11900	12000	13320			
B	6	220	180	40	50	60			
C	16	3000	3000	3200	3100				
D	15	2140	2240	2060	2100	2300	2500	3060	2980
E	13	1260	1420	1740	1920	2320	3300	4260	
F	3	10280	8850	8170	6080	6280			
G	24	360	240	180	40	60	40		
H	4	2700	2680	2660	2640	2540	2400		
I	8	1820	1780	2060	2180	2400	2200	2160	
J	8	2860	2380	2000	2240	1900	3660		
K	3	5980	5400	4260	4820	5560	7900	8020	8140
L	3	5320	5100	6140	6320	7220	7260	8900	11020
M	10	11080	7820	6400	4840	4520			
N	3	60	80	80	140	240	180	320	180
O	20	160	100	100	80	0	40	200	360
P	5	2080	3000	4720	4700	4680	3800	3680	3700

Table 5 continued. *Lycium andersonii* continued.

Root	Depth from surface cm	Length of root, cm 80–90	90–100	100–110	110–120	120–130	130–140	140–150	Dry weight of roots g
		cpm/g dry weight							
Main	–	860	750	700	620	190	600	280	39.31
A	6								1.05
B	6								1.02
C	16								1.16
D	15	2620							2.63
E	13								5.57
F	3								0.48
G	24								4.14
H	4								1.05
I	8								5.45
J	8								1.27
K	3	9060	9960	13240					7.37
L	3	8000							2.62
M	10								0.24
N	3								10.73
O	20	100	80	60					2.47
P	5								3.05

Stem crown materials 2120 (34.3 g); dead main root 5020 (35.5 g); litter 1700; stem 4820 (42.8 g).

growth.

A summary of the numbers of roots found with low medium and high rates of labeling is given in Table 7. There were a few roots with high amounts of label at the tip or high label near the point of attachment to the main root. This is indicative of some pulse effect.

The fact that ^{14}C is uniformly distributed among different roots implies exchange and equilibrium.

TABLE 6. Distribution of ^{14}C in roots of plants from Rock Valley, Nevada, excavated one year after exposure of leaves to $^{14}CO_2$.

Root	Depth from surface cm	*Atriplex confertifolia*—Rock Valley—May 1974 (2,193,000 cpm ^{14}C fixed) Length of root, cm 0–10	10–20	20–30	30–40	40–50	50–60	60–70	70–80	Dry weight of roots g
		cpm/g dry weight								
Main	–	2660	3200	2140	1560	1440	1380			24.10
A	7	1009								0.08
B	10	1480	1840	1610						0.24
C	9	4370	6770	6200	6100	6000				0.19
D	9	8700	7670	10520	9370	17435	21200			0.26
E	8	1020	1230	1650	1920	2570				0.23
G	18	1620	3760	4840	8430	8080				0.96
H	7	1900	1740	1280	1200	1120	1020	1020	700	2.48
I	18	1240	1140	900	920	1180	1060	660		1.13
J	15	2560	2340	2100						0.49
K	13	6860	7060	8720	8500	6920	6700	6040		1.05
L	16	2460	880							0.33

Miscellaneous roots cpm/g dry wt 1340 (3.6 g); large stem 5340 (25.9 g); small stem 4380 (32.8 g); leaves 2540 (25.3 g); litter 10820 (13.8 g).

Table 6 continued.

Grayia spinosa—Rock Valley—May 1974 (1,226,000 cpm ^{14}C fixed)

Root	Depth from surface	Length of root, cm 0–10	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	90–100	Dry weight of roots
	cm	cpm/g dry weight										g
Main	—	2580	2260	1500	1660	1320	1300	1360	1480	1740	2320	20.98
A	5	3720	3520	3400	3460	3080	2545					1.17
B	4	2920	1740	5962								0.24
C	5	7830	3043									0.09
D	6	2310	1130									0.11
E	5	2840	1882	643	93							0.23
F	7	3820	3100	2920	2200	2400	2280	2300				9.94
G	5	8960	7960	5940	4980	3980	4620					4.60
H	11	3220	2840	3540	5820							0.93
I	9	4160	4500	2900								1.23
J	12	2680	2680	2340								1.20
K	13	3780	3040	2050								0.26
L	17	1700	1680	2060								0.42
M	21	1980	1300									0.20

Miscellaneous roots cpm/g dry wt 4320 (2.9 g); small stem 4200 (28.2 g); large stem 7440 (48.9 g); leaves 3780 (23.5 g); litter 160 (41.3 g).

Ceratoides lanata—Rock Valley—May 1974 (1,959,000 cpm ^{14}C fixed)

Root	Depth from surface	Length of root, cm 0–10	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	90–100	Dry weight of roots
	cm	cpm/g dry weight										g
Main	—	3500	2000									26.28
A	7	4000	4710	18040	4800	2080	1160					0.16
B	6	5350	8750	11120	2730	32900	1761					0.31
C	6	18740	19100	13300								0.34
D	10	2960	2660	1580	1420	1800	3020					0.77
E	10	2740	1240	1640	860	860						0.73
F	8	7220	6840	7760	7060	4900	4200	2900	3000	4200	3080	1.24
G	10	4890	6040	8640	25120	5590						0.19
H	9	5340	4720	6320	4740	4580	4460	3590				0.46
I	9	3320	3220	2020	2120	2420	1820	1840				2.86
J	8	18430	16400	11560	7150							0.25
K	10	12520	9060	8960	6580	6060						0.46
L	15	3880	2600	2680	3520							0.48
M	6	4980	3980	2080	1560	1820	940					1.21
N	8	3420	2200	2640	2640	1400						1.15
O	10	1760	2780	2740	3060							1.34
P	18	1380	1200	1100	880							0.95
Q	11	10120	8100	5540	4520							0.34
R	8	240	250	143	357	294						0.27
S	12	1960	1740	1920	1560	1560	1420					0.83
T	8	5440	4520	4780	4360	3520	3260					0.85
U	11	6180	4840	4080	3240	2280	2330					0.59
V	8	4340	3940	3100	4320							0.60
W	9	4960	4880	5380	6220	6580	6260	5480				0.70
X	15											
Y	8	1260	1160	1480	1210							0.25
Z	10	420	40	40								1.30

Other roots 1360 cpm/g dry wt (43.2 g); leaves 4440 (21.8 g); miscellaneous roots 2940 (9.6 g); small stem 10560 (59.9 g); large stem 4440 (54.4 g); litter 12,880 (1.1 g).

Table 6 continued.

Lycium pallidum—Rock Valley—May 1974 (792,000 cpm ^{14}C fixed)

Root	Depth from surface cm	Length of root, cm 0–10	10–20	20–30	30–40	40–50	50–60	60–70	70–80
		cpm/g dry weight							
Main	—	1400	620	300	600	700	700	720	720
A	10	1420	980	540	540	580	620	620	640
B	17	220	240	60	160	140	160		
C	2	280	200	160	220	220			
D	22	480	380	540	956	957	1675		
E	22	360	400	400	160	160			
F	20	200	375	160	100	120	191		
G	29	580	560	560	560	600	660	540	540
H	23	160	106	300					
I	25	220	180	180	120				
J	25	540	560	640	680	560	620	740	800
K	25	200	186						
L	26	240	240	260	260				
M	6 (large)	3680	2720	3740	4260	3580	3660	3340	3700
N	9 (off M)	1040	400	595	538				
O	4 (off M)	1880	1460	1120	1220				

Root	Depth from surface cm	Length of root, cm 80–90	90–100	100–110	110–120	120–130	130–140	Dry weight of roots g
		cpm/g dry weight						
Main	—	800	840	620	520	620	620	80.97
A	10	740	720					2.24
B	17							4.13
C	2							0.72
D	22							0.97
E	22							1.88
F	20							0.55
G	29	580	580					11.26
H	23							0.19
I	25							0.79
J	25	900	620					3.56
K	25							0.15
L	26							1.05
M	6 (large)	3800						14.52
N	9 (off M)							0.33
O	4 (off M)							0.77

Miscellaneous roots 140 cpm/g dry wt (4.2 g); dead crown 60 (62.7 g); small stem 4060 (5.4 g); large stem 3520 (30.9 g); leaves 1440 (5.7 g); litter 1420 (16.2 g).

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TABLE 7. Summary of labeling patterns of the roots from Table 5 and 6.

Species	Date sampled	No. of high S.A.** roots	No. of low S.A.** roots	No. of nonlabeled roots	No. of medium S.A.** roots
	Mercury Valley				
Larrea tridentata	Dec. 1973	3	5	0	7
Atriplex confertifolia	"	3	6	0	3
Ambrosia dumosa	"	0	1	0	8
Krameria parvifolia	"	2	9	1	2
Atriplex confertifolia	"	2	0	0	3
Ambrosia dumosa	"	1	3	2	11
Acamptopappus shockleyi	"	4	1	0	4
Larrea tridentata	"	5	1	0	4
Larrea tridentata	June 1974	0	5	3	0
Atriplex confertifolia	"	0	11	2	2
Ambrosia dumosa	"	0	2	3	8
Ambrosia dumosa	"	1	3	0	11
Acamptopappus shockelyi	"	0	3	0	10
	Rock Valley				
Lycium andersonii	Dec. 1973	5	2	4	5
Grayia spinosa	"	2	3	0	9
Ceratoides lanata	"	8	1	0	0
Atriplex confertifolia	"	2	0	1	
Lycium pallidum	"	2	5	0	7
Lycium andersonii	May 1974	0	4	1	11
Grayia spinosa	"	0	3	0	11
Ceratoides lanata	"	5	3	1	
Atriplex confertifolia	"	2	4	0	6
Lycium pallidum	"	0	5	3	8

*Some roots appeared to have a pulse or a demarcation in the distribution of the ^{14}C.
**S.A. is specific activity of ^{14}C.

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DISTRIBUTION OF PHOTOSYNTHETICALLY FIXED ^{14}C IN PERENNIAL PLANT SPECIES OF THE NORTHERN MOJAVE DESERT[1]

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ABSTRACT.— The distribution of photosynthate among plant parts subsequent to its production is needed to fully understand behavior of vegetation in any ecosystem. The present study, undertaken primarily to obtain information on transport of assimilates into roots of desert vegetation, was conducted in the northern Mojave Desert, where the mean annual rainfall is about 10 cm. Shoots of *Ambrosia dumosa* (A. Gray) Payne plants were exposed to $^{14}CO_2$ in 1971, and the distribution of ^{14}C in roots, stems, and leaves was subsequently measured at 1 week, 2 months, and 5 months. Only about 12 percent of the ^{14}C photosynthate was stored in the root. Much of that stored in stems was available for new leaf growth. Photosynthate was labeled with ^{14}C for 24 plants representing eight species in 1972. Results showed that after 127 days the mean percentage of ^{14}C in roots as compared with the estimate of that originally fixed was 11.8; the percentage in stems was 43.8. The mean ratio of root to root plus stem for ^{14}C was 0.212, but this value was only half that of the ratio for actual weights of these parts of field plants. The correlation coefficient for (^{14}C in roots)/(^{14}C in root + stem) × (dry wt of root)/(dry wt of root + stem) was +0.89. Small stems were the major storage organ for the ^{14}C. To check the validity of the ^{14}C data, root growth of eight perennial desert plants grown in the glasshouse was followed as plants increased in size. The mean percent of the whole plant that was root for eight species was 17.7 percent. The mean proportion of the increase in plant weights that went below ground for the eight species was 19.5 percent. This value is higher than the fraction of ^{14}C found below ground, and therefore the ^{14}C technique underestimates the movement of C to roots. Results of an experiment designed to test the value of the ^{14}C-pulse technique for determining current root growth for some perennial species from the desert indicated that the transition part of roots where root growth continued after exposure to ^{14}C was highly labeled. Old growth contained less ^{14}C than new growth.

The distribution of the products of photosynthesis among leaves, stems, roots, and reproductive parts must be understood if the dynamics of any plant community are to be known. Some data of this nature are available in the literature for desert plant species, but very little is quantitative (Cannon 1870, Dittmer 1964, Markle 1917). Jones and Hodgkinson (1970) give values for root and shoot weights of two *Atriplex* species. It is, of course, recognized that shoot-root ratios of plants and assimilate distribution vary with environmental conditions (Harris 1914, Kochenderfer 1973, Moore and West 1973, Wardlaw 1969).

The new photosynthate or assimilate in plants is subject to distribution among various plant parts, depending upon the phenological state. Such distribution is most likely under control of growth regulators (Richmond and Lange 1957). As phenological events change, some of the assimilate will become redistributed (Schmer and Knievel 1972, Moser 1977). The sinks for such redistribution are often known (fruiting, leaf, stem, or root growth), but the sources are often obscure (leaf, stem, root, or other). In the case of redistribution prior to leaf abscission, the source is known, but the sinks are more obscure. The sources of assimilate for new growth following dormancy or defoliation from mechanical means (grazing, wind, harvest, etc.) are also obscure. Even when the plant part that constitutes the source is known, there remains the question of what really involves available carbohydrates or other assimilates.

Several ^{14}C techniques have been developed recently to study assimilate distribution in plants. The pulse technique (Caldwell et

[1]Findings in this paper appeared, with several modifications, in The belowground ecosystem: a synthesis of plant-associated processes. Pages 303–310 *in* Range Science Department Science Series Report NA 26, Colorado State University, Fort Collins, 1977. We present these findings again for convenience and accessibility to readers interested in the several related papers in this volume.

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al. 1972, Wardlaw 1969), in which one or more foliar applications (pulses) of $^{14}CO_2$ are made and then two points of ^{14}C concentrations are looked for in the root systems, was partially evaluated under glasshouse conditions in the present study. The technique of foliar application of $^{14}CO_2$, in which gross distribution among leaves, stems, roots, and reproductive parts was measured (Gej 1972, Warembourg and Paul 1973, 1977), was also used. Techniques used elsewhere include foliar application of ^{14}C-urea (Clifford et al. 1973) and $^{14}CO_2$ labeling of specific leaves (Morooka and Kasai 1972). In the present study $^{14}CO_2$ was used to gain information on distribution of photosynthate and provide an estimate of annual primary productivity going below ground in perennial plants of a desert ecosystem.

MATERIALS AND METHODS

Photosynthate Distribution (^{14}C) in *Ambrosia dumosa* in 1971 in the Field

On 11 June 1971 about 0900, four *Ambrosia dumosa* (A. Gray) Payne plants in the northern Mojave Desert (1971 rainfall, 14.7 cm; 1972 rainfall, 11.8 cm) were covered with transparent plastic bags of 2 mil thickness, and 125 uCi $^{14}CO_2$ was released into each bag. Considerable water vapor condensed on the inside of the bags. Two hours later the bags were removed and leaf and stem samples were taken from each for determination by Q-gas counting of the amount of ^{14}C fixed. The technique for ^{14}C counting was that of Hendler (1959). All values were corrected to a sample size of 50 mg. Counting accuracy was made to a confidence level of 95 percent. The subsample of leaves and twigs was taken to represent between 5 and 10 percent of all those on the plant. A precise number of leaves was collected in each case, and an accurate estimate of those remaining on the plant was made so that a reasonably accurate assessment of the total ^{14}C fixed by the plants could be determined. Plants were excavated after 1 week, 2 months, and 5 months. Total ^{14}C present in small roots, large roots, small stems, large stems, and leaves was determined.

Photosynthate Distribution (^{14}C) in Eight Plant Species in 1972 in the Field

On 21 March 1972 and 27 March 1972, 24 individual plants representing eight species, *A. dumosa*, *Atriplex confertifolia* (Torr. & Frem.) Wats., *Lycium andersonii* A. Gray, *Larrea tridentata* (Sesse & Moc. ex DC.) Cov., *Atriplex canescens* (Pursh) Nutt., *Ephedra nevadensis* Wats., *Lycium pallidum* Miers, and *Ceratoides lanata* (Pursh) J. T. Howell, were exposed to $^{14}CO_2$ each for 2 h in the field as in 1971. Ten mCi ^{14}C in $NaHCO_3$ were present in 200 ml solution and 5 ml was used for each plant. The $^{14}CO_2$ (250 uCi) was released inside the plastic bag by pouring HCl into the $NaHCO_3$. After 126 to 127 days the plants were excavated and separated as before. At this time most of the leaves had abscised on the species which undergo summer dormancy.

Photosynthate Distribution Determined by Separation of Plants into Parts for Eight Plant Species Grown in a Glasshouse

Eight species of desert plants were propagated in the glasshouse in 1971, some by seedlings and others by cuttings, and planted individually into containers of Yolo loam soil (3.7 kg dry wt.). Nitrogen fertilizer (50 ug N/g as NH_4NO_3 monthly on dry weight of soil basis) was added, and the soil moisture tension was kept at around minus one-third bar during the study. The species employed were *A. canescens*, cuttings; *A. confertifolia*, cuttings; *Atriplex hymenelytra* (Torr.) Wats., cuttings; *E. nevadensis*, cuttings; *A. dumosa*, seedlings; *L. tridentata*, seedlings; *L. andersonii*, cuttings; *Lycium pallidum*, seedlings.

After about two months, individual plants were separated into leaves, stems, and roots at approximately two-week intervals to give a series of plants of different increasing sizes. Dry weights were determined, and the samples were counted for ^{14}C contents. The number of plants per species varied from six to eight replicates.

Evaluation of Pulse Technique for Measuring Root Growth

Glasshouse studies were undertaken in 1973 to evaluate the pulse technique (Wardlaw 1969) for measuring root growth following foliar fixation of $^{14}CO_2$. The idea is that a pulse of ^{14}C assimilate will be transported to the growing point of the roots and that this deposited ^{14}C mostly will not interchange with new assimilate being later transported to roots. Supposedly then, it would be possible to measure root growth extension from a given point in time by identifying that point with ^{14}C label. Also, it is believed possible that growth between two time intervals could be determined by using two separate pulses.

If roots produced annual growth rings, or if new assimilate exchanged with old materials, the technique would be of little value. To assess the utility of the pulse technique, plants were grown in solution culture with Hoagland nutrient solution. Eight species were grown in duplicate. These were *E. nevadensis, A. hymenelytra, Coleogyne ramosissima* Torr., *Atriplex cuneata* A. Nels., *Juncus mexicanus* Willd., *L. tridentata, L. pallidum,* and *A. dumosa.* Plastic bags were placed over the foliage and 5 uCi $^{14}CO_2$ was released into each. The roots were marked with black iron powder so that old and new root growth could be separated. After three weeks the amount of ^{14}C in new root growth in two increments as well as in other parts of the plants was determined by the procedures given above.

RESULTS AND DISCUSSION

Photosynthate Distribution (^{14}C) in *A. dumosa* in 1971 in the Field

In the 1971 ^{14}C-fixation study, the *A. dumosa* plants fixed about 4 percent of the ^{14}C supplied. Between the time of fixation and sampling dates, little of the ^{14}C seemed to have been lost to respiration because recovery after two months was around 90 percent of that originally fixed (Table 1). An interesting aspect of the data was the relatively low levels transferred to the roots (9.4 percent at one week; 12.3 percent at two months; 10.0 percent at five months). This contrasts with 80 percent found for grasslands by Dahlman (1968), Singh and Coleman (1977), and Warembourg and Paul (1973, 1977). The very low level with *A. dumosa* may indicate that the newly fixed ^{14}C is entering a carbohydrate pool before transport to roots, under which conditions the label would underestimate the amount of translocation of photosynthate to roots because of dilution in the pool.

The leaves of *A. dumosa* seemed to serve as a storage sink for some time, but the major storage sinks were twigs and stems (Table 1). *Ambrosia dumosa* is a deciduous plant, so that photosynthate remaining in leaves is lost to the plant at the time of leaf abscission. Stored reserves in the stems become mobilized and are used in early development of new growth when environmental conditions become favorable. In *A. dumosa* the time of new growth development depends mainly on adequate soil water and is somewhat independent of temperature (Wallace and Romney 1972).

The transport of about 10 percent of the ^{14}C label below ground in fieldgrown plants contrasts with the 16.3 percent of new growth of the glasshouse plants compartmented in roots (see below). For solution culture (see also below) the root/root + stem for ^{14}C was 8.2 percent and for dry weight 28 percent.

In the plant sampled 5 months after labeling with ^{14}C, 56 percent of the estimated $^{14}CO_2$ fixed was still present in the plant (Table 1). In addition to respiration losses and losses from abscised leaves, there were losses due to flowering and fruiting and possibly also to consumption by herbivores. A portion (13.5 percent of the 56 percent) was present in new leaves that had grown in response to a late summer rain. At this point the root to root plus stem ratio for the ^{14}C was 20.7 percent, which is considerably less than for the weights of field plants (53.6 percent) (Wallace et al. 1974). One possible indication is that biomass losses from stems (animal, weather) are greater than losses from roots. Root to root and stem dry weight ratios of old plants then would be higher than the same ratio for ^{14}C measured after a short pe-

riod. As mentioned previously, the mixing of ^{14}C in a carbohydrate pool before translocation is another possibility.

Photosynthate Distribution (^{14}C) in Eight Plant Species in 1972 in the Field

The 1972 data confirm the trend indicated by *A. dumosa* in the 1971 study (Table 2). In comparison with the estimated amount of ^{14}C originally fixed, the mean ^{14}C in roots for the eight species was 11.8 percent. It ranged from a low of 3.9 percent with *A. confertifolia* to a high of 22.3 percent for *L. pallidum*. These are the same species with low and high transport values for the glasshouse study (Table 3) and for root to root plus stem dry weight ratios from a field study (Wallace et al. 1974). The correlation coefficients for the root to root and stem ratios for ^{14}C and the ratios of weights for field plants (Wallace et al. 1974) was +0.89. Again the ratios for ^{14}C are much below those for weight. The hypotheses mentioned above for *A. dumosa* presumably apply to all the other species studied. That is, in the field biomass loss is greater for stems than for roots so that the measured ratio is greater than the ratio of new photosynthate distributed between stems and roots. Also there may be some exchange between the labeled assimilate and older carbohydrates due to presence of pools, particularly for *A. confertifolia*, although a large proportion of this species is leaves and seed or flowers.

The transfer to roots of ^{14}C was especially low in those species which retained a high proportion of leaves at time of sampling. This was pronounced for *A. confertifolia*, *A. ca-*

TABLE 1. Distribution of ^{14}C label of photosynthate in plant parts of *A. dumosa* (1971).

	1 week	2 months	5 months
cpm fixed (2 h)* per plant	2,600,000	2,400,000	2,700,000
% remaining	98	90	56
		g dry wt/plant	
Leaves	18.77	9.54	3.96**
Small stem	37.87	12.16	19.43
Large stem	27.99	42.97	25.12
Large roots	36.72	46.82	27.09
Small roots	6.33	8.02	6.38
	% distribution at sampling times of ^{14}C remaining in plant		
Leaves	57.0	22.2 ± 7.31	13.5**
Small stem	25.7	35.4 ± 8.37	43.3
Large stem	7.7	28.8 ± 14.31	25.3
Large roots	8.5	10.4 ± 1.77	15.6
Small roots	1.1	3.2 ± 0.15	2.3
Total	100.0	100.0	100.0
	% of original fixed ^{14}C in stems and roots at sampling times		
Small stem	25.3	31.9 ± 7.5	24.2
Large stem	7.6	25.9 ± 12.9	14.2
Large roots	8.3	9.4 ± 1.6	8.7
Small roots	1.1	2.9 ± 0.14	1.3
Total roots	9.4	12.3	10.0
		^{14}C in stems/^{14}C in roots (ratio)	
	3.50	4.90	3.84
		^{14}C root/root + stem (%)	
	22.2	17.5	20.7

± is plus or minus the standard deviation.
*cpm fixed at 50 mg counting wt
**Original leaves had abscised and a new flush of leaves had grown in response to late summer rain, but some of these leaves had abscised also.

nescens, C. lanata, and *L. tridentata,* in which the mean was 7.1 percent. The mean for ^{14}C found in roots for the other four species was 16.5 percent. The latter may be the more accurate estimate for distribution of new photosynthate below ground for the time period involved. Perhaps a longer time would be needed to evaluate root transport for the evergreen or near evergreen species. Also, temperature and soil water may change transport of assimilates (Schmer and Knievel 1972, Wardlaw 1969). Phenology conditions may also induce transport to roots at later dates.

From the various studies made, it seems possible that only 10 to 20 percent (sometimes less) of the annual photosynthate goes into the root systems. Considering, however, that there are aboveground losses to respiration, herbivores, leaf abscission, wind, flowering, and fruiting, the estimates may be realistic. Net standing biomass of aboveground and below-ground structural plant parts is close to 2.5:1 (Wallace et al. 1980, this volume) in

TABLE 2. Distribution of ^{14}C label of photosynthate in parts of field-grown plants (1972) (after 126 or 127 days).

	Species							
	Ambrosia dumosa	*Atriplex confertifolia*	*Lycium pallidum*	*Lycium andersonii*	*Larrea tridentata*	*Atriplex canescens*	*Ceratoides lanata*	*Ephedra nevadensis*
Number of plants	4	4	4	2	2	2	3	3
^{14}C fixed in 2 h (10^6 Cpm/plant)	3.637	4.411	4.127	3.297	1.046	4.558	4.488	1.643
% remaining at sampling	63.5	86.6	66.2	66.5	77.6	78.5	78.2	90.4
	g dry wt/plant at sampling time							
Leaves	10.9	30.1	1.6	0.0	6.4	39.4	13.4	–
Large stems	48.5	15.8	18.7	22.3	3.2	39.7	11.8	–
Small stems	59.8	16.4	16.1	31.5	3.0	38.7	22.9	–
Roots	118.4	14.7	62.2	25.0	4.2	29.5	9.7	82.4
	^{14}C in plant parts at sampling (10^6 cpm/plant)							
Leaves	0.50	2.41	0.11	0.0	0.36	1.79	0.79	–
Stems	1.24	1.24	1.70	1.76	0.34	1.39	2.48	1.24
Roots	0.56	0.173	0.92	0.43	0.11	0.40	0.24	0.25
	Final distribution of ^{14}C in stems and roots (%)							
^{14}C fixed in 2 h (10^6 Cpm/plant)	20.3	19.7	23.3	17.4	26.5	38.9	15.3	16.2
Small stem	48.7	68.0	41.6	63.0	48.7	38.8	75.9	67.1
Large root	19.7	7.2	23.3	11.0	12.2	13.4	4.8	7.7
Small root	11.3	5.1	11.8	8.6	12.6	8.9	4.0	9.0
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
^{14}C roots* / ^{14}C root + stem	0.310	0.122	0.351	0.196	0.244	0.224	0.087	0.168
	Percentage of original fixed ^{14}C in roots or stem at harvest time							
Stem	34.2	28.1	41.2	53.4	32.5	30.5	55.3	75.5
Roots	15.4	3.9	22.3	13.0	10.5	8.8	5.3	15.2

*Correlation coefficient of $\frac{^{14}C \text{ in roots}}{^{14}C \text{ in root + stem}} \times \frac{\text{g root}}{\text{g root + g stem}}$ in field = +0.89.

spite of the low percentage of new assimilate going below ground. Small stems (twigs) may constitute the major storage site for carbon in these desert plants. The 1971 and 1972 years resulted in relatively little biomass production because of limited rainfall. This may affect the proportion of photosynthate being transported and stored in various plant organs and that lost through reproductive proportions being stored below ground.

Photosynthate Distribution Determined by Separation of Plants into Parts for Eight Plant Species Grown in a Glasshouse

In the glasshouse study on roots, the percentage increase in dry root weight compared with the percentage increase in total weight as plants increased in size indicated a mean percentage of new growth going below ground of 19.5 percent (Table 3). Highest value was for *L. pallidum* (33.7 percent) and lowest was for *A. confertifolia* (4.7 percent). In a companion field study with eight species, the highest root to root plus stem ratio was for *L. pallidum* (62.2 percent), and the lowest was for *A. confertifolia* (29.9 percent) (Wallace et al. 1974). The correlation coefficient between the ratios in Table 3 and the root to root plus stem ratio for the field (last column in Table 3) was + 0.98.

Evaluation of Pulse Technique for Measuring Root Growth

The results of the glasshouse ^{14}C studies of plants in solution culture revealed that the pulse technique (Wardlaw 1969) may have some value in providing an estimate of current root growth (Table 4). There was a hot spot at the transition zone where growth continued after the date of exposure to ^{14}C. The ^{14}C, at least for the three weeks of the study after exposure to $^{14}CO_2$, continued to be transported to the new roots. It is possible that this would not continue indefinitely, but even so there definitely would not be a completely sharp demarcation between roots grown before and after the date of labeling because both old and new growth contained ^{14}C. Carbohydrate pools, exchange among carbohydrates, as well as root developmental biology must be better understood to evaluate such techniques. Caldwell et al. (1972) came to similar conclusions. The root/root + shoot ratio was generally much higher for dry matter than for ^{14}C (Table 4). This indicates that $^{14}CO_2$ may not be an accurate means of determining below-ground biomass.

CONCLUSIONS

The studies indicate that, as an average, somewhere around 10 to 20 percent of the carbon fixed by the perennial shrubs in the northern Mojave Desert was subsequently found below ground after a few months. Two different techniques gave close to the same results, although actual weighing of parts of plants grown under semicontrolled conditions gave higher values for transport to roots than did the ^{14}C procedure. Possible reasons for ^{14}C to underestimate the amount of below-ground transport may be the mixing of ^{14}C pools of carbon, so that the amount transported would be diluted in its content of ^{14}C and also the loss of roots in sampling.

The closeness of the two methods indicates that the proportion of the carbon fixed in photosynthesis in these woody plants that is transported below ground is much less than 50 percent, although for the standing biomass of these species 50 percent or more of it is below ground (Wallace et al. 1974). The differences, however, are not difficult to reconcile because the processes of respiration, flowering, fruiting, leaf abscission, harvesting by herbivores, etc., are constantly causing losses of carbon. In the Great Basin desert, Bjerregaard (1971) found much higher values for below-ground standing biomass than those found by us for the northern Mojave Desert. Grazing has occurred recently in that desert, however, but there has been no grazing in our study site for over three decades, and this may be an important factor in the differences.

Best answers for the questions of partitioning of photosynthate to below ground or to root, perhaps, can be obtained from field studies in which new seedlings are monitored for gas exchange (Koller 1970) for some years and for losses of carbon due to phenological

TABLE 3. Root, stem and leaf relationships for the plants grown in the glasshouse.

	No. of plants	Root	Stem	Leaf
		% distribution		
A. dumosa	9	20.5	44.4	35.1
E. nevadensis	10	14.5	85.5	—
A. hymenelytra	6	19.3	27.7	53.0
A. confertifolia	8	4.3	30.9	64.8
A. canescens	7	12.0	41.8	46.2
L. pallidum	9	26.3	59.3	14.4
L. andersonii	7	21.9	73.0	5.1
L. tridentata	7	23.5	39.6	36.9
Means		17.7		

*Calculated by using the smallest plant as the base.

**C.V. is coefficient of variation of $\frac{\text{root}}{\text{root + stem}}$

***Reference (Wallace et al. 1974).

events or harvesting. After several years the plants could be excavated and below-ground parts measured. If root losses due to soil fauna were minimal, then below-ground transport could be estimated fairly accurately for field conditions. Such experiments would be costly, however, and would require several years. We did a study slightly like this for 40 months (Wallace et al. 1980, this volume). The present estimates, although crude, perhaps would serve most purposes.

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Table 3 continued.

Mean increase dry wt in roots*	Root	Stem	Root / root + stem		C.V.**	Root*** / root + stem (field data)
% in root	g	g	%	SEM	%	%
% in whole plant						
26.4	5.33	10.43	33.8	3.01	26.7	53.6
13.2	1.03	6.08	14.5	0.68	14.8	45.5
19.5	4.52	6.47	41.1	2.57	15.3	–
4.7	1.19	8.59	12.2	1.66	38.4	29.9
12.7	3.15	11.77	21.1	2.01	25.2	40.2
33.7	5.74	12.91	30.8	1.96	19.1	62.2
20.9	6.56	19.20	25.5	2.72	28.1	45.5
25.0	4.78	8.07	37.2	2.94	20.9	55.3
19.5						

TABLE 4. Distribution of foliar absorbed ^{14}C from plants grown in solution culture after new roots had developed three weeks after the $^{14}CO_2$ application.

Species	Leaf	Stem	Root old	Root transition*	Root new	*Root* root + stem ratio
	cpm ^{14}C/g dry wt					
Ephedra nevadensis	9880**	–	380	640	600	0.013
Atriplex hymenelytra	69120	9920	580	2780	1300	0.063
Coleogyne ramosissima	65520	8580	680	2280	800	0.073
Atriplex cuneata	30360	28940	13840	34720	29000	0.352
Juncus mexicanus	15700**		7040	36940	18240	0.451
Larrea tridentata	28180	10240	2700	3040	2080	0.043
Lycium pallidum	43260	6440	1760	34400	34160	0.092
Ambrosia dumosa	20860	13140	1960	14820	7980	0.082
	g dry wt/plant part					
Ephedra nevadensis	17.42**	–	2.06	1.26	0.916	0.21
Atriplex hymenelytra	1.61	1.10	1.01	0.039	0.030	0.50
Coleogyne ramosissima	0.72	1.04	1.09	0.025	0.022	0.52
Atriplex cuneata	1.79	0.63	0.56	0.031	0.037	0.50
Juncus mexicanus	9.02**	–	6.29	0.201	0.029	0.42
Larrea tridentata	3.29	7.95	1.06	0.202	0.089	0.15
Lycium pallidum	1.45	11.51	2.63	0.038	0.046	0.19
Ambrosia dumosa	4.33	5.28	1.85	0.132	0.081	0.28

*New root growth adjacent to the old.
**Mostly stem tissue.

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DEPTH DISTRIBUTION OF ROOTS OF SOME PERENNIAL PLANTS IN THE NEVADA TEST SITE AREA OF THE NORTHERN MOJAVE DESERT

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ABSTRACT.— The root systems of 48 perennial plants, representing nine species from the Rock Valley area within the northern Mojave Desert, were excavated by 10 cm depth increments to determine, by depth of soil, the distribution of roots larger than about ½ mm diameter. The depth of the root zone of all species was relatively shallow and obviously limited by depth of penetration of precipitation (about 10 cm mean annual rainfall).

There were species differences, however, in distribution of roots. Even though a sizeable proportion of the root systems was in the first 10 cm of soil, this portion consisted largely of multiple woody tap roots with relatively few small roots. In all cases except one (*Krameria parvifolia* Benth), more small roots were in the second 10 cm than in the first. From 50 to more than 80 percent of the total root systems were in the first 20 cm. In most cases the majority of small roots was found between 10 and 30 cm in depth. Very fine roots were sampled separately by depth and zone without regard for species because they could not be differentiated by species. Relative depth distribution of very fine roots at Rock Valley for 0–10, 10–20, and 20–30 cm, was about 17, 42, and 41 percent, respectively. The total for the first 20 cm was 59 percent. On a 22 April date, there were 225 kg/ha roots from winter annuals in the Rock Valley area; 19 percent of them were in the first 5 cm of soil in contrast to 8 percent in 10 cm of soil for perennials. On Pahute Mesa located in the southern Great Basin desert area of the Nevada Test Site in *Artemisia tridentata* Nutt. var. *tridentata*, 8 percent of the roots was in the first 5 cm, indicating more shallow rooting compared with the northern Mojave Desert.

Any understanding of the role of soil on desert ecosystems requires that the distribution of plant roots in soil profiles be known. This investigation was to obtain some of this information. Rooting habits of desert plants in the western United States have been studied with conclusions that they generally are not deep-rooted unless they are in places where rain water accumulates (Cannon 1870, Dittmer 1964, Markle 1917, Waterman 1923). These workers recognized that depth of rooting was often limited by caliche layers near the soil surface or by unfavorable soil chemistry or soil physics. None of them, however, reported quantitative information on the amounts of roots at different depths. Consequently, the distribution with depth of roots of several major perennial plants in the Rock Valley area of the northern Mojave Desert was obtained.

MATERIALS AND METHODS

Root systems of 48 individual plants representing nine species were excavated during the spring and summer of 1972. The species, with numbers of individuals sampled, were: *Atriplex canescens* (Pursh) Nutt. (four-wing salt bush) (6), *Acamptopappus shockleyi* Gray (3), *Atriplex confertifolia* (Torr. & Frem.) Wats. (shadscale) (7), *Larrea tridentata* (Sesse & Moc. ex DC.) Cov. (creosote bush) (3), *Ephedra nevadensis* Wats. (Mormon tea) (7), *Lycium andersonii* A. Gray (wolfberry or desert thorn) (5), *Lycium pallidum* Miers (wolfberry or desert thorn) (6), *Krameria parvifolia* Benth. (3), *Ambrosia dumosa* (A. Gray) Payne (burro bush) (8). The numbers in parentheses refer to the number of plants excavated for each species. Nomenclature of the species follows Beatley (1976). These collections were made in connection with other studies that involve the shoot:root relationship of perennial desert plants in the field. The excavations were made by hand shovel and roots were separated by 10 cm depth increments.

The soil was carefully excavated for each plant and often 1 to 3 m^3 of soil was removed. The soil was not screened to remove

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TABLE 1. Distribution by depth of roots from nine perennial plant species collected from Rock Valley to northern Mojave Desert (values are percent of total root system).

Depth cm	*A. shockleyi* (3)	*L. tridentata* (3)	*L. andersonii* (5)	*L. pallidum* (6)
				Large roots
0–10	45.7 ± 9.4	24.4 ± 0.8	25.9 ± 5.4	27.5 ± 4.5
10–20	25.3 ± 7.5	25.4 ± 1.0	15.5 ± 3.6	28.3 ± 4.8
20–30	5.2 ± 2.9	12.6 ± 1.9	15.1 ± 2.6	9.8 ± 2.0
30–40	0.8 ± 0.8	7.0 ± 1.6	9.2 ± 2.0	5.4 ± 0.4
40–50	0.0	3.1 ± 2.2	8.7 ± 3.8	3.5 ± 1.6
Over 50	0.0	0.0	0.0	0.0
				Small roots
0–10	5.9 ± 1.6	2.1 ± 0.7	2.2 ± 0.8	2.9 ± 1.1
10–20	8.5 ± 6.1	8.3 ± 2.6	8.2 ± 2.0	10.5 ± 3.4
20–30	7.1 ± 6.4	7.2 ± 1.7	7.3 ± 1.7	6.5 ± 2.5
30–40	1.5 ± 1.5	4.1 ± 1.5	4.6 ± 1.2	3.2 ± 0.9
40–50	0.0	2.9 ± 1.8	3.1 ± 0.7	2.6 ± 1.1
Over 50	0.0	0.0	0.0	0.0
Percent of Total	23.0	24.6	25.5	25.7

± is standard error of mean.
Numbers in parentheses under species are number of plants in sample.

fine roots (smaller than about ½ mm) but sufficient soil was removed with each plant to obtain the large majority of the root system. We estimate that no more than 30 percent of the root system was missed and this mostly because of very fine roots that were handled separately. Plants were selected to give minimum interference to adjoining shrubs. The fine-root problem was handled as follows: In April and September 1976 at the Nevada Test Site, a series of soil samples 1 liter in volume each were collected on the patterns for samples used by Bamberg et al. (1974). The purpose was to estimate the fine roots and organic debris floated with conventional salts. Only a portion (35 percent) of the organic debris was considered as roots because that was the maximum possible according to our ^{14}C labeling techniques (Wallace et al. 1980, this volume).

RESULTS AND DISCUSSION

The mean weight of root systems of field plants, together with percentage distribution by depth with standard errors for each increment, are given in Table 1. Virtually all the root systems were distributed in the first 50 cm of soil. Most of the biomass was at depths more shallow than that. Means for the nine species showed 39 percent in the first 10 cm, 70 percent in the first 20 cm, 86 percent in the first 30 cm, and 95 percent in the first 40 cm. This shallow rooting is related to the sparcity of precipitation [mean annual is about 10 cm (Beatley 1967, Wallace and Romney 1972)] and with the presence of a caliche layer at 30 to 50 cm. Phenology of the species concerned over a four-year period has been reported (Wallace and Romney 1972) as has the behavior of winter annuals in the area (Beatley 1967).

The portion of the root system in the first 10 cm of soil, though relatively large, was mostly in the form of multiple taproots. Further evidence of this was the small proportion of small roots to total roots in this zone (mean was 3.2 percent for eight of the nine species compared with 8.7 percent for the second 10 cm). Most of the small roots were in the 10 to 30 cm zone. It can be expected that high temperatures of soil surfaces, together with the fact that soil surfaces are drier than lower horizons, are responsible for this behavior. These two factors would account for the sparsity of small roots in the first 10 cm of soil.

There were species differences in root distribution. *Acamptopappus shockleyi* and *K.*

Table 1 continued.

E. nevadensis (7)	*A. dumosa* (8)	*K. parvifolia* (8)	*A. canescens* (6)	*A. confertifolia* (7)
(above 2 mm)				
38.4 ± 5.3	24.8 ± 2.4	39.9 ± 3.3	39.8 ± 5.0	39.7 ± 6.1
19.7 ± 3.6	25.7 ± 2.2	20.1 ± 5.2	14.9 ± 2.2	16.1 ± 1.5
11.2 ± 2.0	10.4 ± 1.7	2.1 ± 2.1	10.6 ± 2.5	6.7 ± 1.5
5.2 ± 1.8	4.0 ± 1.6	2.0 ± 2.0	4.9 ± 1.8	2.8 ± 0.6
1.0 ± 0.4	1.7 ± 1.2	0.0	6.0 ± 2.0	1.4 ± 0.6
0.0	0.0	0.0	1.4 ± 1.4	1.2 ± 1.2
(2 mm or less)				
1.6 ± 1.0	2.9 ± 0.7	16.3 ± 7.7	3.4 ± 1.1	6.1 ± 1.1
5.7 ± 1.1	9.9 ± 1.9	14.3 ± 3.3	10.7 ± 2.6	10.0 ± 3.0
10.6 ± 3.3	6.4 ± 1.6	2.9 ± 2.9	8.4 ± 1.4	7.4 ± 1.6
5.4 ± 2.2	4.4 ± 0.8	2.5 ± 2.5	4.9 ± 1.4	5.6 ± 1.5
1.1 ± 0.5	1.4 ± 0.9	0.0	4.5 ± 1.2	2.4 ± 0.9
0.0	0.0	0.0	1.1 ± 0.7	0.6 ± 0.6
24.6	24.4	36.0	33.0	32.1

TABLE 2. Root sampling in Rock Valley, 22 April 1976, in typical *Lycium pallidum* dominated area, using the pattern of Bamberg et al. (1974a).

	Inter-space (80%)	In canopy (13.3%)	Under plant (6.7%)	Total (100%)
	kg/ha 0–10 cm			
Large roots*	—	—	—	—
Small roots	—	—	—	—
Fine roots	10	3	3	16
Fine roots in organic debris**	26	7	11	44
	kg/ha 10–20 cm			
Large roots*	105	—	32	137
Small roots	54	—	3	57
Fine roots	30	11	11	52
Fine roots in organic debris**	68	7	22	97
	kg/ha 20–30 cm			
Large roots*	143	14	7	164
Small roots	38	7	5	50
Fine roots	30	4	9	43
Fine roots in organic debris**	75	9	15	99
Totals	579	62	118	759
	kg/ha totals by depth			
0–10 cm	36	10	14	60
10–20 cm	257	18	68	343
20–30 cm	286	34	36	356

*The large tap and main branching roots were not included in the sample.

**The maximum amount of the organic debris obtained with salt flotation that would be considered as roots was 35 percent, a value determined with ^{14}C labeling (Wallace et al. 1980); value reported here takes that into account.

TABLE 3. Root sampling in Frenchman Flat, 22 April 1976, in typical *Ambrosia dumosa* dominated area, using the pattern of Bamberg et al. (1974a) (large roots not sampled).

	Inter-space (80%)	In canopy (13.3%)	Under plant (6.7%)	Total (100%)
	kg/ha 0–10 cm			
Large roots (3 mm)*	—	—	—	—
Small roots (1 to 3 mm)	—	—	—	—
Fine roots (< 1mm)	—	—	—	—
Fine roots in organic debris**	15	3	32	51
	kg/ha 10–20 cm			
Large roots*	—	—	—	—
Small roots	—	13	5	18
Fine roots	—	4	1	5
Fine roots in organic debris**	42	8	11	61
	kg/ha 20–30 cm			
Large roots*	—	25	14	39
Small roots	—	5	2	6
Fine roots	18	17	1	36
Fine roots in organic debris**	17	15	3	35
Totals	92	90	69	251

*See Table 2.
**See Table 2.

parvifolia were more shallow rooted than other species. More than 85 percent of the root systems for these two species was in the first 20 cm. Lower stems of *K. parvifolia* were usually covered with about 10 cm of blow sand because of the catchment nature of the shrub, so that roots actually were not as close to the surface as indicated. *Lycium andersonii* roots were more uniformly distributed throughout the root zone than most other species, although *L. pallidum* was somewhat similar. The two species that re-

TABLE 4. Root sampling in Mercury, 22 April 1976, in typical *Lycium andersonii* dominated area, using the pattern of Bamberg et al. (1974a).

	Inter-space (80%)	In canopy (13.3%)	Under plant (6.7%)	Total (100%)
	kg/ha 0–10 cm			
Large roots*	—	—	21	21
Small roots	—	—	4	4
Fine roots	17	—	4	21
Fine roots in organic debris**	18	12	87	117
	kg/ha 10–20 cm			
Large roots*	—	—	9	9
Small roots	—	—	7	7
Fine roots	51	2	7	60
Fine roots in organic debris**	84	5	48	137
	kg/ha 20–30 cm			
Large roots*	—	25	457	482
Small roots	—	5	60	65
Fine roots	27	17	22	66
Fine roots in organic debris**	53	15	75	143
Totals	250	81	801	1132

*See Table 2.
**See Table 2.

main photosynthetically active longer in the season than others (*L. tridentata* and *K. parvifolia*) were not too much unlike other plants, except for the shallow nature of *K. parvifolia* mentioned above. *Krameria parvifolia* had a greater proportion of small roots than did other species.

Depth distribution of the very fine roots for Rock Valley was in kg/ha, 60, 149, and 142 for 0–10, 10–20, and 10–30 cm, respectively (Table 2). This was not different from roots in general. The surface soils of the northern Mojave Desert are low in both large and fine roots, and this probably is related to high soil surface temperatures and low soil moisture of the summer months. This condition (few perennial roots in the surface 10 cm) does support a relatively large number of winter annuals after normal winter rainfall (Turner and McBrayer 1974).

Soil samples were also taken to measure primarily fine roots in Frenchman Flat and Mercury Valley by the procedures of Bamberg et al. (1974). These were not designed to collect the large and intermediate roots, although some appear in the samples (Tables 3 and 4). Indicated were 251 kg/ha for small and fine roots in the site in Frenchman Flat

TABLE 5. Depth distribution of roots from annual plants from different locations on the Nevada Test Site (collected 22 April 1976).

	100% of area, kg/ha			20% of area, kg/ha		
	Mercury	Frenchman Flat	Rock Valley	Mercury	Frenchman Flat	Rock Valley
	0–5 cm depth					
Litter	870	367	–	–	–	–
Large roots*	–	–	–	–	–	38
Small roots	–	–	25	–	–	5
Fine roots	–	–	24	–	–	5
Fine roots in organic debris**	570	181	87	114	36	18
	5–10 cm depth					
Large roots*	–	–	–	–	–	–
Small roots	–	–	20	–	–	4
Fine roots	145	5	27	29	1	5
Fine roots in organic debris**	242	31	76	38	5	15
	10–20 cm depth					
Large roots*	183	–	181	37	–	36
Small roots	196	109	62	29	22	12
Fine roots	227	53	42	45	11	8
Fine roots in organic debris**	444	82	193	99	16	39
	20–30 cm depth					
Large roots*	146	–	–	29	–	–
Small roots	185	–	–	37	–	15
Fine roots	163	25	77	33	5	9
Fine roots in organic debris**	511	104	228	101	21	46
Totals	3013	590	1278	602	118	255
	Totals by depth					
0–5 cm	570	181	325	114	36	66
5–10 cm	387	36	123	77	7	24
10–20 cm	444	82	193	99	16	39
20–30 cm	1006	129	352	201	26	70

*See Table 2.
**See Table 2.

TABLE 6. Roots in soil samples collected in *Larrea-Ambrosia* communities on 24 September 1976. Values normalized 17 percent ash and corrected (organic debris corrected to 35 percent).

	Interspace (80%)	In canopy (13.3%)	Under plant (6.7%)	Total (100%)
	kg/ha 0–10 cm			
Large roots*	—	—	—	—
Small roots	—	—	19	19
Fine roots	25	19	8	52
Fine roots in organic debris**	19	18	81	118
	kg/ha 10–20 cm			
Large roots*	—	—	—	—
Small roots	—	137	48	185
Fine roots	46	34	26	106
Fine roots in organic debris**	16	8	43	67
	kg/ha 20–30 cm			
Large roots*	—	23	42	65
Small roots	—	25	46	71
Fine roots	25	12	12	49
Fine roots in organic debris**	15	5	45	65
Totals	146	281	370	797

*See Table 2.
**See Table 2.

TABLE 7. Root distribution in *Artemisia tridentata* on Pahute Mesa at the Nevada Test Site (organic debris corrected to 35 percent).

Depth cm	Roots, kg/ha Under	Canopy	Interspace	Total	Distribution for 5 cm increments %
		Big roots (over 3 mm)			
0–5	—	—	—	—	0.0
5–10	93	56	260	409	13.7
10–20	590	260	—	850	14.3
		Small roots (1–3 mm)			
0–5	2	10	—	12	0.4
5–10	17	23	140	180	6.1
10–20	70	140	140	350	5.9
		Fine roots (under 1 mm)			
0–5	21	10	—	31	1.0
5–10	32	47	77	156	5.2
10–20	78	77	98	253	4.3
		Fine roots in organic debris*			
0–5	151	34	5	190	6.4
5–10	58	36	100	194	6.5
10–20	69	100	181	350	5.9
		Totals			
0–5	174	54	5	233	7.8
5–10	200	162	577	939	31.6
10–20	807	577	419	1803	30.3
Total	1181	793	1001	2975	100.0

*See Table 2.

and 1132 kg/ha for the site in Mercury Valley. These samples were taken in spring, so they should have shown a component of fine roots due to phenological stage (Caldwell and Fernandez 1975).

Roots associated with winter annual plants are shown in Table 5. Two sets of values are shown. One is based on the assumption that the biomass is uniform and the other (realistic) is that the winter annuals occupy 20 percent of the land area. On this basis the estimated biomass in kg/ha for winter annual roots was 602, 118, and 255 for Mercury Valley, Frenchman Flat, and Rock Valley, respectively (22 April 1976).

The depth distribution of the annual roots was more shallow than for perennial plants, as expected. The first 5 cm of soil had 19, 31, and 26 percent, respectively, for Mercury Valley, Frenchman Flat, and Rock Valley. In the first 10 cm of soil from Rock Valley, only 8 percent of the perennial roots (mostly fine roots) (Table 2) were present. In Frenchman Flat and Mercury Valley they were 20 and 14 percent, respectively, but these values are for 10 cm and those for annuals were for 5 cm.

Another set of soil samples by the same procedure was taken on 24 September 1976 in a *L. tridentata-A. dumosa* community (Table 6). The total root biomass in kg/ha was 797 at this September date, which is essentially the same as the April date in Table 2 (759 kg/ha).

To compare the root patterns of the first 5 cm of soil of the Great Basin desert (an *Artemisia* community) with the northern Mojave Desert, a root sampling procedure as above was used in Pahute Mesa (Table 7) of the Nevada Test Site. The percentage of the roots in the first 5 cm was 7.8 percent, which is about the same as in the first 10 cm of the northern Mojave Desert. In the first 10 cm at Pahute Mesa, 39 percent of the roots were present. Solid rock existing below 20 cm at the site sampled prevented root distribution at lower depths. The root sample of 2975 kg/ha compares with an estimated aboveground biomass of about 3000 kg/ha (Wallace and Romney 1972).

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RODENT-DENUDED AREAS OF THE NORTHERN MOJAVE DESERT

R. B. Hunter[1], E. M. Romney[1], and A. Wallace[1]

ABSTRACT.-- Populations of pocket gophers and rabbits regulate or control the perennial vegetation on relatively rge sites in the northern Mojave Desert. Aboveground shoots are pruned and whole plants are killed by complete ıtting of main roots.

In western Mercury Valley and Frenchman 'lat on the Nevada Test Site are several reas lacking the normal desert shrub cover. Figure 1 is an aerial photograph of several such areas in Mercury Valley. The largest shown covers approximately 60 ha.

Fig. 1. Aerial view of rodent-denuded areas in west Mercury Valley, Nevada Test Site. Largest site (arrow) covers about 60 hectares. Highway transects northeast corner of photo.

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Fig. 2. Grazing rabbits severely prune foliage of transplanted shrubs and newly developing seedlings. Inexpensive wire enclosures offer protection and help ensure survival.

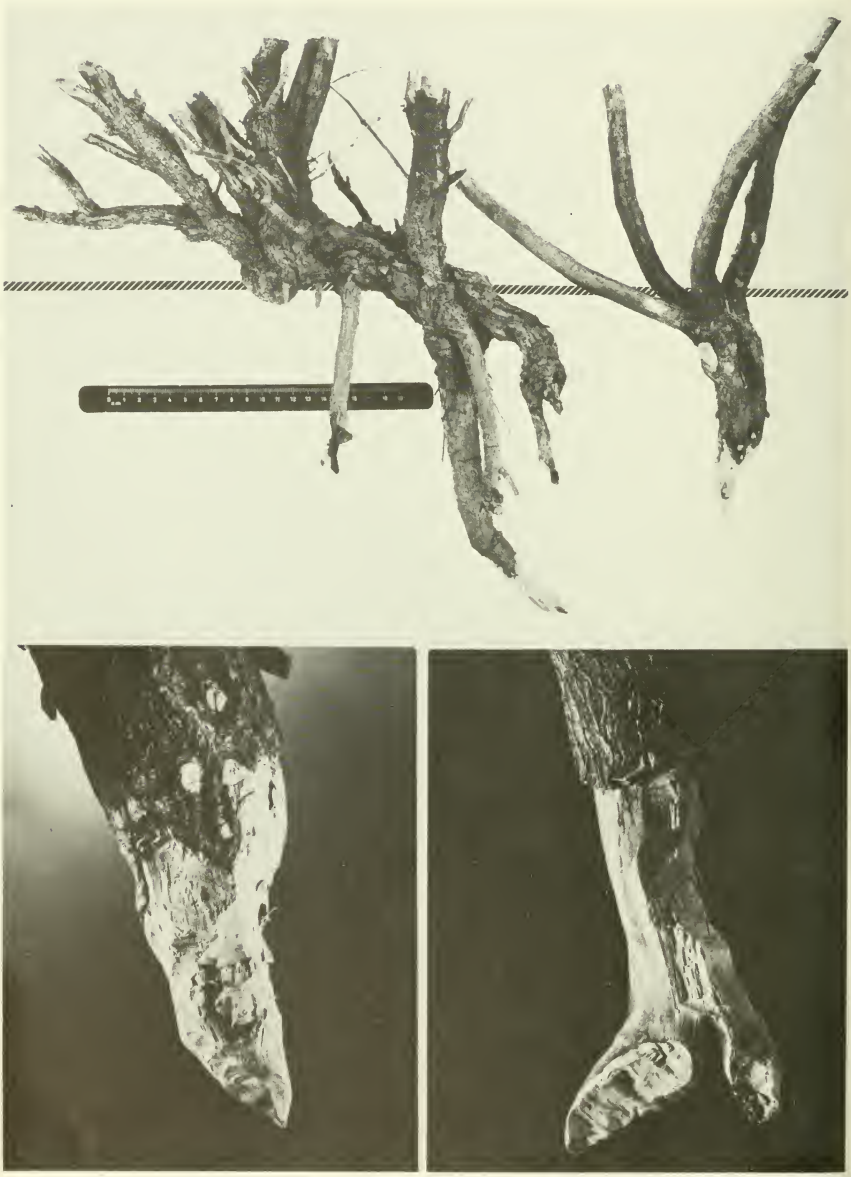

Fig. 3. Example of newly killed *Larrea tridentata* shrubs destroyed by gophers (*Thomomys bottae*).

We have concluded from observations of these areas that they are caused by the activities of burrowing pocket gophers and grazing rabbits. These observations are:

1. The soil surface of the denuded areas is densely pitted with burrow entrances and fresh gopher mounds; the soil is soft, as if freshly plowed; and the surface rocks are uniformly small and retain carbonate deposits, indicating short residence on the surface.
2. Shrubs transplanted onto these areas have been destroyed by severe grazing pressure when left unfenced. Some fenced shrubs also appear to have been killed by burrowing pocket gophers, and nearly all have been pruned to the fences by grazing rabbits (Wallace et al. 1976) (Fig. 2).
3. Dying and recently killed *Larrea tridentata* (Sesse & Moc. ex DC.) Cov. shrubs on the edge of one such area were uprooted, exposing evidence of severe root pruning. The sharp, oblique tooth cuts in healthy wood by pocket gophers (*Thomomys bottae*) were clearly distinguishable from insect damage and decay (Fig. 3).

Further characteristics of these areas are a relatively high population of winter annuals; a gradual transition zone from scattered *L. tridentata* shrubs to a normal shrub community occurring over approximately 20 to 50 meters; and the presence of *Stanleya pinnata* (Pursh) Britt., a small, pithy-stemmed shrub. A few remnant *L. tridentata* shrubs occur within the denuded area, but the absence of standing dead wood indicates the areas have been bare for at least several decades. Many new shrub seedlings are seen, but survival of seedlings to young, well-established shrubs is extremely rare in these areas.

Although rodent population dynamics have been well characterized in the adjacent shrub communities (O'Farrell and Emery 1976), no studies of rodents have been performed in conjunction with these disturbed areas. Nevertheless, their existence, along with visible evidence, indicates that burrowing and grazing animals play a significant role in plant distribution and soil disturbance in the Mojave Desert. The high density of annuals occurring on these areas may be important to maintenance of the desert rodent populations in dry years (Beatley 1969).

ACKNOWLEDGMENTS

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FENCING ENHANCES SHRUB SURVIVAL AND GROWTH FOR MOJAVE DESERT REVEGETATION

R. B. Hunter[1], A. Wallace[1], and E. M. Romney[1]

ABSTRACT.— Fourteen species of native shrubs were transplanted to bare areas of the northern Mojave Desert in 1972 and 1973. By 1978 plants surrounded by small fences were larger (0.26 vs 0.11 m^3 overall average for several species) and survived better (42 percent versus 23 percent) than unfenced plants. These effects are primarily due to reduced grazing of shoots. Loss of shrubs to pocket gophers or other burrowing rodents was not prevented by fencing.

Natural revegetation of disturbed desert lands is a very slow process (Shreve 1917, Shreve and Hinckley 1937, Wells 1961, Shields and Wells 1963, Wallace et al. 1977). Seeding and transplanting of shrubs have often failed as the result of problems such as poor germination, poor growing conditions, grazing by rodents, and inadequate soil preparation (Graves 1976).

Transplanting *Atriplex canescens* (Pursh) Nutt. onto desert lands has been successful in several instances (Springfield 1970, Aldon 1972, Cable 1972, Nemati 1977). Much effort has been put into timing for maximum availability of soil moisture. Our experience with transplants watered through the first summer of growth showed more persistent problems related to grazing and pruning by rabbits and smaller rodents than to drought conditions. The grazing problem has been noted by others working with *A. canescens* (Springfield 1970, Cable 1972, Graves 1976, Shetron and Carroll 1977).

MATERIALS AND METHODS

On 16 February 1972, 100 shrubs of 14 species (Table 1) were transplanted from a glasshouse to a 29 ha bare area in a natural Mojave Desert shrub community on the Nevada Test Site (Frenchman Flat). Each plant in three of eight rows was enclosed within a fence of about 0.5 m diameter of 2.5 cm mesh chicken wire (Fig. 1). Each fence was supported by three lath stakes. All plants were watered monthly through the following summer (10 to 20 liters of water per plant per month).

On 16 February 1973, 62 additional plants representing seven of the species listed in Table 1 were transplanted to a nearby site similarly devoid of shrubs. Three of nine rows were fenced, and the transplanted shrubs were watered through the summer of 1973 in amounts indicated above.

Surviving plants were recorded 31 May 1973, 15 February 1977, and were counted and measured 7 June 1978. Plant volumes were calculated from the height and the average of two width measurements, assuming a cylindrical shape.

A further planting of 381 plants of assorted species in 127 groups of three was made 7 May 1977 in a nearby area where much of the surface had been removed for gravel. All plants were fenced and watered every 4 to 6 weeks through August 1977.

RESULTS AND DISCUSSION

Table 1 reports survival of shrubs at the three census periods for the 1972 and 1973 plantings. By 1978 only four unfenced species survived [*Ambrosia dumosa* (A. Gray) Payne, *A. canescens*, *Larrea tridentata* (Sesse & Moc. ex DC) Cov., and *Lycium andersonii* (A. Gray)]. In contrast, nine fenced species survived. Overall survival rates were marginally improved by fencing.

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Prevention of grazing resulted in greater size of fenced plants (Table 2, Fig. 1). When calculated as percent of average size for each species, the fenced shrubs were significantly larger ($P < 0.05$) than unfenced shrubs.

Failure of shrubs to survive seems to be related primarily to rodent browsing and pruning activity, although a few species may have succumbed to weather and transplant shock [*Salvia sonomensis* (Kell.), *Salazaria mexicana* Torr. and *Stephanomeria pauciflora* (Torr.) Nutt.] Rodents in this area include pocket gophers (*Thomomys bottae*), rabbits (*Lepus californicus* and *Sylvilagus audubonii*), kangaroo rats (*Dipodomys merriami*), and mice (*Onychomys torridus* and *Peromyscus* spp.) (O'Farrell and Emery 1976).

Unfenced palatable shrubs (*Ceratoides lanata* (Pursh) J. T. Howell, *Yucca* spp., *Artemisia tridentata* Nutt.) were killed by grazing of shoots until only stubs were left. Fenced plants, however, also were killed by burrowing rodents, particularly pocket gophers (Fig. 2). Losses continued through 1978 for fenced shrubs.

Plantings made on the gravel excavation site in 1977 survived and grew very well through the first year after transplanting. Only two plants were lost, one of which appeared to be dying within a month of transplanting. Only *Atriplex* species were grazed heavily. The rocky, sandy soil appears to have discouraged burrowing rodents at that site.

Grazing of shoots appeared sporadic and heaviest when most shrubs were dormant and annual plant species were absent (summer and fall).

The fencing technique used is rapid, inexpensive, and effective against non-burrowing rodents. The particular sites planted here appear to harbor an unusual density of burrowing species (Hunter et al. 1980, this volume) seriously reducing the effectiveness of the fences.

Seed production occurred in most surviving species in 1978 (except *Coleogyne ramosissima* Torr. and *Yucca* spp.). Although natural seedling establishment normally may be severely inhibited by grazing animals, we believe that revegetation of sites disturbed by human activities would be enhanced by taking steps to protect newly developing seedlings through the use of inexpensive, fenced enclosures.

ACKNOWLEDGMENTS

This study was supported by Contract EY-76-C-03-0012 between the U.S. Department of Energy and the University of California.

TABLE 1. Numbers of surviving plants transplanted to two disturbed areas in Frenchman Flat in February 1972 and February 1973. Survivors were counted May 1973, February 1977, and June 1978.

	Fenced				Unfenced			
Species*	Original	1973	1977	1978	Original	1973	1977	1978
Ambrosia dumosa	9	8	3	3	18	15	10	8
Atriplex canescens	6	5	4	4	10	9	5	5
Artemisia tridentata	3	3	3	1	6	4	1	0
Ceratoides lanata	5	3	2	2	9	1	0	0
Coleogyne ramosissima	1	1	1	1	1	0	0	0
Grayia spinosa	2	1	0	0	4	1	0	0
Larrea tridentata	10	8	6	5	16	12	11	11
Lycium andersonii	3	2	2	2	5	3	1	1
Lycium pallidum	3	1	0	0	5	0	0	0
Salvia sonomensis	3	0	0	0	6	0	0	0
Salazaria mexicana	1	0	0	0	3	1	0	0
Stephanomeria pauciflora	1	0	0	0	2	0	0	0
Yucca brevifolia	2	2	1	1	4	4	0	0
Yucca schidigera	10	10	6	6	17	16	1	0
Total survival	58	44	18	25	104	66	29	25
Percent survival		76	47	42		62	27	23

*Full names of the species will be found in text except for *Grayia spinosa* (Hook.) Moq., *Lycium pallidum* Miers, *Yucca brevifolia* Engelm. in Wats., and *Yucca schidigera* Roezl ex Ortgies.

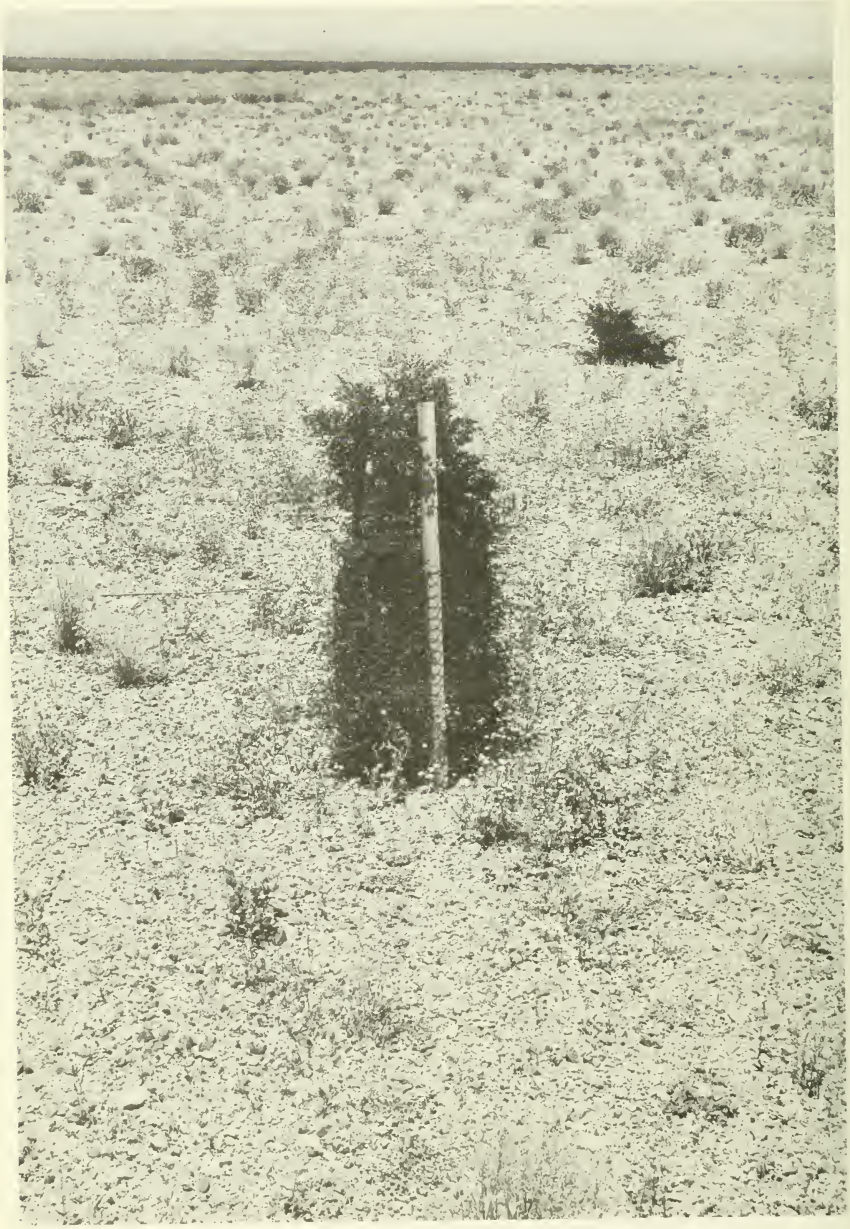

Fig. 1. Inexpensive wire enclosures protect transplanted shrubs from grazing rabbits.

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TABLE 2. Average sizes of fenced and unfenced surviving transplants, June 1978 (Vol, m^3 ± SEM).

Species	Fenced	Unfenced
Ambrosia dumosa	0.093 ± 0.017	0.050 ± 0.010
Atriplex canescens	1.064 ± 0.616	0.263 ± 0.025
Artemisia tridentata	0.108	
Ceratoides lanata	0.171 ± 0.019	
Coleogyne ramosissima	0.026	
Larrea tridentata	0.239 ± 0.087	0.089 ± 0.014
Lycium andersonii	0.022 ± 0.001	0.031
Yucca brevifolia	0.009	
Yucca schidigera	0.040 ± 0.011	
Overall average*	0.260 ± 0.115	0.109 ± 0.018

*Average of all surviving plants, numbers of each species are given in Table 1.

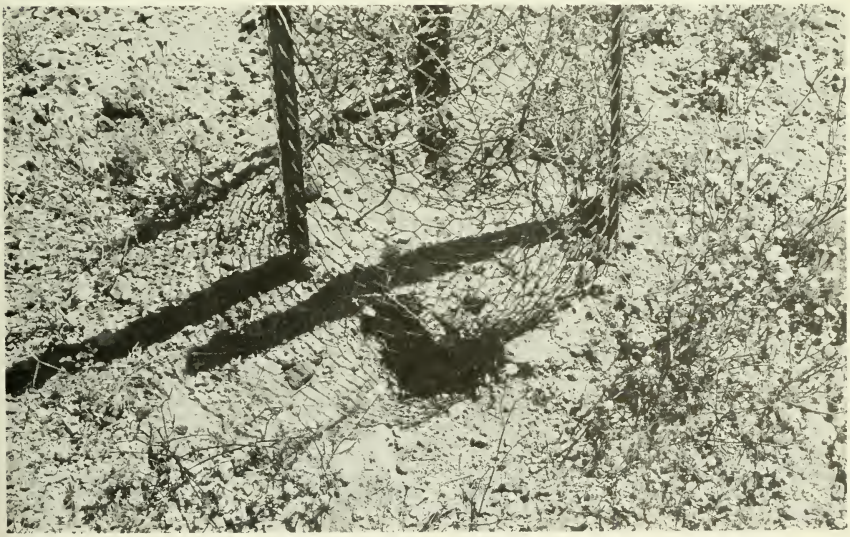

Fig. 2. Pocket gophers (*Thomomys bottae*) destroyed some transplanted shrubs initially protected with wire enclosures.

THE CHALLENGE OF A DESERT: REVEGETATION OF DISTURBED DESERT LANDS[1]

A. Wallace[2], E. M. Romney[2], and R. B. Hunter[2]

Abstract.— The revegetation of disturbed, arid lands is one of the great challenges of a desert. An attempt to encourage it is not an impossible task, however, if the natural and the man-made resources available are utilized and managed. Where rainfall and temperature conditions approach or exceed those of the Great Basin desert, restoration of disturbed land will occur through natural revegetation processes within a reasonable period of time. This is not generally the case in the more arid Mojave Desert areas where the moisture and temperature conditions are less favorable for germination and seedling survival. Restoration of vegetation by natural reseeding can, however, occur within local sites where moisture has concentrated as the result of terrain features forming catchment basins. Otherwise, the natural revegetation processes in the Mojave Desert areas require much longer periods of time (possibly decades or centuries) than are practical for meeting environmental protection standards imposed by current legislation.

Through better understanding of the processes governing revegetation and the ability to control them, it is possible for man to more rapidly restore disturbed desert lands. Terrain manipulation to form moisture catchment basins, selection of seed from pioneering shrub species, preservation of existing shrub clump "fertile islands" in the soil, supplemental fertilization, irrigation, organic amendments, and transplanting vigorous shrub species are some of the important things that can be done to help restore disturbed desert land.

With current stress on maintenance of the quality of the environment and with responsibility for its status placed upon those using a given area, it is increasingly important that we who are involved understand many aspects of the ecosystem in which we work. The facts that deserts are very fragile and that efforts to restore them after disturbance can lead to frustration and failure are well known. We are proceeding in our work with the assumption that our ability to control the factors related to restoration of deserts, whenever the need arises, is proportional to how well we understand the processes governing germination and survival of desert plants. In this report we describe some aspects of natural processes that are of great importance to revegetation problems in the northern Mojave and southern Great Basin deserts (Beatley 1965, Wallace and Romney 1972, 1974, 1976).

Synopsis and Discussion of Experimental Findings

A listing and description of some of the more important behavioral aspects of the deserts in which we work are given below. Details of experiments from which some of the findings were obtained have been previously published (Wallace and Romney 1972, Romney et al. 1973, Romney et al. 1974, Hunter et al. 1975, 1975a, Romney et al. 1977a). The work of Beatley contributes considerably to an understanding of plants under the desert conditions involved in these studies (Beatley 1965, 1965a, 1965b, 1965c, 1966, 1967, 1973, 1974, 1974a, 1975, 1976).

1. Water is the most important parameter governing biological responses in the desert ecosystem; however, equal quantities of water via natural precipitation do not always result in equal responses. Some of the factors

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involved include: (a) rainfall during time when high temperatures cause heavy loss through evaporation, (b) rainfall during the time when plants are in a physiological state of low temperature or high temperature dormancy, (c) high intensity rainfall where loss by runoff is considerable, and (d) cool, spring temperatures that decrease evaporation, enabling a greater proportion of the soil moisture to be used in transpiration.

Because the small amount of precipitation falling upon the northern Mojave Desert (10 to 15 cm per year) varies both in amount and time of distribution (Table 1), and because seasonal temperatures vary consistently during the plant growing season, no two years are really alike. Such has been the case for more than the decade during which we have collected environmental information at the Nevada Test Site. This means that it is not only difficult to predict results, but also that new plant survival is precarious even when transplanted ones are irrigated during the first summer season. A generalized description of why there is year-to-year variation in the biology of the northern Mojave Desert is given in Table 2.

2. Vegetation of the northern Mojave Desert really uses only about 10 to 20 percent of the soil area as a growth medium and the other 80 to 90 percent is used largely as a watershed. This results in the familiar shrub clump or "fertile island" structure characteristic of some deserts (Charley 1972, Charley and West 1975, Romney et al. 1973, Romney et al. 1977a, 1977b). These shrub clump sites have probably been in place for centuries (Wallace and Romney 1972) and are just as structured and fertile as soil in more humid ecosystems (Roberts 1950, Paulsen 1953, Charley and Cowling 1968, Rickard 1965, Garcia-Moya and McKell 1970, Tiedeman and Klemmedson 1973). This means that the water coming into the system is used with the energy of photosynthesis, through decomposition, to maintain just a fraction of the total soil area as highly productive sites. The remainder of the soil serves as needed watershed, and it usually contains some roots. When this soil structure involved with shrub clumps is destroyed mechanically by bulldozers, graders, etc., centuries of the results of biological cycling is destroyed and, by itself, such a damaged desert ecosystem will recover very slowly.

Soil organic matter levels are reasonably high in the shrub clump areas and usually very low in the intervening bare soil areas (Charley 1972, Romney et al. 1973, Romney et al. 1977). Soil organic matter at a given temperature decreases with decreasing rainfall (Jenny et al. 1949). As the climatic conditions of the northern Mojave and other deserts are encountered, upon comparing conditions varying from humid to arid, as in Figure 1, the soil organic matter level does not decrease within the shrub clump sites as it does in the rest of the desert soil area. The generalized curve of that relationship between soil organic matter and precipitation is, therefore, distorted within the range for desert conditions, as illustrated in Figure 1. This structuring of the soil surface into highly productive and poorly productive areas is of utmost importance to the maintenance of the Mojave Desert type of ecosystem.

3. The plant size structure of the perennial plant population of the northern Mojave Desert indicates a reasonably active system in which new individuals constantly enter the ecosystem (Hunter et al. 1975b, El-Ghonemy et al. 1980a, b, this volume). New individuals usually do not enter the system each year, however. Instead, they enter mostly during those years in which rainfall is sufficient for germination and seedling survival. Precipitation records (Table 1) indicate that the above-average rainfall during the winter periods of 1968–1969 and 1972–1973 possibly explains the apparent "pulse" input of new seedlings of certain shrub species (Romney et al. 1980, this volume). The information that only two years out of six were conducive to

TABLE 1. Annual precipitation during period of 1 July to 30 June, Rock Valley, Nevada.[1]

Year	mm	Year	mm
1963–1964	100.7	1970–1971	98.9
1964–1965	121.2	1971–1972	91.7
1965–1966	163.4	1972–1973	275.7
1966–1967	100.9	1973–1974	76.2
1967–1968	153.6	1974–1975	138.4
1968–1969	279.7	1975–1976	61.4
1969–1970	89.6		

[1]Air Resources Laboratory, NOAA, Las Vegas.

new seedling establishment at Rock Valley, Nevada, is important to an understanding of the difficulties one encounters in attempting to restore desert lands without the benefit of supplemental water.

4. New perennial plant seedlings are more apt to become established within the fertile shrub clump areas rather than in the bare spaces between them. Fortunately, however, there are several pioneer species in the northern Mojave Desert that can grow under the hostile environment of disturbed soil, and even in subsoil that is very low in organic matter. El-Ghonemy et al. (1980b, this volume) concluded that the commonly occurring *Atriplex confertifolia* is an important pioneer species useful in the restoration of disturbed desert land.

5. An established shrub population effectively controls germination and survival of new perennial plants by controlling soil moisture. There are two important consequences to consider regarding maintenance and restoration of disturbed lands. One is that as long as the established plants are in place there will be relatively little input of new perennial plants. Establishment of new plants largely depends upon replacement of dying individuals over a relatively long period of time. The second is that destruction of the existing population will so change the soil moisture status that many new plants will become established initially, after which time competition culls out the weaker seedlings and a steady state population once again is established.

In areas having greater than 15 cm annual rainfall, it is highly probable that the new vegetation restored on disturbed land initially

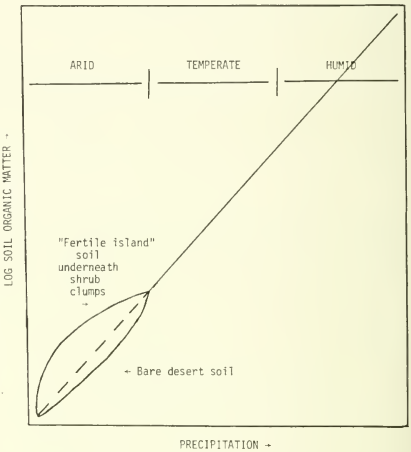

Fig. 1. Hypothetical relationship between soil organic matter content and precipitation. Centuries of biotic activity and recycling and concentration processes have developed the fertility of the soil underneath shrub clumps to levels comparable to soil formed under more humid conditions.

TABLE 2. An example of the annual productivity options for shrubs in the northern Mojave Desert with constant rainfall (10 cm/yr), but with variable time of input and with variable mean seasonal temperatures.

Major seasonal rainfall period			Air and soil temperatures		Estimate of shrub productivity ± 25 percent	
Nov–Dec	Jan–Feb	Mar–Apr	Jan–Feb	Mar–Apr	kg/ha	Percent
E	–	–	C	C	600	200
E	–	–	W	W	300	100
E	–	–	W	C	400	133
E	–	–	C	W	500	167
–	M	–	C	C	800	267
–	M	–	W	W	400	133
–	M	–	W	C	500	167
–	M	–	C	W	600	200
–	–	L	C	C	800	267
–	–	L	W	W	500	167
–	–	L	W	C	600	200
–	–	L	C	W	700	233

E = early season, M = mid-season, L = late season, C = cold, W = warm. Other options than above would occur from different combinations of rainfall input and variable temperatures. Above data indicate differences as great as 267 percent could occur with same rainfall and same evapotranspiration if no runoff or leaching below root zone occurred.

will be a grassland type instead of a reproduction of the original shrub. Range management skills have been developed to improve the grazing potential of rangelands because of this condition, as is commonly done on Great Basin desert lands (Plummer et al. 1955, 1968). Seed availability is a limiting factor in the process, so an artificial seeding of appropriate grass species in disturbed areas generally is done to create a more successful grazing area. One thing that must be taken into account, however, is the likelihood that newly disturbed Great Basin desert areas will become invaded by *Salsola* species (Russian thistle), unless control measures are taken.

6. Inasmuch as soil moisture controls germination of new seedlings to a large measure, the process can be controlled effectively by manipulation of surface terrain to facilitate the concentration of precipitation runoff into catchment basins. These principles have been worked out in desert areas by Evanari et al. (1971). We have emphasized this point in our past discussions on feasibility of cleaning up contaminated desert land (Wallace and Romney 1974, 1976).

7. Animals control seedling survival to a great extent (Plummer 1955, Plummer et al. 1968, Wallace and Romney 1972, 1974, 1976). Not only do rabbits prune plants aboveground, but pocket gophers also destroy plants by eating roots. Even with wire screens to help exclude animals from new shrub transplants, they still have noticeable effects (Hunter et al. 1980, this volume).

Animals also have some positive effects in that they aid in the decomposition and nutrient cycling process. Some species help to conserve the small amount of fixed nitrogen in the system by moving litter underground. Animal activity helps to maintain the shrub clump areas as fertile zones within the ecosystem.

8. The availability of combined forms of nitrogen is vital to an ecosystem. Any disturbance that destroys the fertile shrub clump islands and topsoil of deserts imposes a very severe limiting factor on restoration of vegetation on that land. Biological fixation of nitrogen is very precarious under desert conditions (Hunter et al. 1975a, Wallace et al. 1977). However, a very conservative mechanism results in the presence of sufficient nitrogen to maintain the amount of vegetation made possible by the rainfall. Any attempts at restoration of disturbed sites must consider the nitrogen needs. Fortunately, this may be achievable with fertilizer amendments applied to replace, or supplement, that nitrogen which would be lost to the system by site disturbance of the kind that would occur from cleanup activities (Wallace et al. 1977).

9. Species of vegetation that dominate the northern Mojave Desert have either a low leaf water potential (like *Larrea tridentata* Sess & Moc. ex DC.) Cov. and *Krameria parvifolia* Benth.) or else they are adapted to complete a life cycle during the relatively cool, moist season of the year, followed by dormancy during the hot, dry periods [like *Ambrosia dumosa* (A. Gray) Payne, *Grayia spinosa* (Hook.) Moq., and *Lycium andersonii* A. Gray]. Two of this last group do not go into dormancy when irrigated during the hot period of the year, but *Grayia spinosa* does (Wallace et al. 1970, Wallace and Romney 1972). Revegetation procedures using transplants of rooted cuttings of deciduous shrubs must take into account the dormancy behavior of each species. Transplants that are dormant during the hot, dry season are best maintained that way rather than attempting to force them to break dormancy and undergo new vegetative growth out of season. Rooted cuttings from a number of Mojave Desert shrub species can be used for transplanting stock, especially if planting time can be arranged during the late fall or early spring months when seasonal moisture is most favorable (Wieland et al. 1971).

10. Response of vegetation to water in the northern Mojave Desert is rather complex, the result of several interacting factors. Among the more obvious aspects of water is timing, which itself can be rate limiting. Water can be of relatively little value if it is supplied at a time when it will be lost by evaporation or during a phenological stage of development when no response can be expected. During most early spring seasons in the northern Mojave Desert, there are periods when water is not limiting to plants. Soil moisture from winter rainfall is present, but the period of plentiful supply will depend upon the recharge supply for that year and

upon the temperature conditions that determine how fast the plants use the available water supply.

Response to supplemental irrigation, therefore, is not always a simple, predictable matter, yet some extremes in shrub responses have been documented (Romney et al. 1974, Hunter et al. 1975a). If winter rainfall has been sparse, the response of some shrub species can be dramatic when irrigated during the spring growth season. If, however, the soil moisture recharge level is high from heavy winter rainfall, the supplemental irrigation may do nothing more than help extend the growth period until the soil eventually dries out. This extension of normal growth period by relieving water stress can increase the biomass production of some shrub species severalfold, but other plants cannot respond as much because of slow growth patterns imposed by their genetic nature. If additional water is to give further yield increase, the species in a community must be changed to the kinds of plants that respond more to water. This is why extra water tends to change desert areas into grasslands (Wallace and Romney 1972).

Under desert ecosystem conditions, a given amount of water will sustain a given amount of primary productivity. If the amount of water were increased to a higher level and maintained year after year, the system would adjust to the new level with a new productivity plateau (Fig. 2). Water could again become the rate-limiting factor for this new growth plateau, but it also could be nitrogen or some other nutrient. It could even be genetic so that no additional productivity could occur even with input of more water and nutrients. This barrier may be overcome with increased density of species, but additional nitrogen would also have to become available to sustain that added productivity. Eventually another plateau would be reached following a somewhat hypothetical series of changes as illustrated in Figure 2. Supplemental nitrogen may not be necessary until the second- or third-stage limiting zones are reached, providing the nitrogen fixation and nutrient cycling processes are not overstressed until then. With time it can be expected that an equilibrium would be reached where nitrogen fixation could supply any new needed nitrogen to maintain either of the two higher plateaus, if the nitrogen present were permitted to cycle within the system (Day et al. 1975). The relationship among plant species, water supply, and available nitrogen supply must be understood for a given system if these factors are being manipulated in revegetation work.

Reasonable survival of transplanted shrubs occurred in some small field plot experiments where the effectiveness of protecting new transplants from grazing rabbits by wire screens was demonstrated (Table 3). In addition, the new transplants received periodic irrigation during the late spring and summer months after planting. Results indicate that several shrub species can be used effectively to restore vegetation on disturbed Mojave Desert land with reasonably inexpensive husbandry procedures.

11. The parasitic plant (*Cuscuta nevadensis*) Jtn (dodder) can regulate survival of perennial plants in the desert (Wallace et al. 1980, this volume). Its presence generally is not widespread over large areas, but it may concentrate heavily in specific localities having ideal environmental conditions for its growth. Especially during cool, moist springtime weather, this plant can infest and kill a number of perennial species. We have observed its effects on *Ambrosia dumosa* (A. Gray) Payne, *Acamptopappus shockleyi* A. Gray, *Atriplex canescens* (Pursh) Nutt., *A. confertifolia*, *Ceratoides lanata* (Pursh) J. T. Howell, *Coleogyne ramosissima* Torr., *Encelia virginensis* A. Nels., *Grayia spinosa* (Hook.) Moq., *Hymenoclea salsola* Torr. and Gray, *Lycium andersonii* A. Gray, *L. pallidum*, *Mirabilis pudica* Barneby, *Prosopis juliflora* (Sw.) DC., var. *torreyana*, and *Psorothamnus fremontii* (Torr.) Barneby. Dodder probably infests many other plant species in the Mojave Desert. Beatley (1976) identified five different species of *Cuscuta* active in the central-southern Nevada area.

12. Many desert plant species exist as local ecotypes highly adapted to the local climatic and edaphic environment (Plummer et al. 1955, 1968). Unless plant material used for revegetation of a given site comes from that site (i.e., seed or stock for making transplants), difficulties may be encountered in restoration of the site.

TABLE 3. Percent survival of transplanted shrubs, Nevada Test Site, 1976.*

Plant species	W. Frenchman Flat		N. Frenchman Flat		Yucca Flat	
	Fenced	Unfenced	Fenced	Unfenced	Fenced	Unfenced
Ambrosia dumosa	50(6)**	50(10)	0(3)	50(4)	—	—
Atriplex canescens	33(6)	0(10)	100(3)	83(4)	60(5)	0(60)
Artemisia tridentata	—	—	100(3)	17(4)	100(7)	90(30)
Artemisia hudoviciana	—	—	—	—	75(4)	55(9)
Ceratoides lanata	0(6)	0(10)	67(3)	0(4)	20(5)	0(5)
Chrysthamnus nauseosus	—	—	—	—	33(3)	33(3)
Grayia spinescens	—	—	—	—	60(5)	8(12)
Larrea tridentata	50(6)	60(10)	100(3)	67(4)	—	—
Lycium andersonii	33(6)	10(10)	—	—	0(3)	33(3)
Yucca brevifolia	—	—	—	—	28(7)	44(9)
Yucca schidigera	67(8)	0(10)	67(3)	17(4)	—	—

*W. Frenchman transplanted 2/20/72; N. Frenchman 2/16/73; Yucca Flat 12/18/71.

**Values in parentheses indicate number of specimens transplanted with or without protective wire enclosures. Shrubs were watered upon demand during the first six months after transplanting.

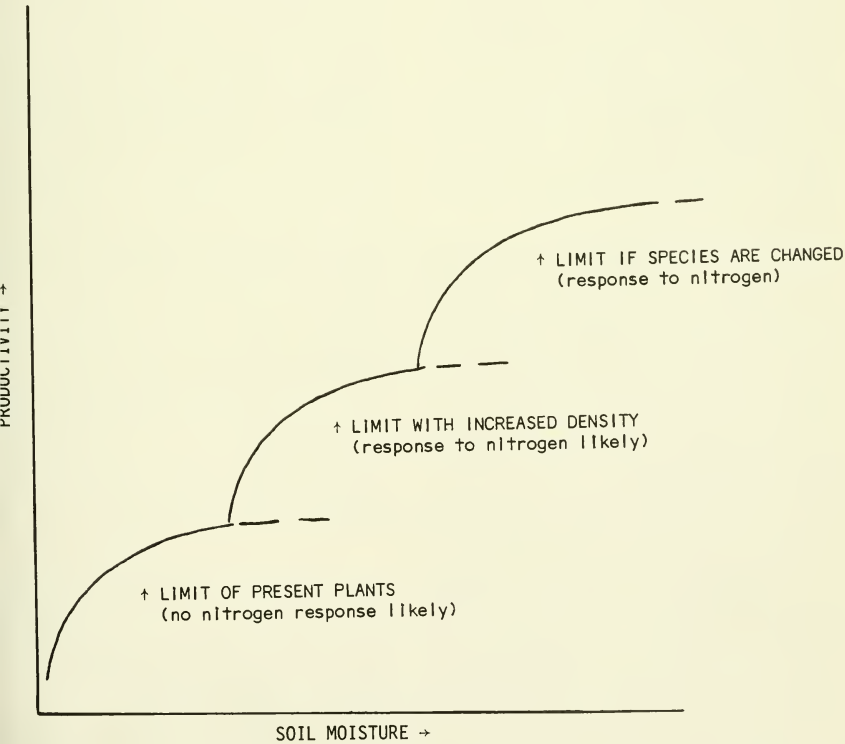

Fig. 2. Hypothetical response of desert vegetation to supplemental moisture. Advancement to the second and third productivity plateau requires successive change in density of species and change of population to more efficient plant species (Romney et al. 1977b).

13. Revegetation of disturbed areas under natural, unmanipulated conditions is more complete and faster in areas having higher rainfall and lower mean temperatures. As one goes from the northern Mojave to the southern Great Basin desert (i.e., southern to northern areas of the Nevada Test Site), changes in climate such as this occur. The Great Basin areas reestablish themselves much faster than those in the Mojave Desert when disturbed. This results primarily from the greater seed germination and seedling survival under higher rainfall conditions.

Several sites were mechanically disturbed in the Great Basin part of the Nevada Test Site during nuclear testing activities in 1957 (Dick and Baker 1969). The condition of these study sites has been examined periodically to follow the natural revegetation processes underway. In May 1976, the following annual plant count was made on 10 × 10 m plots: 450 in plowed site, 13 in scraped site, 168 in disked site, 250 in control site. The high variability in annual plant distribution observed in the general locale for 1976 would indicate no effects of the plowed or disked treatments compared to undisturbed areas. There still remained, however, some indications that earlier removal of topsoil from the scraped site caused reduction of annual plant populations. Data in Table 4 indicate the extent of shrub restoration on these disturbed sites compared to the undisturbed control area. These data are estimates obtained from nondestructive, dimensional measurements of shrubs and grasses growing in the study sites. The methods of analysis and some other examples of results obtained by those methods elsewhere have already been reported (Wallace and Romney 1972, Romney et al. 1973, 1974). Represented among the species included in these estimates are *A. canescens*, *A. confertifolia*, *Artemisia spinescens* D. C. Eat., *C. lanata*, *Chrysothamnus viscidiflorus* (Hook.) Nutt., *Oryzopsis hymenoides* (Roem. & Schult.) Ricker, *Sitanion jubatum* J. G. Sm., and *Sphaeralcea ambigua* A. Gray. Excellent natural recovery has occurred in these disturbed areas through reseeding from species growing in the adjacent area during the 18-year period following the initial disturbance. The plowed and disked plots now show about one-third recovery compared to normal, but the plot having had the top soil scraped from it shows about one-fifth of normal.

14. Nuclear testing activities have in some cases destroyed the natural vegetation in local fallout areas by heat and blast damage and by radiation, or through mechanical damage from site preparation. These disturbed fallout areas have been useful for studying natural restoration of vegetation.

Artemisia is the dominant genus of plants growing in the southern Great Basin desert of the Nevada Test Site (Beatley 1976). We have had occasion to study its behavior for more than a decade following some of the nuclear test events (Wallace and Romney 1972, Romney et al. 1971). As mentioned above, sufficient data have been obtained to substantiate that the pulse hypothesis occurs for the establishment of new *Artemisia* plants (Romney et al. 1980, this volume). New shrub seedlings may have germinated from seed deposited earlier in the area before the disturbance occurred or from seed dispersed from adjacent undisturbed areas. The main trend of succession in the restoration of vegetation in these disturbed sites has been a heavy influx of *Salsola* species during the first three years after disturbance, followed by a steady conversion to grasses. Even though new shrub seedlings have become well established in numbers during the first decade of time, the disturbed sites now give the appearance of having been restored to grassland. This, of course, eventually will change as competition from developing shrubs forces out the newly introduced grasses.

Table 5 contains data taken from two study plots located within one of the damaged fallout areas and from a nearby control

TABLE 4. Natural recovery of vegetation on disturbed soil in Area 13, Nevada Test Site (soil was disturbed in 1957).

Kind of soil disturbance	Condition of perennial plants, 1976*		
	No./ha	% cover	kg/ha
Undisturbed	12,000	27.6	3,200
Plowed	9,000	9.7	1,185
Disked	9,300	10.5	1,233
Scraped	6,000	4.8	653

*Estimates made by nondestructive, dimensional measurements (Wallace and Romney 1972).

area. Sites were selected within areas where vegetation had been totally killed, partially killed, and undisturbed by radiation from fallout debris (Rhoads et al. 1969, Romney et al. 1971). Rainfall conditions varied considerably from year to year during the decade of time in which periodic observations were made (approximately like those in Table 1). As the result, many new seedlings would have germinated and subsequently died during wet and dry periods between the years when plot inventories were made. The results in Table 5 indicate a reasonably stable condition of seedling establishment in the control area populated with about 1000 mature, live *Artemisia* shrubs. Approximately the same numbers of shrubs had been growing on the disturbed plots as on the control plot, based upon shrub carcass counts. Seedling restoration has appeared to be more rapid on the partially killed plot than on the totally killed plot, but in either case the numbers that have germinated and survived are sufficient to eventually restore the disturbed fallout area to its original condition. The numbers of grasses on the disturbed plots indicate the succession trend to grassland compared to the undisturbed area. The density of *Ceratoides lanata*, *Chrysothamnus* spp., and *Tetradymia axillaris* seedlings was much higher on the disturbed plots than normally occurs in the adjacent, undisturbed area. The invasion and establishment of these species from external seed sources probably was made possible by the more favorable moisture conditions in areas where the competitive *Artemisia* shrubs had been destroyed. An interesting, rather complex trend of shrub species succession should occur in this disturbed fallout area between now and the time it passes through the grassland and shrub complex phases back to its original condition. The most important point in Table 5 is that disturbed sites in the Great Basin desert areas of the Nevada Test Site and Tonopah Test Range will restore themselves through natural revegetation processes within a reasonable period of time.

TABLE 5. Vegetation recovery on Pahute Mesa plots initially disturbed by fallout debris in 1965.

Plant species	New seedlings and grass clumps on plot		
	1967	1970	1976
Partially killed plot (100 × 100 m)			
Artemisia tridentata (80)*	35	390	1,170
Ceratoides lanata	5	5	5
Ephedra nevadensis	60	63	60
Grayia spinosa	20	28	55
Lycium andersonii	8	8	5
Mixed grasses	400	5,000	<5,000
Totally killed plot (100 × 100 m)			
Artemisia tridentata (0)	111	2	62
Ceratoides lanata	2	4	6
Chrysothamnus nauseosus	1	3	21
Ephedra nevadensis	1	0	0
Grayia spinosa	15	25	34
Mixed grasses	500	5,000	<5,000
Salsola iberica	<7,000	2,000	< 500
Tetradymia axillaris	2	4	1
Undisturbed control of plot (100 × 100 m)			
Artemisia tridentata (1,000)	6	14	65
Ephedra nevadensis	85	85	85
Grayia spinosa	14	14	14
Mixed grasses	100	80	120

*Values in parenthesis indicate number of original shrubs still living in plot as of September 1967. Each of the plots had about 1000 shrubs before disturbance, based upon dead shrub count.

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