COMPARATIVE AUTECOLOGICAL STUDIES OF *EUROTIA LANATA* AND *ATRIPLEX CONFERTIFOLIA*

by

Juan M. Gastó

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Approved:

Neil E. West
Major Professor

Lesley D. Love
Committee Member

Herman H. Wiebe
Committee Member

George B. Coltharp
Committee Member

Gaylen L. Ashcroft
Committee Member

E. J. Gardner
Dean of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

1969

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Juan M. Gastó

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ABSTRACT

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by

Juan M. Gastó, Doctor of Philosophy

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Major Professor: Dr. Neil E. West
Interdepartmental Curriculum: Ecology

Some comparative ecological studies of *Eurotia lanata* and *Atriplex confertifolia* were conducted at Curlew Valley, Utah, and in the greenhouse and growth chamber at Utah State University.

Factors controlling seed production were examined and the important ones were found to be characteristic of the site and stand, utilization history, and yearly weather variations. *A. confertifolia* showed less variable seed production than *E. lanata*.

Seed germination was tested in the growth chamber on surface (0-2.5 cm) and subsurface soil samples taken from the following contiguous plant communities at Curlew Valley: pure *E. lanata*, *A. confertifolia*, *Atriplex nuttallii*, *Artemisia tridentata*, and the mixed stand of *E. lanata* and *A. confertifolia*. Seed germination percentage was larger in the surface soil samples. There was no significant difference in seed germination in the different soils.

Eurotia lanata and *Atriplex confertifolia* seedlings grew satisfactorily in the growth chamber in all the above soils, indicating that the restricted distribution of these species is not regulated directly by the soil. The soil itself would permit a

broader distribution of both species.

Seedling emergence occurred mostly during late March and early April. The pure stand of A. confertifolia and the mixed stand were most unfavorable for seedling emergence and survival. The ecotone was the most favorable environment for maintaining a large seedling density. Seedling density was higher on the grazed areas than inside the exclosure while mortality was greater on the ungrazed areas.

Differential mortality related to the size of the seedlings occurred early in the growing season. The seedlings surviving the longest were larger than those dying younger. The largest cohort density shrinkage occurred during the first growing season. The rate of mortality of the surviving population during the second growing season was slightly reduced and largely reduced during the third year. During the fourth and fifth year, the cohort shrinkage was negligible.

Most plant growth and development occurred when the soil moisture matric potential was low, usually near or below -1500 Joules per kilogram. During March and April the soil moisture matric potential of the upper layer where most of the roots are concentrated was high and the potential evapotranspiration was low.

The greatest variability in soil moisture content throughout the year occurred at the 30 cm depth, decreased at the 60 and 90 cm depths, and was minimal at the 90 to 150 cm depths. Soil moisture matric potential of the deeper layers was usually greater than that of the surface soil. In the surface layers, the matric potential for the pure shadscale associated soil was always less than that found

under the other stands.

A. confertifolia and *E. lanata* are physiologically capable of living under the physical environment where other species or ecotypes in the surrounding stands naturally live. Their range of tolerance is beyound the magnitude of the environmental factors found in the area.

The intra- and inter-specific interference of *E. lanata* and *A. confertifolia*, as modified by environment, is probably responsible for the presence or absence of the species in a particular location through its influence in the rate of population growth.

(293 pages)

INTRODUCTION

The significance of plants as indicators of the general characteristics of the environment where they grow has long been emphasized. It has been shown in many places under the most varied conditions that there is a close relationship between the various factors which constitute the physical components of the environment and the organisms which can successfully live, grow, and reproduce under those conditions. These organisms, which by mere observation or by experimentation and research have been found to most faithfully indicate a certain kind of environment or sometimes a single factor of that environment are known as "indicators".

Plant indicators are of great concern to ecologists since ecology is the science that studies the mutual relations between organisms and environment. Ecology, then, starts from the premise that the individual organisms, the population, and the community which naturally develops in a certain place is not a random occurrence. Plant indicators are a consequence of a long series of natural and complex processes. Only a certain organism or group of organisms could develop under specific conditions.

If this premise is true, there is then, a cause-effect relationship between environment as a whole and the organisms which occupy it. The organisms themselves, living together as an organized group and acting as a whole, and with all their attributes, are an effect of the environment over a long period of time.

The presence of pure stands of shadscale (<u>Atriplex</u> <u>confertifolia</u>

Torr. and Frem.) and of winterfat (Eurotia lanata(Pursh) Moq.) or of mixed stands of both species has to be related to the environment. These stands are indicators of the environment acting upon the plant community. Thus, the main objective in this study is the search for a satisfactory explanation for the presence of these particular plant communities which are so often found in the salt desert shrub type of North America. The question arises as to what are the mechanisms which cause the presence of pure stands of E. lanata and A. confertifolia or the mixed stand of both species in some places and not in others? The answer to this question is of primary importance to ecologists because of simple scientific curiosity, and to range scientists because it could eventually lead toward better use of the range.

More complete knowledge of the interrelationships of these plant communities to their environment would permit the range scientist to manipulate plants and environment. Thus, it would induce compositional and structural changes in the community leading toward increased primary productivity, hence increased utilization by livestock and wildlife. At the present time, an increase in the area of winterfat at the expense of shadscale would be of extreme economic significance. The former constitutes a valuable forage resource for livestock, while the latter is only of limited value and much lower productivity.

The environment, however, cannot be manipulated blindly. As disastrous results indicate, simple experiments of season and intensity of grazing, and exclosures per se are not the answer. There are probably more basic explanations to aid management decisions. If there is a real desire to understand and manipulate plants and environment in order to replace one of these communities by another, more intensive study should be conducted.

The removal of less desirable species and their replacement by others can be more economically and permanently accomplished by inducing plant successions in the desired direction. This would lead toward a more productive disclimax of more favorable botanical composition. The induction of succession in a certain direction and at a relatively fast rate requires the knowledge of the factors responsible for the vegetational changes. These causes are not clearly understood at the present time.

During the past few years several attempts have been made for this purpose. At first it was believed that the presence of individuals of one species was simply the consequence of a single factor in the soil acting independently upon the vegetation. After preliminary studies it was found that the simple effects of salinity concentrations in the soil solution was not the complete explanation of the distribution of these two species. Later, other research was conducted to explore the relationships which could tie certain physical and chemical characteristics of the soil with the species distribution in the area. Both sets of researchers finally reached the conclusion that of the major edaphic characteristics studied, none acting alone was the real cause of the presence of these species.

There could be, however, minor characteristics of the soil, not yet studied, which could explain the distribution of these species in the area. One of the main objectives of the present research has been to study this possibility from an empirical approach. The testing of the hypothesis, that there is a limiting factor, in Liebig's sense, is then the main objective in this part of the study. The two species, if grown alone under laboratory conditions in soils where these and other plant communities naturally develop, constitute a test to prove the edaphic influences independent of the climatic variations. If both species can successfully grow and reproduce in soils from any one of these plant communities, this would mean a rejection of the idea that there is an inherent characteristic of the soil which is the overriding factor of plant distribution. This could lead to acceptance or rejection of the hypothesis that there is a single soil characteristic which would be the real and overriding cause of the distribution of these species.

Another part of this study includes examination of water relations, a facet of the plant-environment relationship not previously investigated. It is thought that a difference in the water use might be a real contribution to the explanation of the differential distribution of the communities examined.

The previous individualistic studies of plant indicators conducted on the area have not shown a satisfactory relationship between plants and environment. Another possible line of explanation to this phenomenon could be based on the principles of population ecology. This study includes considerations of population dyamics which could be closely related to a more complete answer to the patterns found. The main interest here is focused on the reproduction of the population and community and not on the individual itself. Perhaps the real answer to this cause-effect relationship is found in the effect of soil and other plant species which naturally occur and act together on the reproduction characteristics of the population as a whole. This view opposes the current approach which implicitly considers the growth of the individuals acting independently. This approach has been greatly emphasized in this research, especially where related to seed production, germination, seedling establishment, and growth.

Eurotia lanata is one of the most important species growing in pure stands and covering large areas of comparatively highly productive salt desert range lands. However, many of the lands which could be potentially covered by this species are now covered by shadscale or by shadscale dominated communities. This considerably reduces the potential production of the site. Perhaps some of the studies included in this research would help in the understanding of these mechanisms and so contribute to an increase in production of these lands.

REVIEW OF LITERATURE

The indicator value of plants as a consequence of the general influence of the environment has long been recognized. Clements (1920, 1928) concluded that every plant by its responses to the environment furnishes valuable criteria which can be used as an indicator. The consideration of this concept can be based upon five criterias: species and genera, life-forms, habitat-forms, growth-forms, and communities. He did not include the concept of ecotype as an indicator but considered the species as a good and reliable one. However, both he and Tansley and Chipp (1926) agreed that the community is a better integrator of the environmental conditions under which it develops. Communities are more delicate indicators of certain habitats and habitat factors because they integrate complex conditions. However, they also consider that certain species are excellent indicators of particular conditions.

Sampson (1939) stated that plants are the most reliable measurements of surroundings, since the plant indicator concept is based on a cause-effect relationship, where the plant is taken as the effect of the environment. However, his explanation is not clear when stating that any plant species may be to some extent, an indicator but only a few are sufficiently restricted by growth conditions. This could be interpreted in two ways. One is that the limits of tolerance (Shelford, 1937) to the environmental factors of certain species are too broad, or that there is not a very clear cause-effect relationship for those species. Both explanations could lead the interpreter to opposed and divergent conclusions.

Perhaps some of the disagreement on this subject could be better understood if Gerard's (1965) ideas are taken into consideration. Before interpretation of the environment-plant relationships is made, and the measurements of the vegetation can be meaningful, they must be directed to the right thing. Thus, in order to achieve meaningful results in scientific research dealing with the study of this relationship, entitation is more important than quantitation. Following this same line of reasoning, McIntosh (1967) has concluded that the vegetation measurements give valuable information only when the entity for which they are made is meaningful.

There is a general agreement that the community in a strict statistical sense is not homogeneous. Some defined limits of heterogeneity must be delimited instead of ignoring the error involved and accepting the existing heterogeneity as a fiducial limit of uniformity (McIntosh, 1967).

Some of these ideas perhaps are involved to a relative degree in the paper of Gates, Stoddart, and Cook (1956). In their conclusions, it seems that there was not a clear distinction between the alpha and the gamma indexes of diversity. The first one as indicated by McIntosh (1967) is the diversity of a single stand or community, while the other shows the diversity of a number of samples of a community taken from a range of different environments.

The interpretation and understanding of the environment-plant relationship may not be as good as if discussed from information taken from a wide range of environments. This is mostly because the genetic constitution of the species under such varied conditions may be different and so a large and non-accounted part of the data obtained would simply indicate gamma heterogeneity. It seems important when studying the cause-effect relationship to make a clear distinction between both sources of heterogeneity, but to start working with the alpha diversity first since it is more likely to provide clearer initial information.

In an absolute sense, the community and stands are heterogeneous, and thus if there is a clear cause-effect relationship, the environment also has to be heterogeneous. Each environmental factor acts independently or holocoenotically on the community influencing and modifying the plant community (Allee and Park, 1939; Billings, 1952). Most of the work conducted on shadscale and winterfat has been done with the assumption that the distribution of both species can be thoroughly explained with a single factor or by the law of Factorial Approach of Villar (1929). Most of the studies which include salinity concentration (Kearney et al., 1914; Shantz and Piemeisel, 1940; Stewart, Cottam, and Hutchings, 1940; Shantz, 1938), sodium exchange capacity, one-third atmosphere percentage saturation extract conductivity, soluble sodium (Gates, Stoddart, and Cook, 1956) and those that include bulk density, particle size distribution, compressibility (Mitchell, West, and Miller, 1966), are in this category.

With all this information, there is probably enough evidence to believe that the single factor approach is not satisfactory to explain the distribution of these two species. Thus, it is logical that a more holocoenotic consideration of the influence of the environment on organisms is probably needed. The possibility shouldn't be discarded, however, that one factor may exert a relatively greater influence than the others.

The distribution of the individuals in a plant community is rarely random in a statistical sense (Ashby, 1948; Goodall, 1952; West and Baasher, 1968). Using Liebig's ideas (Liebig, 1855; Browne, 1942) it could then be thought that there is a minimum or a limiting factor in the sense later given by Wollny (1891) and Billings (1964) which includes both maximum and minimum effects. Some research information has indicated that certain environmental factors are present in such amounts as to restrict the communities to certain values between certain limits. Such is the case of the results presented by Gates, Stoddart, and Cook (1956) in which there are five main soil characteristics for which a different mean and deviation exist for the soils rooting shadscale and winterfat. Their results can now be analyzed in the light of later research as indicating that part of the variability is due to ecotypic variation as it has been demonstrated by several pieces of research (McMillan, 1960; Billings, 1952; and Tisdale, 1962) and specifically for winterfat by Workman (1967) and Workman and West (1967, in press), Clarke and West (in press), and Plummer, Christense, and Monson (1968). Germination of seeds from four locations at different sodium chloride levels resulted in significant differences in germinating percentages between the seeds collected at several sites in Utah. Different ecotypes were also demonstrated by reciprocal transplants. The seedlings from each of the four locations were better adapted to their own soil than the seedlings from the other three locations. This variability is then due to the gamma heterogeneity as was so well predicted by Gates, Stoddart, and Cook (1956).

A smaller scale study of ecotypic variation in Eurotia lanata was made by Clarke and West (in press). Studies of seed germination from three sources, collected from three different stands in the same general area of the present research in Curlew Valley, show that germination percentages differ significantly between seed source. They concluded that highly localized genetic differences within the species may enable some strains to germinate more readily than others at higher salinity levels.

There is not any information available indicating that the alpha heterogeneity, or variability within the stand, could also be due to ecotypic variation. However, the work of Clarke and West first mentioned could be indicative that some ecotypic variations within the stand is possible because of a limited effective pollination distance. On the other hand, there has not been geographic isolation and the environmental conditions are quite uniform. If this is the case, the differences in range found for each particular soil characteristic has to be explained on another basis. This could be done using Rübel's (1935) ideas in relation to the replaceability of ecological factors. If this is the case, a second factor influences the vegetation and so there would be a difference in the tolerance range between a minimum and maximum where the species can be found.

A biological phenomena is dependent, according to Hooker (1917), not on a single variable, but on a constellation of factors. This line of explanation fits perfectly with his definition of the Law of Minimum. He has stated it as when a quantity is dependent on a number of variable factors and must be a function of one of them, the quantity is that function which gives the minimum value. In this way, a certain factor could be the limiting one for a certain species, ecotype or biotype with various quantitative values, if there are other factors which would modify, compensate, or replace the action of that on the organism, or if it would modify the reaction of the organism itself.

Liebsher's (1895) Law of Optimum also gives a satisfactory explanation to this variability in the edaphic limiting values found for the same species in different areas and samples. According to this law, the plant is capable of utilizing a growth factor occurring in limiting amounts in proportion to the other growth factors occurring at the optimum value for the plant. Thus, as the other factors of the soil vary, the limiting values vary.

All of this rationale is based on the premise that the vegetation is in equilibrium with the environment. However, if there is no equilibrium, it does not necessarily have to be the cause-effect relationship in the way already discussed. If this is the case, winterfat and shadscale stands could simply represent different seral stages toward equilibrium, representing the same sere. This possibility has already been proposed by Gates, Stoddart, and Cook (1956), but even now, and with all the additional information that exists, it seems very improbable. The main reason is that it has been repeatedly reported that there are many environmental differences associated with both species and stands, even though a general and satisfactory explanation has not yet been found.

One of the most frequently utilized tools to discover environmental differences between sites where Eurotia lanata and Atriplex confertifolia occur has been the use of transects and soil trenches across ecotones and alternes such as those utilized by Mitchell (1965) and Mitchell , West, and Miller (1966). Despite the obvious advantages of such studies in searching for probable sharp environmental differences, there are also some negative arguments which could induce wrong conclusions. Cain and Castro (1959) and Nytzenko (1948) have indicated that when vegetation is poor in species, it is frequently found that single species in a synusia dominate large areas. Under these circumstances, there is not effective competition from other species and thus the same species dominates larger areas than if a more varied flora exists, and many closely related species are competing for the same habitat. However, since the balance is so delicate, even slight environmental changes in the complex lead often to a new constant dominant, different from the former and abruptly delimited. In other words, this indicates that abrupt changes in vegetation could both be caused by considerable and sharp differences in the environment, mostly the substrate as indicated by Whittaker (1953), Hull and Martin (1939), Mason (1946), and Raven (1964), or simply by very gradual and slight environmental differences. Because of the simplicity of community composition, gradual and minute changes in the environment break the equilibrium and cause abrupt changes to other synusia (Nitzenko, 1948; Hanson and Churchill, 1961). The results reported by Mitchell, West, and Miller (1966) seem to fit this line of reasoning.

There is also another argument against the use of transects across alternes and is based on the edge-effect (Odum, 1959). The edge, ecotone, or alterne, constitutes per se a different stand in which the species composition and abundance differs from both adjacent stands. Thus, this intermediate zone is not a gradual transition between these stands or communities, but a different one, structurally, compositionally, and also functionally.

Besides all this, the location of the alterne itself, could lead to wrong conclusions, since it may be displaced for a short or longer distance if dissemination agents are acting differentially over one of the two contiguous stands.

This line of thought makes one ponder the possibility that a different interpretation could perhaps be given to some of the ecotone studies as well as those relating to the environmental characteristics of the environment, especially from measurements taken near the contiguous stand.

Theoretically, there is a simultaneous succession of soil and vegetation, no matter what the parent material. Vegetation is part of the edaphic environment and soil is a function of it besides of other environmental factors. Thus climax vegetation can only be found when there is a climax soil (Billings, 1941). The species that can grow in any soil and seral stage are those in which the magnitude of each of the environmental factors lie between the ranges of tolerance for the species. Billings (1946) has also indicated in this respect that the matrix community of the shadscale desert occurs on zonal soils of mixed minerological composition and that some of the species that compose it are characterized by having a wide tolerance limit, such as Atriplex confertifolia. Those species which have a narrower range of tolerance make the interzonal vegetation of the edaphic islands inside the general matrix, as is the case of Eurotia lanata.

Most of the plant ecological research conducted in the desert shrub types of the Great Basin has been directed toward soil relationships, especially those dealing with salinity and other chemical properties. However, not much emphasis has been placed on other aspects of this problem. Carrodus and Specht (1965), in South Australia, found that the distribution of Atriplex vesicaria and Kochia sedifolia is usually correlated with the depth to which the soil is wetted by normal rainfall. One of the differences between both species is that the first can reduce the percentage of moisture to a significantly lower level than K. sedifolia. Besides this, the depth of penetration of water was three times deeper under the Atriplex than under the Kochia.

Some of the disagreements found in the results of studies on the two species considered in the present investigation may arise from the method of sampling. Roberts (1950) and Fireman and Hayward (1952) have indicated that the influence of the vegetation on the soil is very important. In this respect, the last two authors found that the soluble salt content and the percentage of exchangeable sodium in the soil under shadscale shrub crowns was much higher than in the adjacent bare areas. This heterogeneous distribution of salts under shadscale could also be a logical explanation for the spatial distribution of the individual plants and for the presence of certain species in certain soils.

Harper (1961) has emphasized the importance of the microenvironmental characteristics of the soil surface in relation to seed germination. Thus the limiting factor may be the amount of germination sites available for the seedlings. Baasher (1961) and West and Baasher (1968) have demonstrated that winterfat tends to have a more random dispersion pattern under heavy grazing, whereas it becomes more regular as range conditions improve. This could be of great influence on the germination site availability and thus on the perpetuation and stability of a particular community. Dale (1964) has also confirmed the fact that the influence of the germination site is reflected on the germination percentage, establishment of the seedling, and even later, in the weight of plants and size of the root system.

The soils which support Eurotia lanata and Atriplex confertifolia can be easily altered by the action of vegetation. Kinsinger and Eckert (1961), in one experiment conducted under greenhouse conditions, reported that Halogeton glomeratus mulch leacheate considerably reduces germination of certain grasses and forbs. Its effects are greater as the concentration increased. Since the yield of vegetation from these two species is well correlated with ground cover (Kinsinger and Strickler, 1961) and since the leacheate production should be also proportional to the ground cover and yield, it seems logical that the environment-vegetation relationship should be studied with the micro-environmental influences of the vegetation in mind. General averages of soil samples taken at different depths, but without considering their location in relation to the existing vegetation, could give results which would easily lead toward wrong conclusions.

Hull (1962) seeded and grew E. lanata and A. confertifolia in the greenhouse in soils taken from shadscale and sagebrush communities. The seedlings grew well in cans with soil from the two locations. Nevertheless, no seedling, not even those of shadscale, emerged from soils taken at a depth of 6-18 inches and 18-36 inches from the shadscale soils. Only slight differences were found on the percentage emergence of both species in both kinds of soil. This suggests that there is not a direct relationship between species and germination in the particular soil where the community grows naturally. Seed germination could also be directly related with the presence of these two species under various environmental conditions.

Workman (1967) and Workman and West (1967, in press) have reported that there are significant variations in the germination of Eurotia lanata seeds under different levels of salinity. For all the seed sources studied, the percentages decreased as the sodium chloride varied slightly but significantly for each of the four different sources of seed. Germination percentages of seeds from the four sources were nearly equal at 3.0 and 4.0 percent concentration, and also showed severe restriction of germination. Hilton (1940, 1941) found that the highest germination of Eurotia lanata occurred when seeds were placed in a 0.5 percent NaCl solution and was slightly lower in distilled water. It also gradually declined, up to 1.5 percent and abruptly for higher concentrations.

Hussain (1966) found in this research that most shadscale seeds germinated with zero percent salt content and a few of them at a concentration of one percent, but no germination at all was found at two, three, or four percent. Twitchell (1955) concluded that only a short period of soaking was required to remove the chlorides, and so resulted in a higher percentage of germination of fourwing saltbush (Atriplex canescens). According to him, the higher germination after the treatment is an indicator that the chloride inhibits germination. However, Springfield (1964) has reported that soaking the fourwing saltbush seeds to remove the chlorides or any other inhibitor is not necessary.

Beadle (1952), working with several species of Atriplex in Australia, and Mayer and Poljakoff-Mayber (1963) with the same group of plants in Israel also have reported a decrease in germination with an increase in the salinity concentration. They related these results to seeds with various concentrations of salts in the solution surrounding them, as well as with those covered by bracteoles and without an addition of salts.

The low and high temperature regimes used by Workman (1967), Workman and West (1967, in press) and Springfield (1968a, 1968b) to study the germination of winterfat prove that there is slight influence of temperature. Although the seed source by temperature interaction appears important, the results were not significant. Springfield (1968b) studied water potential and temperature in relation to germination. He found that the germination of this species was decreased and delayed as moisture potential decreased. However, these decreases were proportionately less at lower temperatures. This means that soil drying may not be as detrimental to germination during cool weather. Temperature of germination also interacted with seed source. Statler (1967) and Eckert (1954) also mentioned the importance of temperature on the germination of this plant. The U. S. Forest Service (1948) indicates that this species germinates at 50 F nictotemperature and 77 F phototemperature, while Hilton (1941) reports that the maximum germination and seedling production occurs at a fairly constant mean temperature of 70 F. However, the most remarkable result in his study was the finding of a wide thermal tolerance since no marked decrease was found at 42 F nor at 72 F for 18 hours and 86 F for 6 hours. Temperatures above 86 F resulted in reduced germination and higher mortality of seedlings. Continuous temperature near freezing slightly retarded germination, however, and seedling growth was temporarily reduced until the temperature was raised again.

The temperature requirements for germination of several species of Australian Atriplex also pointed to a wide range of tolerance (Burbridge, 1945). The germination of A. confertifolia at 65-85 F was 69.1 percent, while only 30.9 percent at 35-65 F (Hussain, 1966). Springfield's (1966) studies with fourwing saltbush seeds have suggested that moisture stress can affect germination to a different degree according to the temperature. These results are in agreement with those found by the same author (1968b) for winterfat.

The germination of E. lanata seeds is, in general, very high under normal conditions. Asay (1959) found that the seeds treated by mechanical means germinated better than those treated with acid, but both had lower germination than the untreated ones.

Great variability in the germination of winterfat has been indicated by Wilson (1931), who reported values ranging from 5 to 88 percent from seeds collected at several dates and places.

Winterfat seeds were viable after two and one half years of storage (Bradley, 1942). There is, however, a loss of viability of seeds after the first full year (Wilson, 1931; Springfield, 1968a). Seeds of the harvest year had a 97 percent germination, while those of the previous year showed 87 percent and those of two years before were only 23.5 percent. After three and four years, the germination percentage is negligible (Hilton, 1940, 1941). Not only the period of storage but also the time of collection is important. Seeds collected in October showed less germination than those collected in November with germination increasing after two months storage.

Springfield (1968a) concluded that one and two year old seeds germinated better than older seeds. However, he also indicated that seeds 4.5 and 6 years old produced greater germination values, especially at temperatures of 6.1 C and 13.9 C. Retention of viability depends largely upon the year of collection as well as on certain undefined physiological characteristics of the seeds.

For shadscale, the germination percentage was higher in seeds collected during November as compared to those collected during September. This variation may be due to the fact that embryos are not fully mature at the earliest date and need more time in the plant to develop full viability (Hussain, 1966).

The differences in germination percentages reported for these species may also be due to the individual plant differences (Vest, 1952; Vest and Cottam, 1953; Workman and West, 1967). Riedl et al., (1964) reported significant differences in germination of seeds from different plants, even when collected on the same date. These individual differences between plants were also measured later from the vigor of the seedlings from these seeds.

The mechanism of germination in the soil could also be affected by germination inhibitors. Evenari (1949) has defined them as substances produced by plants or substances of related structures not found in plants which inhibit or delay the germination of seeds of the same or other species. The failure of germination or a reduction of it may be due to inhibitor substances, and not to conditions such as lack of oxygen, high temperature, etc.(Knipe and Herbel, 1966; Mayer and Poljakoff-Mayber, 1963; McCalla and Haskins, 1964; Martin, 1951). Reid, Verstraten,and Wilkie (1963) have reported antibiotic effects of sagebrush in Wyoming. These substances, especially if water soluble, could be important in the synchronization of germination with soil moisture conditions (Went, 1949; Koller, 1957).

Muller and Muller (1956) have reported that in some desert plants the production of a toxic material does not constitute any competitive advantage under natural conditions. The ineffectiveness of toxicity under natural conditions may be due to microbial activity, soil colloids, or inactivation by xeric conditions. This can be referred to as an ecological effect which modifies and so differs from the physiological effect of one plant over the other under laboratory conditions.

Vest (1952) and Vest and Cottam (1953) reached the conclusion that the mechanical durability of the bracteoles of shadscale fruits lasts longer than the chemical inhibitor in affecting the germination of the seeds. The fruits remain on the ground for several years before the germination starts. It only occurs when the bracteoles show symptoms of disintegration. Breakdown of bracteoles was proved to be caused by a fungus.

The most common method used to study the presence of inhibitors is to germinate seeds in petri dishes with the addition of the solution to be tested (Stout and Tolman, 1940, 1941). Vest (1952) made an extract of _A._ _confertifolia_ bracteoles by grinding them and soaking the meal in water five times its weight for 20 hours. This extract was later diluted to various proportions. Vest (1952) and Vest and Cottam (1953) found that the bracteoles contain a water soluble substance which inhibits germination, and the water extract of these bracteoles completely inhibits the exised seeds. The dilution of this extract, however, reduces its inhibitory action and the percentage of germination increases as the concentration decreases. Strickler (1956) has indicated that under field conditions, _E._ _lanata_ fruits germinated under five other vegetation types but did not become established. He did not indicate any conclusive explanation for these results but postulated that it may be related with plant exudates affecting the seedlings. The absence of winterfat seedlings observed by Strickler

(1956) on an ecotone with A. confertifolia could be indicative of this influence. However, there are also many other possible explanations.

Al-Rabbat (1963), after conducting seeding experiments with winterfat, reached the conclusion that the depth of seeding was important in the germination and establishment of this species. An increase in the depth had adverse effects, while the best results were obtained at 1.2 cm or less. Soil compaction before planting also had positive results on seedling emergence. Good results from shallow plantings were also obtained by Riedl et al. (1964) and Bridges (1941). Wilson (1931) and Hilton (1940, 1941) also concluded that it should not be seeded deeper than 1.2 cm, and the first author also reports that it could even germinate without covering if the weather conditions are favorable. Statler (1965, 1967) reports that the best seeding depth in Wyoming was 0.6 cm, while he pointed out the importance of the date of seeding, of which the best was May 17. At that date, there was sufficient moisture and the soil was warm enough for germination. After conducting several seeding studies, Brown (1962) reached the conclusion that there is very little chance of successful establishment of many of them. Plowing and drilling proved to give good results, with a density of 4.4 plants per square meter being established after one complete growing season. Brown (1962) found that from the seedlings emerging in the spring, only 2.1 to 30.6 percent survived until the spring of the following year. Bridges (1941) reported better results at deeper depths than 1.2 cm for shadscale, which was the worst treatment for this species.

The success of reseeding native range with these two shrubs has been reported by Plummer (1966). E. lanata and A. confertifolia and other shrubs at the Desert Range Experiment Station in Utah were still persisting and comprised even larger percentages in the botanical composition than on the nearby native range, twenty-five years after seeding. Tueller (1966) studied the factors influencing the establishment of winterfat in different vegetation and soil types and reported that all seeding attempts during three years were failures. In each case the establishment was less than 0.25 plants per foot of row and survival was negligible. However, if these young plants succeeded in surviving beyond the seedling stage, they would be definitely established.

Direct seedings of both introduced and native species, in the shadscale zone are low, contrasted with those in the sagebrush zone. Many problems were outlined by Bleak et al. (1965), but perhaps the most important appears to be the arid climate. Springfield (1963) in New Mexico reached the conclusion that seedbed preparation is necessary for good stands.

Seed size varied between 13,500 seeds per pound when grown under irrigation, while 27,500 and 34,500 seeds per pound when grown at two other range localities (Tueller, 1966). Wilson (1931) gives a value of 91,000 seeds per pound, while Plummer, Christen, and Monsen (1968) indicate an average of 112,275 seeds per pound for winterfat and 64,920 for shadscale. Since there is such a variability in the seed size, it could be thought that it is important in relation to seedling development. However, the first author reached the conclusion that even large vigorous seeds, twice as large as those found in the field under natural conditions, did not increase the success of seeding. Similar results are reported by Nelson (1962).

If conditions for growth of winterfat are favorable, seed production could be large. Wilson (1931) has reported values as high as 70 and 80 pounds of seed per acre under irrigated conditions in New Mexico. No information has been found for seed production under range conditions. Winterfat and shadscale seedlings were found by Harper (1959) to be more abundant on grazed areas than on non-grazed control plots. West and Stoddart (1964) found that the number of seeds per plant of winterfat in Curlew Valley, Utah, as well as in other locations, was greater for grazed than non-grazed plants. Protection, in general, resulted in an increase in vigor, and higher yields were obtained inside the exclosure than outside. This would seem to indicate that the lower reproductive capacity of the protected plants of winterfat is due to a loss of individual plant vigor.

It is possible that seedling production could be influenced to a large degree by the seed production of the population. The amount of seedlings could be affected by temperature, since it has been found by Telwar (1961) that a -23 C temperature killed winterfat plants although they grew better at 4.4 C nictotemperatures. Grazing is one of the most important factors in seed and seedling production and establishment of this species (May, 1963).

Halogeton plants start to appear in closely clipped plots but not on those moderately and lightly utilized. The increased abundance of this plant is a consequence of the weakening of E. lanata (Tueller, 1966). The increase of halogeton or any other annual could have considerable effect in the soil such as has been reported by Eckert and Kinsinger (1960). This effect in soil could finally affect seedling establishment.

Inter- and intra-specific seedling competition could also be important in the understanding of the synecological relationships of these two species. Ferguson (1962), who studied methods of establishing Purshia tridentata, reached the conclusion that from the standpoint of seedling survival, planting more than one seed per spot appears to be advantageous, thus finding a positive interference on their seedlings. Later, Ferguson and Basile (1967) concluded that the chance of any seedling surviving until the end of the growing season increased as the number of seedlings emerged per spot also increased. This could be explained on the basis of the creation of a beneficial environment, which is created where several seedlings grow together, thus increasing the survival rate. One of the negative consequences of this grouping is speeding the date of emergence, thus increasing the chances of frost damage.

With annual plants there is a negative effect on bitterbrush seedlings. In cheatgrass stands, Holmgren (1956) has indicated that only a few bitterbrush seedlings were capable of survival the first summer because of interference of the annual. However, the same seedlings were more able to compete with broad-leaved annual weeds than with the grasses. Those seedlings that grow during the first season free of competition are more vigorous and subsequent competition didn't affect them.

Heady (1956), working with natural mulches on an annual grassland, found that the amount of litter present on the soil surface directly affected the vegetation. The increase in mulch increased the herbage production as well as induced changes in the botanical composition and size of the plants. Under natural conditions, the slow changes in the amount of natural mulch present on the soil surface may facilitate, under certain circumstances, the introduction of new species during successions (Olson, 1963). The alteration in the mulch productivity parameter with the rate of decomposition modifies litter and soil conditions. Thus, a modified microenvironment may further alter, in turn, the successional pattern and climax. The amount of litter on the surface could be greatly influenced by the utilization. It is usually larger on the ungrazed areas than on the grazed ones (Evanko and Peterson, 1955), and thus may influence the amount of water infiltration on the soil or the availability of germination sites.

The most evident differences between grazed and ungrazed areas is usually the density and botanical composition of the range (Costello and Turner, 1941). West (1966) has reported that in Curlew Valley, Utah, after ten years of comparing exclosured with grazed vegetation, the most important change was the loss of density and areal extent of winterfat and perennial grasses in heavily grazed situations. _E. lanata_, when heavily grazed by livestock rodents, and lagomorphs loses ground to shadscale and big sagebrush. The utilization of 20 percent of the current years growth of _E. lanata_ during the summer prevented seed production, while a winter clipping up to 95 percent of the current growth allowed at least some viable seeds to be produced (Eckert, 1954). Ants and other seed eaters could also have important consequences on the reproduction of the community (Bohart and Knowlton, 1953; Wight and Nichols, 1966). Range utilization is perhaps the factor which has the greatest influence in the reproduction of these species populations.

Besides those aspects related with reproduction of the plants at seed production, germination, emergence and establishment, other properties of the population are also important. Longevity of the plants, which has barely been studied, is also of considerable importance. Asay (1959) reported the life span of winterfat plants to be from 17 to 74 years with a mean of 36 years. The season of use is extremely important in relation to mortality of these two species. Cook and Stoddart (1963) have indicated that desert plants can be grazed in late spring only if herbage removal is 30 percent or less. The desert ranges are best adapted to winter grazing and when used in this season, there is less mortality of plants.

Most researchers who have dealt with salt desert shrub vegetation have tried to explain the distribution and presence of one species on a certain area, solely based on one environmental characteristic and that is soil, especially certain factors such as soil salinity (Shantz, 1925; Shantz and Piemeisel, 1940; Kearney et al., 1914; Billings, 1945). Other workers (Gates, Stoddart, and Cook, 1956; and Mitchell, West, and Miller, 1966) have also included some other edaphic characteristics.

Went, Juhren, and Juhren (1952) presented a more general discussion on all the possible mechanisms which may be responsible for the presence or absence of one species in a certain area. They are grouped into the following categories: distribution and presence of seed, differential germination, competition, soil differences, climatic differences, pest and diseases, and differential survival. However, they also indicate that in most plant communities these mechanisms are mixed and it is impossible to isolate them. The inherent unity of the stand rests upon the fact that it is not merely the response to a particular environment but it is at the same time, the expression and indication of it. The visible continuity and the sessile nature of the plant community are peculiarly helpful in indicating the environmental limits under which the community develops. Thus, it provides the fullest possible integration of all physical factors (Clements, 1949).

There is, however, an indirect effect of the environment acting in relation to competition. Litav, Kupernik, and Onshan (1963) have demonstrated the high mortality of the seedlings of a low shrub species is due to the presence of annual plants which exert their influences, even after completing their life cycle. The same seedlings are successfully established and the rate of mortality greatly reduced when they are grown free of competition. In this case, the environment acts directly upon the annual plants, and the annuals are the ones that limit the establishment of the perennial plant seedlings. This evidence goes even further when they improved the environment for growth by adding irrigation and fertilizers. The negative effect on the seedlings was due to the greater increase in the growth and developmental rate of the annual, and so greater competition. This antagonistic effect could be explained on the basis of negative influences induced by roots or plants exudates, as has been suggested by Woods (1961).

In order to have a clearer picture of the ecological relations of the area, a dynamic understanding is also necessary. Clements (1940) has indicated that the badlands of the sagebrush disclimax are characterized in initial stages by colonies of annual halophytes, while the first stage of importance is formed by low perennial species of Atriplex nuttallii, A. corrugata and others. These are followed by A. confertifolia, while the final stage comes after the invasion by Artemisia tridentata. Hutchings and Stewart (1953), McArdle and Costello (1936), and Weaver and Clements (1938) have indicated that winterfat on certain soils represents the climax stage.

Shadscale and winterfat are often found on extensive areas forming pure stands. However, they can also be found as components in some other communities (Allred, Beck, and Jorgenson, 1963) indicating a different and broader range of environmental tolerance. Branson, Miller, and McQueen (1967) concluded that soil moisture relationships are the primary cause governing the presence of different plant communities in the salt desert shrub vegetation type. Quantities of soil salts also appeared to be important as a cause of community differences. The major effect is in the osmotic potential contribution to total soil moisture stress. This is the explanation why the so called halophytic species are not always found under saline conditions. Harris and Young (1936) demonstrated that alkalinity rather than salinity is important as a determining factor of the distribution of these desert species. This is an effect of the soil on the vegetation, since from the evidence they obtained these plants play a minor role, if any, in bringing about chemical changes in the soil that might influence the type of vegetation a habitat may ultimately carry.

The moisture regime in the soil under different stands may differentially affect the vegetation, thus directly influencing the botanical composition of the community. Since on the average, the amount of precipitation received on continuous stands should be similar, the differences in water balances should then arise from differential water use, movement, and evapotranspiration.

A large number of empirical or semi-empirical equations have been derived to estimate the potential evapotranspiration of an area, using climatological data such as Blaney and Criddle (1950), Penman (1952), and Thornwaite (1948). Some of these formulas, in addition, include a vegetational factor. Tanner (1960) considered that the energy balance method which measures the radiation exchange at the surface is a reasonable method for daily estimates. Taylor and Haddock (1956) also concluded that the amount of water removed from the soil is largely determined by weather factors and is quite insensitive to the water potential of the soil, and the availability of water depends on the rate the energy is used by the plant in removing water at a required rate.

Most of these formulas, however, have been developed for irrigated crops and are only useful between the limits of the available moisture in the soil, that is one-third and fifteen atmospheres of moisture tension. Because of the difficulties of direct soil moisture measurements, a large number of the empirical formulas which have been developed for estimating the evapotranspiration uses readily available climatic data such as temperature, humidity, and wind speed. Other formulas also include net radiation and soil heat flux (Halsted and Covey, 1957).

Many papers have presented information which leads to the conclusion that energy availability is not the only important factor influencing evapotranspiration. Makking and Van Heemst (1956) demonstrated that the real evapotranspiration falls below the potential one when the soil is drying. The rate of reduction depends on the moisture tension of the soil and on the intensity of the potential evapotranspiration. Bierhuizen (1958) demonstrated under laboratory conditions that the rate of transpiration increases with the increase in available moisture content from the wilting point and becomes nearly constant at higher water potentials.

Lemmon, Glasen, and Satterwhite (1957) went even further and concluded that evapotranspiration is a function of soil, plant, and meteorological factors. In summary, they concluded that evapotranspiration cannot be predicted strictly on the basis of meterological variables, and that the soil water potential is not the only factor governing water loss. The plant itself is important on the system of water transfer.

The moisture condition in the soil may be the main factor governing the distribution of the shrubby vegetation (Branson, Miller, and McQueen, 1967). The capacity of these plants to tolerate a low water potential in the soil may be a better indication than the salt content alone. In this respect, the total water potential is a better measurement of this factor than the osmotic potential alone.

Rickard (1967) found that in two adjacent stands of greasewood and sagebrush, the soil moisture accumulated during fall and winter appears to be a consequence of decreased evaporation losses and lack of transpiration from shrubby species, which are leafless during winter and early spring. These results are also confirmed by Rickard and Murdock (1963) who found that the soil moisture was nearly maximum in early March and became steadily depleted after this time. They also confirmed the hypothesis that _A_. _confertifolia_ was found on areas with more restricted moisture than other nearby communities and the permanent wilting percentage of the surface soil of the Eurotia - Atriplex community was unduly high with regards to its moisture equivalent value.

DESCRIPTION OF STUDY AREA

The field studies described in this chapter were conducted in Curlew Valley, Box Elder County, Utah. In addition to the work carried on directly under field conditions, a part of this research was done in the greenhouse and growth chamber at Logan.

Curlew Valley is located in the northwestern part of Utah. The location of the area corresponds approximately to the coordinates 45° 15' north latitude and 113° 5' west longitude. The immediate study area is in a lacustrine valley located at 1350 meters (4430 feet) above mean sea level and 10 kilometers (6 miles) north of Kelton (Mitchell, 1965). The area has been used by the College of Natural Resources of Utah State University for many years and constitutes the main center of research for the salt desert shrub vegetation in the northwestern part of Utah.

Besides the climatological influence of the elevation on the vegetation itself, there is also the historico-edaphic influence. The soils were formed under a lacustrine influence by the direct genetic origin of the prehistoric Lake Bonneville. The influence of the lake is even more significant since it has been indicated (Eardley, Gvosdetsky, and Marsell, 1957), that the elevation of this area corresponds approximately with that of the shore line at the Stansbury stage. The same authors have indicated that the average elevation was around 1363 meters between 23,000 to 13,500 years ago. However, the shore line elevation fluctuated between 1356 to 1365 meters. This variation in elevation of the shore line and the location of the experimental areas explains to a great degree some of the soil variabilities found in the area both in relation to their parent material as well as in their physiographic characteristics.

The shore lines, as well as other influences of Lake Bonneville, are at present time almost unmodified (Gilbert, 1890). There are, however, some intersecting streams which have interrupted their continuity on small areas, but the embankments, beaches, and bars are almost as perfect as the day when the lake began lowering its level.

The differences in the water level of this prehistoric lake were influenced mostly by temperature and precipitation changes which occurred during the late Pleistocene (Wright, 1896; Flint, 1957). There were two main high water levels interrupted by a lower level caused by an arid climate. These variations in water level caused a whole series of changes on the parent material of the soil where the study was conducted.

The effects of wave action from lake waters are now clearly understood, and a characteristic profile of equilibrium has been developed (Gilluly, Waters, and Woodford, 1959). The water movement along shore lines influences the erosion,deposition, and transport of materials, thus developing the characteristic profile. This profile is influenced mostly by size and shape of particles and by the characteristics of the wave action. Thus a different physiographic aspect may indicate also different soil characteristics. Gvosdetsky and Hawkes (1953) have shown that there is a strong zonation of the soils at the Stansbury level, and that this zonation could also be the cause of the pattern of distribution of the plant communities which now covers the area.

The water level and the location of the shore line was also influenced by the littoral vegetation which developed around Lake Bonneville. The beach composition and mobility is influenced by the characteristics of the vegetation which developed under the environmental conditions which existed when the lake was formed (Scott, 1963; Perkins, 1963).

The physical characteristics of the soils where the study was conducted has been described by Mitchell (1965) and by Mitchell, West, and Miller (1966). They reached the conclusion that the soil profile under the pure _E._ _lanata_, _A._ _confertifolia_, and that of the mixed stand and the ecotone of both species are essentially identical. The only differences between them was a slight increase in root concentration and in the hardness of the C_{Ca} horizon going from the pure winterfat toward the shadscale community. The same fraction of the soils from these three locations was completely uniform in composition. These results, as well as the X-ray analysis, also corroborate the findings that there were no basic differences in the physical or morphological composition of the soil between these two pure communities. Especially noticeable is the fact that the soil texture, bulk density, and compressibility of the upper two horizons are extremely homogeneous. They concluded that not any obvious evidence of the influences on the vegetation by soils exists, and vegetation does not seem to induce soil changes.

The role of some soil chemical and physical factors in the distribution of these two species in the salt desert shrub vegetation type was studied by Gates (1956, 1958) and by Gates, Stoddart, and Cook (1956). The only five significant differences between these communities, including some in Curlew Valley, were for total soluble salts, saturation extract conductivity, exchangeable sodium, one-third atmosphere percentage and soluble sodium. Shadscale was found on areas with 0.53 percent salt, while winterfat was found on areas with 0.36 percent. The exchangeable sodium was also greater for shadscale, 3.7 m.e. per 100 grams of soil, while for the other species, it was only 2.5 m.e. The field capacity for soil moisture was also greater for shadscale. They concluded that the density of the plants had little correlation with these soil characteristics. Since they found a comparatively wide tolerance range for these species, they suggested the possibility of ecotypic variation.

Billings (1945) has described the cold desert vegetation of the Western Great Basin in relation to soil characteristics. He indicated that the subsoil of those areas where shadscale naturally develops is usually saline, but questioned the universal association of shadscale with this characteristic. He observed a tendency to find shadscale on areas with saline subsoil, but judged it not to be a requirement of the plant. Evans (1926) referring to the Salt Lake Valley also indicated the close association of this plant with a high content of salinity in the soil.

Shantz and Zon (1924) also reached the conclusion that *A. confertifolia* is a salt tolerant plant, but there is not a universal association between them. It can occur in areas where the salt concentration of the subsoil is as great as 1.15 percent or even higher, but it thrives best where the concentration is much lower, around 0.09 percent. In later papers, Shantz (1925) and Shantz and Piemeisel (1940) have restated the same conclusion.

The general characteristics of the soil in relation to the horizontal arrangement of the species in the salt desert shrub vegetation type has been described by Kearney et al., (1914). They indicated that sagebrush occurs chiefly on coarse textured soils with low salt content, while shadscale occurs in the center of the valley on soils with a high salt content below the depth of 1 or 2 feet. Fine textures, high salinity and a midsummer moisture deficit are the main characteristics of the habitats where shadscale naturally grows. However, they also indicate, that in other areas shadscale is also present where there is not a highly saline subsoil, and where the soil is too dry and gravelly for sagebrush. Thus, from this presentation, it is clear that A. confertifolia naturally occurs in areas of variable edaphic characteristics. To relate it with a single, simple factor or explanation is not adequate in understanding its behaviour. Winterfat also occurs in areas where there is some salinity in the subsoil but such values are generally lower (Shantz, 1938). Shantz reports that it is a dominant of climax vegetation on certain soils in that region. However, the edaphic or climatic reasons which restrict winterfat to certain environments and not to others are not clearly explained or understood.

There are, then, some definite soil characteristics associated with sites where shadscale and winterfat naturally grow forming pure communities (Shantz and Piemeisel, 1940). Shadscale usually grows where salt content on the surface is low but in the subsoil at 2 or 3 feet depth, the percentage of salinity rises above 2 or 2.5 percent. Winterfat, however, grows in soils of fine texture with low salt content in the upper 2 feet, but with only up to 1 percent in the subsoil, and has higher water requirements.

The communities studied are: one of pure shadscale, another of pure winterfat and a third, a mixture of both species. The winterfat community appears monospecific. There are, however, some occasional scattered shrubs of *A. tridentata* growing alone or in groups of a few individuals. There are also some rare, isolated plants of *Sitanion hystrix*. In the open spaces in this community, there is often found during the wetter growing seasons variable amounts of annual plants, among which the most outstanding for its abundance is *Halogeton glomeratus*. There are also some other occasional annuals which represent a very small percentage in the botanical composition (Figures 1 and 2).

The botanical composition of the pure shadscale communities is almost one hundred percent *A. confertifolia*. There are, however, some occasional individuals of *Sitanion hystrix*. Among the annuals *Halogeton glomeratus* represents most of the cover by this group of invaders. Occasionally there are also some individuals or groups of *Bromus tectorum* (Figure 3).

In between these two areas there is a third community represented by a mixture of *Atriplex confertifolia* and *Eurotia lanata*. Besides these two perennials there is the grass, *S. hystrix*, which is uniformly present in all this area and constitutes a large percentage of the botanical composition. Among the annuals, *Bromus tectorum* is the most important. *Halogeton* is also conspicuous, but contributes a smaller percentage. Other annuals are only occasionally represented (Figure 4).

The pure stands of both species are divided by a fence into two

Figure 1. General view of the grazed E. lanata stand. The isolated taller shrubs are Artemisia tridentata. The Wildcat Hills are in the background.

Figure 2. Close up of a sector of the ungrazed E. lanata stand. Soil cracks, surface litter and microrelief are the main characteristics of the microhabitat. A dime is used for size comparison.

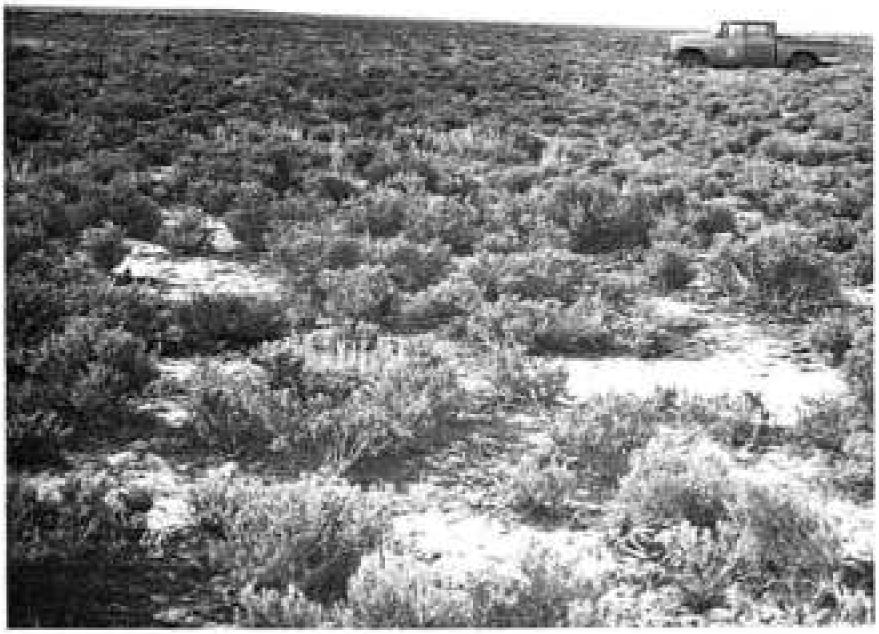


Figure 3. General view of the grazed stand of A. confertifolia. Most of the small plants are seedlings of Halogeton glomeratus.

Figure 4. General aspect of the mixed stand of A. confertifolia - E. lanata. The annuals in between the shrubs are mostly Bromus tectorum.

conditions. One of them corresponds to the exclosures in which both livestock and rabbits have been deprived of its utilization. The exclosures were constructed in 1955 and have been maintained up to the present date. Both exclosures now have, approximately, a similar botanical composition, with a slight difference in the percentage of perennial grasses, which is higher in the ungrazed area. However, the density in the excluded areas was larger than in the grazed stands (West and Stoddart, 1964).

There is, finally, another type of vegetation which in this paper has been called the E. lanata - A. confertifolia ecotone. It corresponds to an area mostly covered by winterfat but which has scattered shrubs of A. confertifolia, and it is located around 0 to 30 meters from the pure E. lanata stand. These ecotones are present in the winterfat area, both in the grazed as in the ungrazed portion (Figure 5).

The vegetation of the area is known with the general name, the salt desert shrub vegetation type. This type is particularly important in Utah since it covers approximately 49 thousand square kilometers (12 million acres). This is about 22 percent of the land area of the state. Curlew Valley is part of the "West Desert" or the Great Basin side of the Wasatch Mountains (West, 1966). The area represented by this type of vegetation in the whole United States is approximately 15.4 million hectares (38 million acres) (Branson, Miller and McQueen, 1967; Kuchler, 1964).

The potential natural vegetation for the whole area corresponds, according to Küchler (1964), to the Saltbush-greasewood type, which is physiognomically characterized by open stands of low and dwarf shrubs,

Figure 5. Fence line contrast of an area inside and outside the E. lanata exclosure. At left the exclosure and at right, the constrasting grazed area. In the front part is the ecotonal E. lanata - A. confertifolia while in the back is the Eurotia lanata stand.

and half shrubs. The main dominants in this type are A. confertifolia and Sarcobatus vermiculatus, while other important components are Artemisia spinescens, Atriplex spp., Eurotia lanata, Kochia americana, Graya spinosa, and several others. Shreve's map (1942) is more specific and indicates the extent of the shadscale community and that of the winterfat. Flowers (1934) has described this same vegetation in a similar way and with approximately the same subdominants. However, he named it the shadscale association.

The most conspicuous primary consumers of the vegetation are the blacktailed jack rabbit (Lepus californicus, Gray). Because of their abundance, size and amount of forage consumed, they are one of the most important herbivores (Wagner, 1964; Currie and Goodwin, 1966).

This whole area is moderately grazed most years by sheep. The season of use is during the latter part of winter and early spring, while the rest of the year it remains unused. During the 1968 and 1967 seasons, the area was not grazed at all by domestic livestock while during the previous season, it was intensively utilized.

Another important primary consumer is the harvester ant (Pogonomyrmex owyheei, Cole), which probably is not as important in energy flow in the ecosystem as they are in some other ecological relations of the plant community such as the reproduction and mortality of the perennial shrubs (Sharp and Barr, 1960).

Climatological data, mainly temperature and precipitation, have been recorded since 1956. Appendix table 13 and figure 6 indicate the mean monthly precipitation for the ten-year period between 1956 and 1965, as well as the absolute maximum and minimum for that same period (Fears, 1966). Besides this, the monthly values for the years 1966 to 1968 are also indicated (Cook and Stoddart, 1966, 1967). Appendix table 14 indicates the long term monthly temperatures, as well as the mean maxima and minima. A general description of the study area and the location of the plots and exclosures is indicated in figure 7.

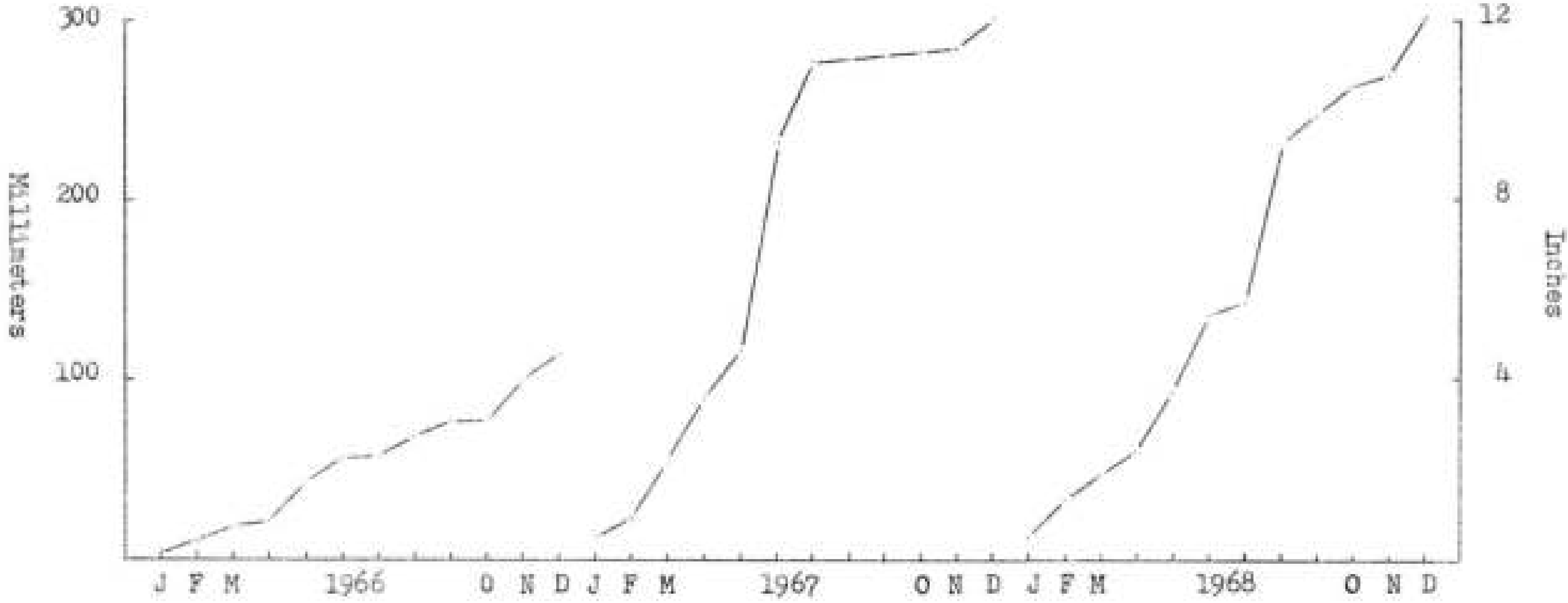


Figure 6. Accumulative monthly precipitation at Curlew Valley for the period 1966 to 1968.

Figure 7. Aerial photograph of the study area in Curlew Valley. (a) E. lanata exclosure, (b) A. nuttallii exclosure, (c) pure A. confertifolia exclosure, (d) pure A. confertifolia, grazed, (e) grazed mixed stand, (f) grazed pure E. lanata stand, (g,h) location of ecotonal studies in Mitchell's (1966) study.

MATERIALS AND METHODS

The main objective of this study was the search for environmental factors, in addition to grazing pressure, which may cause changes in the relative importance and distribution of *Atriplex confertifolia* and *Eurotia lanata* in the Great Basin Desert. The study as a whole was divided into seven parts to accomplish these objectives.

The first part of this study concerns phenology. Phenological development was determined throughout the year. During the early and most active part of the growing season, determinations were made once a week, while later in the season readings were made only every two weeks or once a month during the winter.

The phenological development of twenty permanently marked, mature plants were studied in each experimental area. The areas included the pure stands of *Atriplex confertifolia* and *Eurotia lanata*, both in the grazed area as well as in the ungrazed area. The data provided in this study actually only represent ungrazed plants since the area was not utilized by livestock at all during 1967 and 1968.

A phenological scoring system was used. Scores were as follows: 1. Winter dormancy, 2. Apical buds swelling, 3. Twigs elongating, 4. Floral buds developing, 5. Flowers opening, 6. Fruit developing, 7. Fruit disseminating, 8. Fall dormancy, 9. Fall bud swelling, 10. Fall twig elongation, 11. Fall floral buds developing, 12. Fall flower opening. Each individual plant was scored at each reading to the closest 10 percent by estimation of proportion of plant parts involved.

Seed production of these two species was studied in pure stands as well as in a mixed stand of both species. The influence of grazing on the amount of seed production was also included as part of this research. In doing this, comparisons were made of seed production in adjacent areas, one of which has not been grazed by livestock, small rodents or lagomorphs since 1955, while the other has been grazed almost every year excepting the 1967 and 1968 seasons. The first area is referred to as "exclosure" or "ungrazed" while the other is the "grazed area" or "outside the exclosure". The comparisons of the grazing effect on seed production were only made on the pure stands of both species.

Twenty plants bearing fruits were randomly chosen in each location, and of each species. For pure stands, both grazed and ungrazed conditions were evaluated while in the mixed stand of both species, no control over grazing was exercised because of lack of an exclosure. Plants were covered on the third week of August, 1967 and in 1968 with nylon net bags such as suggested for bitterbrush by Seegrist, Neal, and Hubbard, 1966. Bagging the plants permitted a complete count of winterfat and shadscale fruits and seeds. The nets were removed in December of the same year the plants were bagged (Figure 9, page 62).

The fruits collected in the field were brought to the laboratory where they were counted. However, for those collected in the 1968 season, only a sample was taken and weighed and thus an estimation of the total fruit and seed production per plant was made.

In this study a fruit was considered a mature ovary with the accessory structures surrounding and protecting the seed. However, often no seed was found inside the external structure. A seed was defined as a visible embryo and would presumably develop into a new plant if sown.

The percentage of fruits filled with fully developed seeds was also calculated. During the first season, the calculations were made separately for each plant, while the following year only the mean of all plants at each location was determined. A sample of one hundred fruits per plant was analyzed for seed fill, if the plant produced as many or more seed; while if the plant produced less, all the fruits were analyzed. On the other hand, during the second season, only a general sample of 300 fruits was taken from each of the five sampling areas, and the percentage of the filled ones was calculated. The product of the number of fruits per plant times the percentage filled gave the number of seeds per plant.

Mean percentage of fruits filled was calculated in two different ways during the 1967 season. The first method involved adding the percentage filled on each plant and dividing by the number of plants. The other value is a weighted mean in which those plants with larger numbers of fruit contribute to the mean in a larger proportion. It was calculated by dividing the total number of seeds produced by all the plants of the same species in each area, by the total number of fruits of all plants of the same species.

The weight of 1000 fruits was arithmetically calculated for the 1967 season for each plant and area after determining the number of fruits and seeds and their respective weights. For the 1968 season, the weight of 1000 fruits was calculated by weighing 200 fruits from each area and species and multiplying by five. The seed weight per plant was calculated arithmetically using the values previously calculated from the weight of 1000 seeds and the number of seeds per plant.

The transformation of individual plant values into area values required the calculation of the plant density of each species in each area. The total density and the density of plants with and without fruits was determined. The product of the number of individuals bearing fruits per unit of area times the mean value per individual gives as a result the value expressed on a surface basis. Results were expressed per ten square meters, since often the seed and seedling production densities were so small that only a fraction of a seedling would have been represented in fractional area units.

The density of A. confertifolia was determined in the field by using ten rectangular plots of 4.50 square meters, that is 0.75 by 6.00 meters. The winterfat density was determined by using 20 circular plots of 0.89 square meters. For E. lanata, this calculation was arbitrary since it is not always possible to distinguish in the field one individual plant from another. The criteria was to consider as one individual plant a group of stems living together at an average distance of less than 5 to 7 cm from each other and separated 7 to 10 cm or more from other groups of stems. In any case, this gives a general impression of a group or unit. Whether or not this represents the actual number of plants per unit of area, it is not known, but the important thing is that the criteria used for determining density and bagging for the seed production study were the same.

No analysis of germination was made from the seeds collected in the nylon net bags. The reason is that since the bagged plants probably underwent some substantial modification in the microenvironment under which the seeds were formed and developed, this could have influenced their germination and introduced unknown effects. Since the main objective of this part of the study was to determine the amount of viable seeds per plant and per unit area, and since previous results have shown some contradictory results and extreme variability, only hypothetical calculations of germination were made. Percentages of germination reported by some of the previous workers on these two species under the most varied conditions were used and combined with the actual values of seed production obtained in this research.

The third part of this study consisted of the analysis of the germination characteristics of these two species under controlled environmental conditions. The study was conducted in a growth chamber under a 13-hour light period and 11-hour dark period with 15.0 C and 4.5 C temperatures respectively; no control of the relative humidity of the air was possible.

Seed germination was conducted on soil samples taken from Curlew Valley from five sites of close proximity rooting pure winterfat, pure shadscale, mixed winterfat-shadscale, pure nuttall saltbush (Atriplex nuttallii) and pure big sagebrush (Artemisia tridentata). This study was conducted to determine if there are any inherent characteristics of the soil, physical, chemical or biological, which would induce an antagonistic effect on the germination of seeds from these two species. Such effects could reduce or increase the germination percentage, or even completely prohibit germination on a different soil.

The soil samples were taken from Curlew Valley, on the second week of June, 1967. Samples were taken at random from ten different spots at each site. Two sets of samples were taken,one which corresponds approximately to the upper 2.5 cm of soil or soil crust which naturally forms in some soils. The other set represents the soil found from 2.5 to 25.0 cm depth. The reason they were split into two sets of samples is because the deeper sample more typically represents the upper 25 cm of soil without a concentrated effect of the vegetation, while the surface sample may possess a much greater effect of vegetation on soil. The latter design probably gives more of an indication of soil on vegetation while the former one better represents the effect of vegetation on soil.

These soils were thoroughly mixed in the laboratory and later used both for the germination study and the evaluation of seedling growth and development.

Samples of these ten soils were placed in small square pots of 1 cm per side and 7 cm deep. The soil samples used in all the germination and seedling studies were not sterilized or otherwise treated.

Twenty-five well developed seeds of A. confertifolia were buried about 0.6 cm deep in the soil of each pot. They were covered with a thin and transparent polyethylene shield, in order to protect them from excessive evaporation. Pots were watered every day with distilled water.

A second germination analysis was conducted in petri dishes. This test employed the same ten soils, but this time twenty-five seeds each of shadscale and winterfat were placed on the surface of the soil, inside the petri dishes. Moisture percentage was kept around saturation.

The shadscale seeds used were collected in Rush Valley, Utah, thirty-two months before and stored at room temperature. Those of the other species were collected twenty months earlier near La Sal, Utah.

The reason two sets of germination analysis were made, one with buried seeds and the other on the surface, was to try to detect if there was any difference between them and so distinguish between possible chemical and physical causes. The germination on upper and deeper soil was made to evaluate possible biological soil influence on germination.

Continuing with this line of research conducted under homoclimatic conditions and absence of interspecific competition, an experiment was conducted to test the influence of soil on seedling growth. The same ten sources of soil were used, but this time they were placed in pots filled with three kilograms of soil.

Seeds of both species were germinated in petri dishes on a peat moss substrate. Once they germinated and the seminal root was approximately 1.0 to 1.5 cm for E. lanata or 0.5 to 1.0 cm for A. confertifolia then they were carefully transplanted to the pots, where they were irrigated with distilled water. The soil was continuously kept around field capacity.

Six seedlings of E. lanata were planted in each pot whereas two or sometimes three seedlings per pot of A. confertifolia were established. On the 25th day after transplantation, the pots were thinned with only the three tallest seedlings of E. lanata being kept while only the two tallest of A. confertifolia were allowed to develop further. The small number of plants in this last species was due only to the difficulties in obtaining them. They remained in the growth chamber 55 days and then were moved to the greenhouse because they started to etiolate.

Measurements of the shadscale plants were made after 30, 50, and 75 days, whereas measurements of winterfat were made at 40, 70 and 110 days after they were seeded. The measurements taken were: total maximum height of the plant, the number of leaves and the dry weight of the top. The number of leaves refers to those longer than 0.3 cm for the first species and 0.5 cm for the second.

Later the same experiment with only E. lanata was repeated in the greenhouse. Measurements were made at 80 and 125 days after seeding. Total maximum height, number of leaves and dry weight of the plants were measured the same as described above. In addition, the total stem length and the percentage of plants in flower were also calculated. The first of these values represent the sum of all the stem length of the plants, while the other, the proportion of plants which have at least one flower.

The soils in which these germination and seedling growth studies were conducted were analyzed for cation exchange capacity, organic matter, texture, moisture percentage at -33 and -1500 Joules/kg, total salinity, total nitrogen and pH.

Another part of this research dealt with seedling emergence, their survival and growth, under field conditions in Curlew Valley. A series of transects of 0.15 by 25.0 meters were established before the 1966 season. Two transects were located on the grazed area of pure Eurotia lanata and three on the ungrazed area, another on the ungrazed ecotone, and two on the grazed ecotone. Finally, another was established on the mixed stand of the two species and one on the pure stand of shadscale. Later in 1968, the number in those last two stands was increased to a total of three transects in each location.

The designation "ecotone" for some of these transects is in some respects arbitrary. They are located in areas predominantly with E. lanata but with occasional plants of A. confertifolia. The area, in general, has been denominated for a long time as pure winter-fat stand, in the center of which is a large exclosure. Four of the transects are located inside the ungrazed area, and another four are located near each of them but on the grazed area. The results from the grazed and ungrazed transects are, in many respects, comparable thus providing information for the study of the effect of grazing on seedlings.

Each seedling was identified with a large plastic turkey leg band and a numbered metallic tag, secured to the soil surface with bobby pins. After the seedling germinated and emerged, it was tagged for later identification. The date when a seedling was first tagged is an indication of the approximate date of emergence. The location of each seedling was also recorded in respect to distance from other adult plants of the same or different species and to other seedlings. The nature of the ground cover where the seedling was found, in relation to litter, was also recorded.

Periodic measurements of seedling development and growth were also made. The height of the plant, the number of elongated leaves and the product of both, along with the date of mortality and circumstances under which the plant died were determined.

A sixth part of this research consisted of the study of water relations in these stands. The soil moisture content below 15 cm and its variability throughout the year was measured by the neutron scattering method. The principles on which this method is based and its description has been made by Taylor, Evans, and Kemper (1961).

Ten plots were established in the grazed stands of E. lanata and A. confertifolia, as well as in the mixed stand of both species. The plots were located at random along a 30-meter transect. Each plot consisted of an aluminum tube introduced into the soil profile as deep as 1.60 meters while 14 cm were left above ground. Measurements were made at variable time intervals, according to the time of year. Measurements were more frequent during April through June, usually at weekly intervals, while during the last part of June and July at bi-weekly intervals, and the rest of the year at monthly intervals or occasionally.

Measurements of soil moisture by volume were made at 30, 60, 90, 120, and 150 cm depth. The curve which expresses the relationship between moisture percentage and soil matric potential was determined for each stand and at each depth. Four soil samples were randomly taken and analyzed in the pressure plate membrane at -33, -67, -100, -300, -500, -1000, and -1500 Joules per kilogram. Later the value calculated by this method was transformed into moisture percentage by volume using the bulk densities calculated.

Moisture percentage by weight in the upper 2.5 cm was assessed in the same 3 areas. Twenty soil samples were taken at random from 2 transects of 30 meters each. Each sample was placed in a separate tin can and sealed with a plastic tape. Their moisture percentage was later calculated gravimetrically after determining the wet weight and the oven dry weight of the soil sample. The soil samples were dried in the oven at 105 C for 48 hours or longer. The location of the sample in relation to the nearest adult plant was also recorded.

In a similar way, 10 samples were taken on each area at a depth of 5.0 cm, that is between 2.5 and 7.5 cm. Another group of samples was taken from the same areas but from 0.0 to 15.0 cm depth, and the moisture content determined in the same way.

The root biomass was determined in the three locations, and at the same depths at which the moisture determinations with the neutron probe were made. Only the dry weight of the finer roots, those of less than 1.5 mm diameter, was included in this study. The soil samples from where the roots were taken, were obtained with a soil auger of 7.8 cm diameter. The procedure used in its determination was as described by Shuurman and Goedewaagen (1965). They were separated from the soil by immersing the whole sample in a container full of water and later removing the floating particles. After carefully washing of the roots in water, the thicker roots were removed as well as the soil particles. Finally all roots extracted were oven dried and weighed.

The last part of this research included the study of soil salinity and reaction on the upper surface of soil and its variation throughout the year.

The salinity determination as well as the soil reaction were made in the laboratory using the same soil samples taken for the determination of soil moisture percentage on the upper surface of soil at three depths from 0 to 15 cm. The wheatstone bridge was used with the saturation paste, as described by Richards (1954). The pH of the samples was also determined on the paste with an electronic indicator.

RESULTS AND DISCUSSION

Phenology

The results of this study indicate that during the years studied plants interrupted their dormancy and started to grow during the second half of March or early April. At this time of the year there was abundant moisture in the surface layers of soil, where most of the roots are concentrated. Moisture accumulates in the soil during the winter, when the water losses are reduced because of the low temperature and thus reduced evapotranspiration.

During the 1967 season, the apical buds of E. lanata were still dormant by March 22, as indicated from a phenological index of 1.0. Those of A. confertifolia were already swelling at that date and had a phenological index of 1.6. Some plants were still dormant and their index was 1.0 while others had one hundred percent of the buds swollen and thus their index was 2.0.

One week later, on March 29, the mean phenological index of E. lanata was 1.7 and most of the plants had at least some buds swollen. On April 12, most of the plants had all their apical buds already swollen and thus their mean index was 2.0. A. confertifolia had also an index of 2.0 and most of the buds were already swelling but there was no twig elongation.

During the second half of April twigs of both species started to elongate. On April 26, the phenological index of E. lanata was 2.8 and 2.7 for A. confertifolia. This means that on the average 80 and 70 percent of the twigs, respectively, were elongating. By May 10 and 17, the twig elongation increased and an average of 100 percent of the twigs were already elongated.

By the end of May, the phenological index of the individual plants of E. lanata was around a mean of 3.3 and had a range of 3.0 to 3.9. This means that a mean of 30 percent of the twigs had floral buds developing. On shadscale the mean was 4.0 and the range was 3.0 to 4.8, indicating that while some plants were still elongating their twigs, others already had 80 percent of their flowers opened.

On June 5, the mean index for E. lanata was 3.8 while the range was from 3.0 to 5.0. In other words, while some plants were still in the twig elongation stage, others already had all their flowers opened. A. confertifolia was more developed at this time of the year, and the mean index was 4.2 with a range of 3.0 to 5.0. Field measurements on June 14 showed that the range of variability of the index for both species indicated twig elongation to flower opening was occurring but the mean index was slightly higher.

By this time of the year the mean index of all the individual plants studied was not a good indicator of the developmental stage of the population. There were some individual plants which never produced flower buds or flowers, and thus the mean was lower, and did not adequately represent the overall phenological stage of the population.

The phenological determinations conducted at the end of June indicate that most of the plants had an index between 5.0 and 6.0 while about one-third of the plants had an index of 3.0. The latter half of June was when fruits developed and some flowers were still opening.

The data of July 19 indicate that the plants were in two different phenological stages at this time of the year. Most of them were developing their fruits and had an index of 6.0 while others had an index of 3.0. No flowers were found at this time of the year. This situation continued until the first part of August.

Seed dissemination was initially observed on August 13. Plants at this time of the year had only two different indexes, 7.0 which means fruit dissemination or 3.0. Dissemination was most intensive during September and October but continued during the winter season. Dormancy of the plants was recorded on September 18 when leaves were actively falling.

The beginning of the 1968 season was similar to the previous one. The total annual precipitation recorded for the area was similar but the distribution throughout the year was different (Table 13). During 1967 intensive rains occurred from March to July, with a maximum of 114.7 millimeters in June. However from August to November less than three millimeters per month were received. The early rains explain why there was such a large proportion of the plants developing flowers and fruits, and the late drought explains why the dormancy started earlier in September.

The 1968 season was dry during the first part of the year with only 15.1 millimeters in March, 12.4 in April and 33.0 millimeters in May. Only 8.2 millimeters were recorded in July. This explains why the plants and seedlings were starting their dormancy by the end of July. The precipitation data from the rain gauge was also corroborated with actual soil moisture determinations in the field. Soil moisture content was very low when plants started their dormancy.

The intensive rains which occurred in August, which added up to 88.0 millimeters, broke the dormancy and activated the plants and seedlings. Plants grew again and dormancy was re-entered during the first week of October.

The drought which occurred during the first part of the season was probably responsible for the total lack of fruit production on the plants of E. lanata studied. Seed production on A. confertifolia was less affected by the drought than those of winterfat.

The early growth of these two species was less affected by variations in precipitation since it depends mostly on moisture accumulation during the cold part of the year. The moisture storage capacity of the soil is larger than the moisture demands for the initial growth of E. lanata and A. confertifolia. Thus bud swelling always started and no death of plants was recorded at this time of the year. Later in the season when there was not enough moisture in the soil, dormancy ensued.

Seed Production

On an individual plant basis, during the 1967 season, a larger number of fruits per plant was formed on the mixed stand of both species (Table 1, Figure 8). Shadscale produced 2204 fruits per plant while winterfat produced 299. These values are much greater than those for the respective pure communities. This is perhaps the most obvious and interesting of all the results concerning seed production (Figure 9).

It is also interesting to note that the ungrazed stands of both

Table 1. Fruit and seed production during the 1967 season of *Eurotia lanata* and *Atriplex confertifolia* growing in pure and in mixed stand.

Stand	Utilization	Fruits							Seeds	
		Number per		Weight (g) per			Percentage filled		Number per	
		Plant	10 sq m	Plant	1000 Fruits	10 sq m	Per Plant	All Fruits	Plant	10 sq m
				Atriplex confertifolia						
Pure	Grazed	807	1903	6.55	8.47	15.47	14.4	18.2	146.9	350
Pure	Exclosure	715	1746	6.34	9.20	15.49	16.5	18.4	131.6	317
Mixed	Grazed	2204	4117	15.77	7.13	29.46	24.7	25.1	553.2	1032
				Eurotia lanata						
Mixed	Grazed	299	11140	0.96	3.57	39.77	15.6	14.0	41.7	1554
Pure	Exclosure	55	2095	0.20	3.46	7.24	17.3	23.5	12.9	491
Pure	Grazed	89	5191	0.31	3.40	17.63	21.0	17.3	15.4	898

Table 1. Continued

Stand	Utilization	Seeds			Adult plants		
		Weight (g) per			Density per 10 sq m		
		Plant	1000 Seeds	10 sq m	With Fruit	Percentage With Fruit	Total
		Atriplex confertifolia					
Pure	Grazed	0.123	0.840	0.029	2.36	46.5	5.08
Pure	Exclosure	0.098	0.746	0.023	2.44	44.0	5.34
Mixed	Grazed	0.530	0.957	0.099	1.87	42.1	4.44
		Eurotia lanata					
Mixed	Grazed	0.034	0.820	0.127	37.26	71.2	52.38
Pure	Exclosure	0.012	0.971	0.046	38.09	30.6	124.63
Pure	Grazed	0.016	1.028	0.093	58.33	42.1	138.44

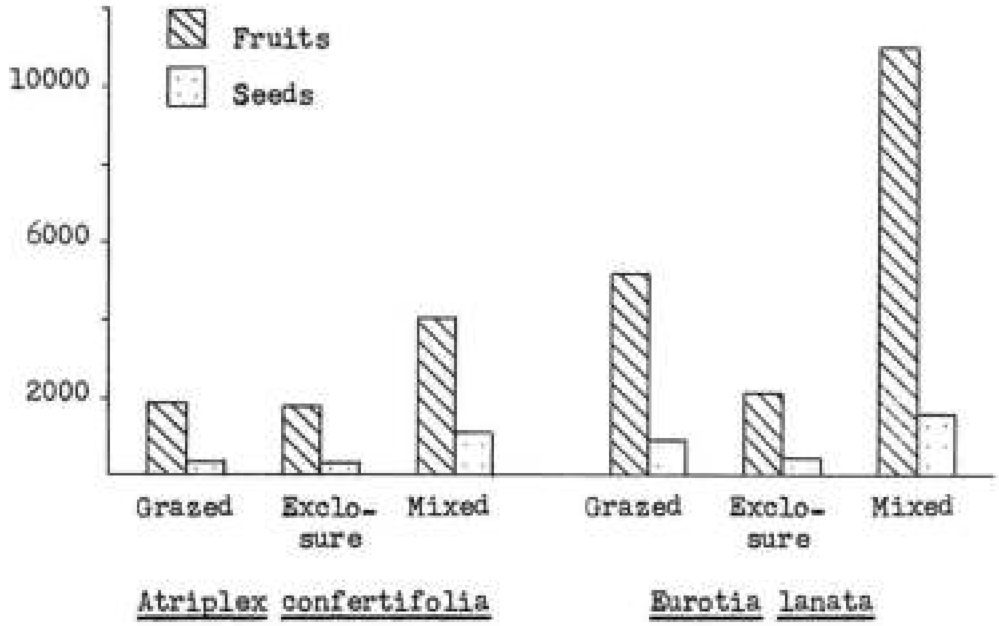


Figure 8. Fruit and seed production of E. lanata and A. confertifolia grown in pure and in mixed stands during the 1967 season.

Figure 9. Nylon net bag covering an ungrazed A. confertifolia plant, for the seed production studies.

species have the least number of fruits per plant, that is 715 for the shadscale and 55 for winterfat. On the other hand, the number of fruits per plant is considerably greater in the grazed stand. The difference between grazed and ungrazed is, however, by far less than that between the pure and mixed stands.

On an area basis, the numerical proportion of seed produced under the three conditions in which each species was growing was slightly changed, but the order remained the same. The number of fruits per hectare or per 10 square meters in both species was highest in the mixed stand, intermediate in the grazed ones and the lowest in the exclosures.

The fruit production on a weight basis could also be indicative of the effect that these three different contexts have on both species. The _Eurotia_ _lanata_ plants in the mixed stand produced about five times more fruits than those in the exclosure, while only three times more than those on the grazed area. Shadscale plants produced approximately two and a half times as many fruits in the mixed stand than in any of the other two situations, where seed production was very much alike. Nevertheless, the grazed plants produced slightly more seeds than the ungrazed ones.

The weight of one thousand fruits of winterfat was very similar under the three conditions of growth. The variability found between plants by far exceeds any possible difference between the stand means. Shadscale also showed some differences in weight. The lowest mean corresponds to those plants growing on the mixed stand, while the largest to those growing in the exclosure. However, for this species, the differences in stand means were also small in relation to their total variability.

The yield of fruits on an area basis also holds a similar relationship to that of the weight per plant. In the mixed stand, the yields of both species are much larger than on the pure stands. For shadscale there is practically no difference between the grazed and ungrazed areas, while for the other species, the yield was almost two and a half times larger on the grazed area than in the exclosure.

The number of fruits and seeds is perhaps a good indicator of the capacity of the plant to produce new seedlings later. Larger numbers of seed per plant indicate that the individuals which produced them are physiologically well fitted to develop fruits and seeds. However, this physiological reaction is not the cause by itself and is a consequence of the combination of all the environmental factors acting upon the plant, as well as the internal reactions of the organisms.

The environmental factors include all the edaphic and climatic influences. The edaphic influences include level of fertility, texture, water retention, structure, organic matter, infiltration, etc. The climatic factors include the relative humidity, temperature, frost during seed formation, availability of precipitation during this process, etc. The biological factors are important, and among those deserving special attention are the ones related with the effects of organisms upon environment as well as inter- and intra-specific competition.

On an area basis, the number of seeds and fruits are important too, representing the capacity of the population to produce new seedlings. The population reaction is also a good integrator of the environmental factors acting upon it. Summarizing, it seems clear that a better understanding of the reproduction in a community would come only after knowing the individual plant behaviour as well as their group reaction when in the population.

The weight of the fruits and seeds produced is not as good an indicator of the reproductive capacity as numbers per unit area. It really represents only the amount of energy invested by the plant, on an individual basis, or by the population on an area basis. A better indication of the reproductive capacity comes perhaps from the size of fruits and seeds expressed by weight. Seed size could later be an important factor in the development and survival of seedlings since larger seeds have more chance to survive vigorous conditions (Salisbury, 1943).

The number of seeds per plant and per unit area, as well as their weight, keeps the same basic relationship which has already been expressed in the previous paragraphs. The larger values are those found in the mixed stand, while the smallest are those on the ungrazed, pure stands.

All of this previous information reported here could be summarized in one sentence. That is, the largest reproductive capacity interpreted in terms of seed and fruit production was found on the mixed stand of both species, while the lowest on the unutilized areas.

The percentage of fruits filled with seeds reflects how favorable the conditions were after the flowers were pollinated. This could be related with the moisture availability during the post-pollination period, with availability of nutrients to the plant from the soil and to the seed from the plant, to the temperature during this period, or to any other factor.

The mean percentage of fruit filled for all the plants of winterfat sampled was 15.6 percent on the mixed stand, 17.3 in the exclosure and 21.0 percent in the grazed area. These results demonstrate that the best conditions for seed fill occurred in the grazed stand of E. lanata, while the least favorable occurred in the mixed stand.

The large differences consistently found between the grazed and ungrazed stands seems very logical after considering the intensity of grazing of this highly preferred species by all kinds of livestock and rabbits. For shadscale, the differences are small. This is understandable since the plants are usually only slightly utilized or not utilized at all.

The mixed stand of shadscale and winterfat shows the largest differences in most results. There is, in the first place, a completely different inter- and intra-specific interference. The plant densities of each species in this mixed community are less and thus the utilization of the plants could also be different from that on the pure stands. Winterfat usually grows protected by large and spinny plants of shadscale. Its plasticity is clearly manifested through a different growth habit. Plants are taller, and the basal ground cover is proportionally reduced with seed and fruit production being greater.

The grazed and ungrazed stands of winterfat look very similar in many respects. There are of course, differences in size and density of adult plants but they are minimal in comparison with those of the mixed stand. The question that now arises is: do those plants in the mixed stand really represent the same ecotype or under different environmental conditions is plasticity all that is involved?

It has been demonstrated by Workman and West (1967, in press) that different ecotypes of winterfat exist. Large genetic differences have been found for different areas where considerable distances, geographic barriers, and environmental differences are involved. Here the situation is different in that only a short distance and to a certain degree, relatively similar environmental conditions are involved. Data presented by Clarke and West (in press) however, indicate that the E. lanata plants from a mixed stand and pure stand in Curlew Valley actually possess different ecotypes in terms of at least salinity tolerance at germination. However, the plants of winterfat found inside and outside the exclosure should correspond to the same ecotype since the exclosure has only been established for 12 years and the life expectancy is estimated from 17 to 74 years with an average of 36 (Asay, 1959).

The percentage of filled fruits on an area basis is more important for the population than the mean values calculated per individual. If there is no correlation between the number of fruits per plant and the percentage filled, both the individual and population means should be identical. This is not the case, however.

Fruit filled on the pure stand of shadscale average 18.2 percent for the grazed area, and 18.4 percent for the ungrazed, while 25.1 percent in the mixed stand. These values are slightly higher than those obtained on an individual basis. In the mixed stand of E. lanata as well as on the grazed pure community, fill is less than the percentages found for fruits harvested inside the exclosure. The winterfat plants from inside the exclosure had a smaller percentage of fruits filled per plant than fruits filled per area. This difference in the mean value of fruits filled leads to the conclusion that there could be a correlation between size of the seed yield per plant and the percentage fill.

It is important to define the above because it has been observed in the field that, in general, the plants which are found on areas with a lower density of the population and community such as near ant hills, roads, or other open spaces usually have larger numbers of fruits per plant. If this could be demonstrated quantitatively in the field, it would indicate that there is a density dependent factor for fruit production. If it could now be demonstrated that there is also a density dependent factor for percentage fill, these two would be additive and the number of seeds would increase because of a larger number of fruits as well as a larger percentage fill.

The value which better integrates all the information presented in this section is perhaps the production of viable seeds, on an area basis. The calculation involves knowledge of two values, the seed production on an area basis and the percent of germination.

Seed production was calculated in this study and the values are presented in table 1. The percent of seed germination of both species was not calculated.

Seed germination could have been determined under standard laboratory conditions. However, since the main objective in this study was to learn about their ecological relations, it would have been meaningless work. Seed germination in the laboratory has no ecological significance unless there is a clear knowledge of its variability in relation to the environmental functions which could influence it. These relations are not thoroughly understood at the present time.

The main objective of this part of the study was the determination of availability of viable seeds per unit area, in order to later relate this value with seedling production.

The availability of viable seeds per unit area was calculated by using the seed production results from this study plus the results of the germination studies reported by several authors (Workman and West, 1967; Springfield, 1968; Vest, 1952).

Seed production of winterfat was 1554 seeds per ten square meters in the mixed stand with 898 seeds per ten square meters on the grazed stand and only 491 seeds per ten square meters in the ungrazed stand. The production of viable seeds per unit area, calculated by combining the results reported in the previous paragraph with those of Workman and West (1967), varied a great deal. This variation was induced by three main factors: seed source, concentration of the sodium chloride solution used to moisten the seeds, and temperature (Appendix, table 15).

The greatest influence was that of the concentration of the solution. The seeds from the La Sal source, at the low temperature regime showed 98 percent germination at 0.0 concentration, 94 percent at 1.0 while only 47 at 2.0 percent concentration, 5 at 3.0 percent, and no germination at all at 4.0 concentration. This means that the number of viable seeds produced per ten square meters when the concentration of sodium chloride is 0.0 corresponds to 1522 on the mixed stand, 880 in the grazed and 481 in the ungrazed stand. At one percent NaCl concentration, these values are respectively 1461, 844, and 461 viable seeds per ten square meters. Even at a concentration as high as 3.0 percent, the number of viable seeds produced per ten square meters would have been 78 in the mixed stand, 45 in the grazed stand, and 25 in the exclosure.

The values of the salinity determination on the upper 2.5 cm of soil as well as those from 2.5 to 7.5 and those of the upper 15.0 cm are low (Table 12, page 205 and appendix tables 48 and 49). This demonstrates that a high number of viable seeds could be produced. Computations indicate that seed germination likely would exceed by several times the number of seedlings emerged, as indicated in appendix tables 26, 31, and 36 and figures 20 and 21 on page 107, figure 29 on page 118, figure 42 on page 130, and figure 45 on page 132.

Salinity is obviously the most influencial factor in seed germination studied by these authors. However, despite the fact that on certain areas it could be extremely high, under natural conditions, winterfat is restricted to areas with a much lower concentration (Gates, Stoddart, and Cook, 1956). Some of the plant communities, which usually develop on the surrounding areas where winterfat occurs, have salinity concentrations below the absolute limit determined by Workman and West (1967). They are between 3.0 and 4.0 percent concentration of sodium chloride, or under certain circumstances of temperature and seed source greater than four.

The general area of distribution where winterfat is usually found, has no limitation based on viable seed production in relation to salinity which could explain, by itself, the natural limits of this species. The Law of Limiting Factors in relation to viable seeds is not the explanation.

Differences in temperature are thought also to influence the total amount of viable seeds produced. In general, the high temperature regime produced slight increases of germination affecting the number of viable seeds produced. At 0.0 percent concentration of salinity and high temperature, there would be a 99 percent germination instead of 98 at low temperature. At 1.0 percent NaCl concentration and high temperature regime, the germination was 82 percent instead of 94 at low temperature. At 3.0 percent NaCl, the same 5 percent germination level occurred at high and low temperature regimes. At 4.0 percent NaCl concentrations, the germination was 1 percent instead of none for low temperatures.

The high temperature regime would mean a hypothetical production of 1274 viable seeds per ten square meters in the mixed stand, 736 viable seeds under the grazed conditions and 402 viable seeds on the exclosure. Despite the decrease in amount, in relation to the low temperature treatments, the differences should not be effectual in nature.

The difference in seed source is also small in relation to the total variability. Both seed sources reacted differently to the concentration of sodium chloride. Cisco seed source germination was depressed more as the concentration increased, than seed from the other source. Thus, at 1.0 percent concentration of sodium chloride and low temperature only a 40 percent germination was found. Extrapolating these results would mean a viable seed production of 622 per ten square meters on the mixed stand, 359 on the grazed and 196 on the exclosure; at 2.0 percent concentration of sodium chloride 653, 377, and 206 viable seeds per ten square meters, respectively, while at 3.0 percent of sodium chloride concentration, 31, 18, and 10 viable seeds would be produced per ten square meters.

The water potential has also been found to be important in influencing the number of viable seeds. Appendix table 16 combines Springfield's (1968) results with those of seed production actually obtained in this study. Seed source, temperature at germination, and moisture stress are analyzed in relation to viable seed production.

The number of viable seeds of winterfat decreased as the moisture stress increased. Thus at 0.0 atmospheres, and at 2.3 C, Springfield's Horse Springs seed source gave 80 percent germination. This would mean 1243 viable seeds per ten square meters in the pure stand, 718 in the grazed area, while only 393 viable seeds would occur in the exclosure. This value would decrease slightly at 3.0 atmospheres to 1103, 637, and 349 viable seeds per ten square meters, respectively, while at 15 atmospheres, it would allow only 497, 287, and 157 viable seeds per ten square meters.

The decrease in the number of viable seeds would be smaller at low temperatures and larger at high temperatures. At the highest temperature tested, the percentage of germination decreased from 89 percent at 0.0 atmospheres to 11 percent at 15.0 atmospheres, while at the low temperature, it was reduced from 80 percent at 0.0 atmospheres to 32 percent at 15.0 atmospheres. This means that the number that could be produced in this last case would be only 171 viable seeds per ten square meters in the mixed stand, 99 in the grazed area and 54 on the ungrazed area.

Seed source has only slight influence in the production of viable seeds. The influence of moisture stress and temperature is similar, regardless of where the seeds were collected.

The low temperatures in the early spring and the high moisture present on the soil surface at that time of year are the mechanisms which allow the plant to have the highest number of viable seeds under the environmental conditions where it naturally grows. Early germination in March and April, when the conditions are more favorable, means a larger number of viable seeds produced. In this respect the germination studies previously conducted and the seed production results reported here clearly indicate that the winterfat communities have developed a mechanism which permits them to have high efficiency in viable seed production. Early in the spring the number of viable seeds found is greater than at any time of the year. Besides this, the environmental conditions are also more favorable for seedling development and establishment.

Shadscale has shown considerable variability on the production of viable seeds (Vest, 1952; Hussain, 1966). The results of appendix table 17 show that the number of viable seeds is zero when the bracteoles are covering the seed no matter how large the seed production of the population. Since this cannot be sustained if the species is to thrive, there has to be some mechanism which transforms some of these originally unviable seeds into viable ones. This mechanism is based on two factors. One is the washing away of the inhibitory substances existing in the bracteoles by the action of precipitation and soil water movement. There is also a mechanical impedance of the bracteoles themselves on the germination and growth of the seeds contained inside them. Thus, these bracteoles have to be destroyed in the soil by some agent. This is done by the action of soil microorganisms, especially fungus (Vest, 1952).

The process of making these seeds viable requires variable amounts of time according to the microenvironment where the seed remains in the soil. There are also variable microhabitat conditions which could have differential influences because of differences in soil moisture and because of micro-organismal activity.

The increase in germination as the concentration of the bracteole extract, as well as a dilution of 1:3 and 1:5, showed no production of viable seeds. However, a greater dilution such as 1:10 would mean a hypothetical production of 464 viable seeds per ten square meters on the mixed stand, 157 on the grazed area, and 143 in the exclosure. Now if the dilution increases to 1:20, the production also increases to 671, 227, and 206 respectively, while on distilled water, it was even larger with 774, 262, and 237 viable seeds per ten square meters.

The date of harvest is also important in the viability of seeds. The largest values are those determined for the sample of seeds harvested on December 16 in which are 155 viable seeds per ten square meters on the mixed stand, 52 on the grazed area, and 47 on the exclosure. High numbers are also projected for those seeds harvested on April 1 with the same values as before; while those harvested on April 15 would yield 310, 105, and 95 viable seeds per ten square meters respectively.

There are two main possible causes involved. One of them is a probable plant-seed relationship in relation to the date of separation from the mother plant which could affect later the physiology and viability of the seed when seeded in the soil. The other is the climatic and other environmental influences on the seeds during the post-harvest period. If this is the case, the influences of the general environment could be most variable since there are so many possible microhabitats in the soil which could differentially influence the hydric, thermic, biological, and other factors on the seed.

In general it could be concluded that both species have different seed production per unit area and in relation to the community they inhabit. Besides this, the germination percentages which characterize both species are extremely different, as well as the factors involved in their germination. Because of this, the number of viable seeds produced by both species is different in each case, and the factors which influence them produced changes of different magnitude in shadscale and winterfat dominated communities.

The factors which influence winterfat are oriented toward the production of the largest germination early in the spring when the conditions are more favorable. Seeds of E. lanata germinate early in the spring whenever the environmental conditions, mostly soil moisture and temperature, are favorable for it. The seeds or their pericarp does not require any chemical or physical modification produced by external agents to be viable.

The mechanism involved in shadscale regeneration is different. It is oriented toward the production of viability at a non-uniform time, that is, a spacing in production of viable seeds. This means shadscale seeds are produced whenever the environmental conditions are favorable for the parent plant, but these seeds are not viable. Viability of seeds is influenced by completely different mechanisms than production.

Atriplex confertifolia initially produces non-viable seeds. The percentage of viable seeds determined by Vest (1952) is zero when the environmental factors have not yet produced the necessary changes to modify the same chemical and physical properties of the seed coat structure. Leaching of the inhibitory substances in the bracteoles as well as softening them requires time and the action of several environmental factors surrounding the fruit.

The 1968 season was in many respects different from the previous one. The main difference was the reduction in fruit and seed production both on an individual plant basis, as well as per unit area (Table 2).

The percentage of E. lanata plants with fruits was 9.0 in the mixed stand, 0.5 percent on the ungrazed stand and 0.2 percent on the grazed one. However, in the pure stands of winterfat in areas where the normal density of plants occurred, the percentage of plants with fruits was 0.0. No plant with fruit was found under those conditions. The only individuals bearing fruits were located at the edges of ant hills, roads, or openings where some plants were lacking. Thus, during this season, the production of winterfat fruits and seeds was only local.

The yearly variations in weather affected the fruit and seed production of winterfat in two ways. The percentage of plants bearing fruits was reduced, as well as the number of fruits per plant. From

Table 2. Fruit and seed production during the 1968 season by *Eurotia lanata* and *Atriplex confertifolia* growing in pure and in mixed stands.

Stand	Utilization	Fruits: Number per Plant	Fruits: Number per 10 sq m	Fruits: Weight (g) per Plant	Fruits: Weight (g) per 1000 Fruits	Fruits: Weight (g) per 10 sq m	Fruits: Percentage Filled	Seeds: Number per Plant	Seeds: Number per 10 sq m	Adult plants: Density per 10 sq m With Fruits	Adult plants: Density per 10 sq m % with Fruits	Adult plants: Density per 10 sq m Total
						Atriplex confertifolia						
Pure	Grazed	337	543	1.31	3.88	2.10	15	51	82	1.61	31.6	5.08
Pure	Exclosure	332	833	1.44	4.34	3.61	19	158	396	2.51	47.0	5.34
Mixed	Grazed	69	163	0.25	3.73	0.61	12	20	47	2.36	53.2	4.44
						Eurotia lanata						
Mixed	Grazed	35	165	0.13	3.81	0.63	37	13	61	4.71	9.0	52.38
Pure	Exclosure	14	9	0.04	2.85	0.02	28	4	2	0.62	0.5	124.63
Pure	Grazed	129	36	0.39	3.00	0.11	37	48	13	0.28	0.2	138.44

the results obtained during the 1967 season, as well as those determined during the previous one, it is clear that seed production per plant, as well as the chance for plants to bear fruits, is a density dependent factor. However, no mathematical relations were determined in this respect.

The mixed stand of winterfat and shadscale showed a better production of seeds both on an individual plant basis as well as per unit area. Besides, since plants were more spaced in the field and their density was lower, seed production was greater and not localized around natural openings in the vegetation or bare ground.

The largest seed production of winterfat per unit area was found in the mixed stand, the same as the previous season. The lowest seed production was in the exclosure.

The yearly variability of A. confertifolia seed and fruit production was less than for E. lanata. On the average, the percentage of shadscale plants with fruits was similar for the two seasons, while for winterfat, the plants in 1968 had only a fraction of the fruits of the 1967 season. Besides this, the number of seeds produced per ten square meters of shadscale community was proportionally less reduced than that of winterfat.

The percentage of filled fruits of shadscale was similar during the two years the study was conducted while for winterfat, much larger values were found in 1968.

Seed production was shown to be highly variable. The main factors influencing it are the stand where they grow, utilization, plant density, and the weather variations from year to year. A. confertifolia showed a lower variability than E. lanata in relation to these factors as was determined from actual data of fruit and seed production per plant as well as per unit area, weight of 1000 fruits, percentage of filled fruits, and percentage of plants bearing fruits.

Seed production of E. lanata kept the same basic relationship in the 1968 season. However, the production of seeds and fruits was less than the previous year.

Germination

The differences in environmental characteristics which affect those communities forming pure stands of E. lanata, A. confertifolia, or the mixed community of both species have usually been related to some soil factor. However, until the present time no single edaphic factor has been found to perfectly delimit the distribution of either species.

Results of the soil-community relationship studies have not been clearly interpreted. If a certain factor is found to be related quantitatively with the species, it is indicated as such. However, explanations are not clear in stating if the presence of the species is due to the capability of the adult plant to grow and survive under those conditions, or if the seedlings are capable of establishment, or even if the seeds are capable or unable to germinate.

Soil analysis of the most varied kinds could be run on these soils, such as major elements, as well as secondary and minor elements, salinity, plant exudates, microorganisms, etc. All of these would provide indirect information in relation to these problems. There is always the possibility that the wrong factor is being analyzed and thus the lack of correlation is due to "entitation" of the factor chosen and not to a possible explanation involving the quantitation of the real factor.

If there is any factor of the soil, which per se is responsible for the germination or lack of it, it would be best found by the analysis of seed germination on the soil itself. If the germination values determined for these two species on different soils show some effect of limiting factors, then the physical, chemical, and biological analysis of the soil should determine which is the factor.

The purpose of this part of the study was to analyze the germination of shadscale and winterfat on soil samples taken from five different sites supporting plant communities which naturally develop in the surroundings of the two species in question.

The results of the analysis of emergence of A. confertifolia seeds, seeded in pots under uniform climatic conditions in the growth chamber, could help interpret this problem (Appendix table 18, Figure 10).

The two check treatments show, in general, slightly higher germination percentages than the other soil treatments. When the seeds were placed over filter paper, germination occurred faster. Since the seeds were not buried, germination was detected immediately. Besides this, the germination conditions were also different, since the seeds received light and the atmosphere surrounding them was that of the petri dish and not that of the substratum.

Peat moss also behaved in a similar way. That is, the emergence percentages were high from the beginning. A higher germination percentage was shown for this medium than any of the soil treatments, from the fourth to the last day after seeding. Another important

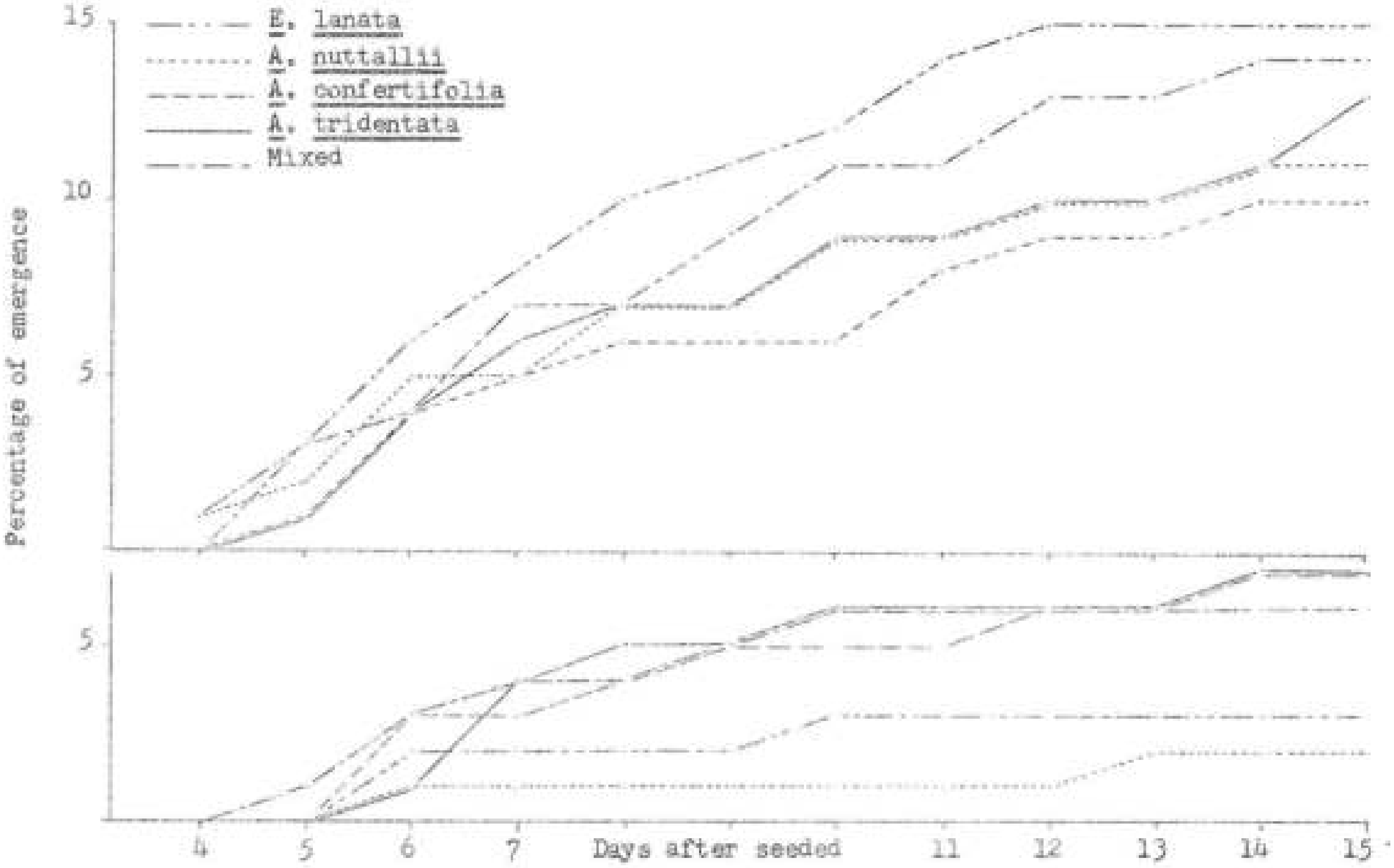


Figure 10. Percentage emergence of <u>A. confertifolia</u> seedlings seeded in pots with Curlew Valley soil. The soil samples were taken from areas where natural communities of <u>E. lanata</u>, <u>A. confertifolia</u>, <u>A. tridentata</u>, <u>A. nuttallii</u>, and the mixed stand of <u>E. lanata</u>, <u>A. confertifolia</u> naturally grow. The upper graph represents the emergence in the upper 0 to 2.5 cm soil samples, while the lower is from soil taken from the 2.5 to 25 cm depth.

feature is that the germination increased until the tenth day and after that no more germination occurred. Something similar occurred on the filter paper. Most of the seeds emerged during the first eleven days. Peat moss differs from the soils used in this emergence study in that it is looser, it has larger air spaces, the permeability is greater, and the mechanical resistance to growth and emergence of the seedling is less.

The analysis of emergence from soils associated with the five different plant communities showed a very striking result. The percentages of emergence of the shadscale seeds were greater on those soils originally taken from the surface 0 to 2.5 cm, on any of the five stands studied. The lowest emergence was obtained on the soils from the deeper layer, that is from 2.5 to 25 cm, no matter from under which community the soil was taken.

The total emergence of A. confertifolia 15 days after seeding was greatest in the surface soil from the E. lanata stand, 15 percent; 14 percent for the mixed stand of shadscale and winterfat, 13 percent for the Artemisia tridentata stand, while only 10 percent for soil taken from the Atriplex nuttallii and on the A. confertifolia communities. This means that the lowest percentage emergence was found on soils where stands of the very same species was growing.

The total emergence of the seedlings on the deeper soil samples was smaller than on those from the surface layer. However in this case, the higher percentages were found on the shadscale and sagebrush soil, 7 percent; the mixed stand, 6 percent, while the lowest emergence was found in the winterfat and nuttall saltbush soils, 3 and 2 percent, respectively.

The soil analyses conducted on these substrata show some striking differences (Appendix table 19). The percentage of organic matter found was in all cases greater on the surface samples. This could have directly influenced the percentage of emergence, or it could be a factor indirectly related with others which directly influence other soil properties. In this category could be included soil structure, porosity, fertility, infiltration, permeability, water retention, gaseous exchange, modulus of rupture, etc. Whether some of these factors or the organic matter is directly related with the increase in germination percentage is not known.

The cation exchange capacity showed small variability from one soil to the other, and from the surface to the deeper soil layer. The only large difference was found for the A. confertifolia soil. This could be easily understood considering the greater percentage of clay in this soil. In any case, it would seem completely unsatisfactory to try to explain the differences in emergence based on this soil characteristic.

In all the soils, with the exception of that from the shadscale stand, the clay percentage of the surface layer was less than that of the deeper layer. The sand percentage was greater on the surface layer than on the deeper ones. The only exception to this was Atriplex nuttallii. Despite the fact that there are certain constant relationships between the soils from the surface layer in relation to those of the deeper one, it seems that in a quantitative and direct way, the texture itself cannot explain the differences in germination.

The pH of the surface layer was usually 7.8 while the deeper layer shows values of 8.0 or 8.1. The only exception to this is the soils from the shadscale community where both values were 8.0. The difference in value is, in the first place, too small to be meaningful. Besides this, it could not explain the differences on germination in the soils from different stands.

The salinity concentration as measured by the electrical resistance method indicates smaller values for the upper surface of soil. The only exception is the shadscale soil where electric resistance and salinity were less in the surface layer than the deeper stratum.

The germination of A. confertifolia when seeded in petri dishes on the surface of the substrata is different than the results obtained when buried in soil as described previously (Appendix table 20, Figure 11).

The largest percentage germination at the end of the ten-day period was 34 percent. The germination on filter paper was much less than that on the different soils.

There was also a slight tendency to have a higher percentage germination on the soils from the upper layer than in those from the deeper layer. The percentage of seeds germinated in the soil from the surface layer of the shadscale stand was 19 percent, while only 15 percent in that from the deeper. In the A. tridentata soil, the germination percentage was 24 and 21 percent, while in the Atriplex nuttallii soil, it was 22 and 14 percent. In the mixed stand the percent germination was higher in the surface layer, 25 percent, while in the deeper soil sample it was only 16 percent. There was one exception where the germination was higher on the soil sample from the deeper layer, and this was the soil from the E. lanata stand.

The soils used in this experiment were not sterilized. The

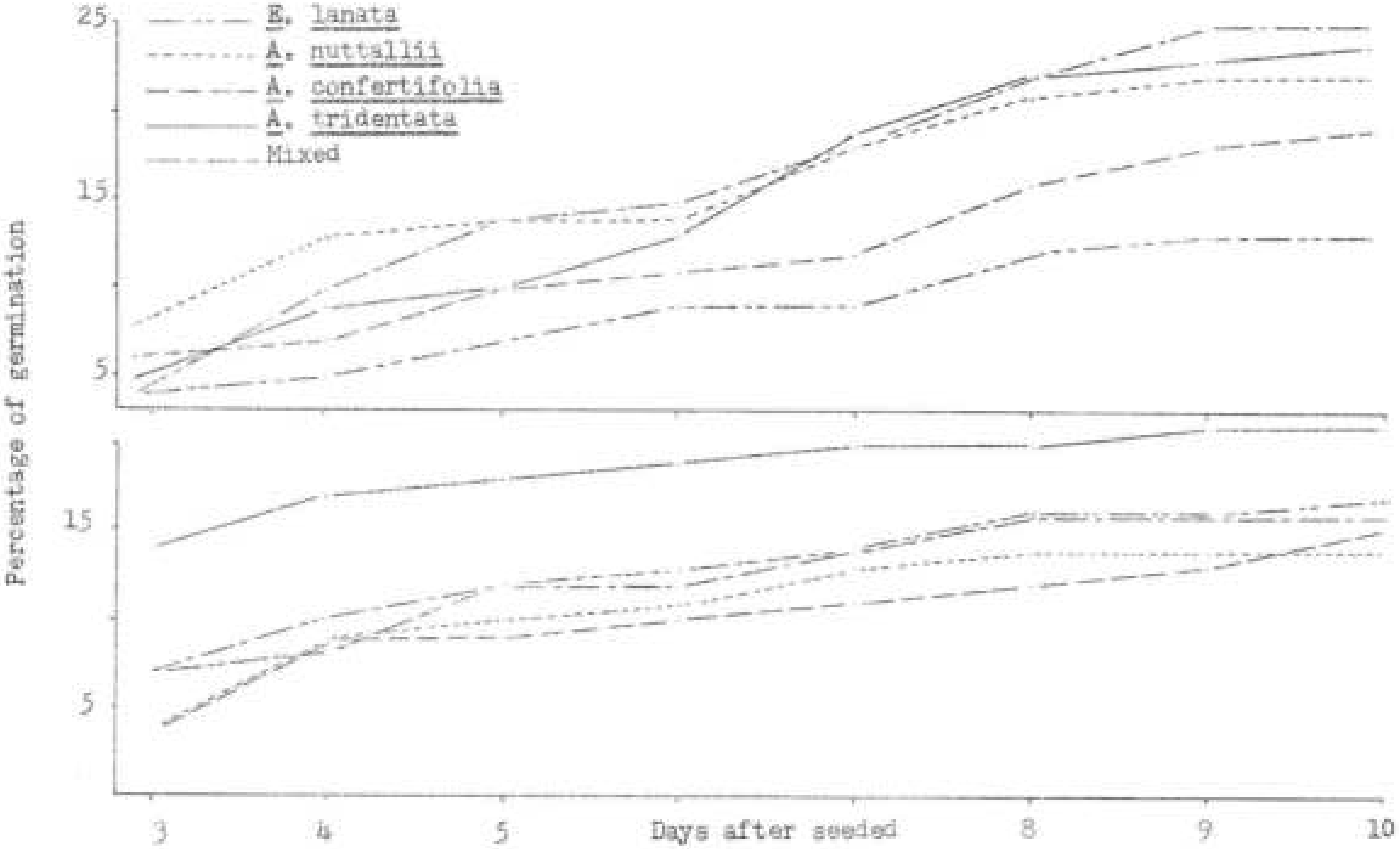


Figure 11. Percentage germination of A. confertifolia seeds, seeded in petri dishes with Curlew Valley soil. The soil samples were taken from areas where natural communities of E. lanata, A. confertifolia, A. tridentata, A. nuttallii, and the mixed stand of E. lanata, A. confertifolia naturally grow. The upper graph represents the emergence in the upper 0 to 2.5 cm soil samples, while the lower is from soil taken from the 2.5 to 25 cm depth.

reason was to test the possible effect of the existing microorganisms as well as the existence of plant exudates on the soil and their effect on the germination. The high temperature necessary for sterilization could have destroyed these possible effects. Perhaps contamination of the dishes is what increases the variability of the results. Despite this, some conclusions can be reached.

The difference in germination in the soils from the upper and the lower surface layers is very clear. There are certain soil characteristics that induce higher percentages of germination under the soil from the surface layer than in the deeper one. The difference in emergence percentages obtained in the previous study where the seeds were buried were much larger. This is an indication that the edaphic effect could be largely influenced by physical properties of the soil. However, in the germination analysis conducted in petri dishes, when the seeds were placed on the surface of the soil, they were mostly under the influence of the chemical characteristics of the soil. The physical influence was less important since they were only touching the surface part and the soils inside the petri dishes were saturated or nearly so.

Before starting germination and emergence analysis, it was thought that if there is any influence from exudates produced from the plants, they would be more concentrated and obvious in the upper layer of soil where there is a larger concentration of organic matter. However, the results clearly show that the conditions for germination were better in soils from the surface layer.

The results of these two germination analyses also show that there is not any specificity of shadscale seed germination and emergence, for soil where the stands naturally develop. Shadscale seeds germinated and emerged well in the soils from under all five plant communities studied. The percentages of germination were smaller in their own soil than in those from other plant communities. Thus the presence of shadscale stands in certain areas cannot be explained on direct differential germination of the species on the particular soil. If this was the case, shadscale would have less chance to form stands in the places where it naturally grows than on the soils where other communities develop.

The substrata where the seeds germinate are of great importance in affecting the germination percentages. Because of this, the germination site should be of extreme importance in determining the distribution of this species. This result was later corroborated in other parts of this study. Seedling production under natural conditions was largely affected by germination site. Seedlings were not produced at random but concentrated on certain microhabitats or germination sites (Table 7 on page 144).

Winterfat germination was less influenced by the substrate. The percentage of germination in petri dishes, when seeded on the surface of the substrate, shows little or no difference between treatments (Appendix table 21).

The germination over peat moss was 36 percent. This means that it was about as high as on the other substrata. There were, however, slight differences in the germination percentages between soil substrates, but not any clear tendency to have larger values in the surface soils.

The effects of the substrata when seeded on the surface show mostly the influence of the chemical characteristics rather than the physical. Winterfat did not show significant differences on the various soils. However, the physical influences of the edaphic factors could be of importance such as has been previously demonstrated by Springfield (1968). If this is the case, germination site should be important in regulating plant distribution, rather than the soil itself. Winterfat shows similar percentages of germination on all of the five soils tested no matter whether they come from the area where they naturally grow forming pure stands, or if they come from under other communities.

The soil itself and its influence on the germination and emergence of E. lanata does not explain any possible interrelationships which could restrict the area of distribution of this species. Winterfat seeds did not have higher germination percentages in its own soil, than in any other.

The hypothesis that there is some limiting edaphic characteristic which restricts the germination of E. lanata or A. confertifolia only to the soils where they naturally grow should be rejected. Under the conditions where the experiments were conducted, it was demonstrated that under uniform climatic conditions in the growth chamber, seeds germinated in all these soils. The limits of germination tolerance for both species are much broader than the magnitude of the edaphic factor variability, both for their own soils as well as those rooting the other surrounding plant communities.

The lack of specificity in germination conditions is outstanding. E. lanata and A. confertifolia seeds did not germinate better in their own soil than in those where other stands naturally develop. Germination site could be important in regulating the seed germination and establishment. The vegetation present on the area influences the amount and availability of germination sites. If this is the case then the influence of vegetation on soil, especially on the microhabitat, is more important than the influence of the soil itself on the germination.

In a quantitative way, a combination of the edaphic influences on seed production, germination, emergence, and seedling growth and establishment could be influencing the distribution of the species on the area. The soil has a large and direct influence on the growth of the vegetation and on the seed production. Besides this, germination site plus differential seed production, results in a differential germination rate. A germination rate too low, lower than the mortality rate, would finally result in the absence of the species from those soils where the germination rate is not enough to replace the dead plants.

Seedling Growth in Controlled Environments

Responses of Atriplex confertifolia in the growth chamber and greenhouse shows the influence of soil under uniform climatic conditions. The results of this study indicate that there is a differential soil effect on the growth of the seedlings of this species (Appendix table 22, Figures 12, 13, and 14).

The number of leaves is a good indicator of the size of the plants. Plants had the largest number of leaves when grown in pots containing soil samples taken from the upper 2.5 cm of soil from

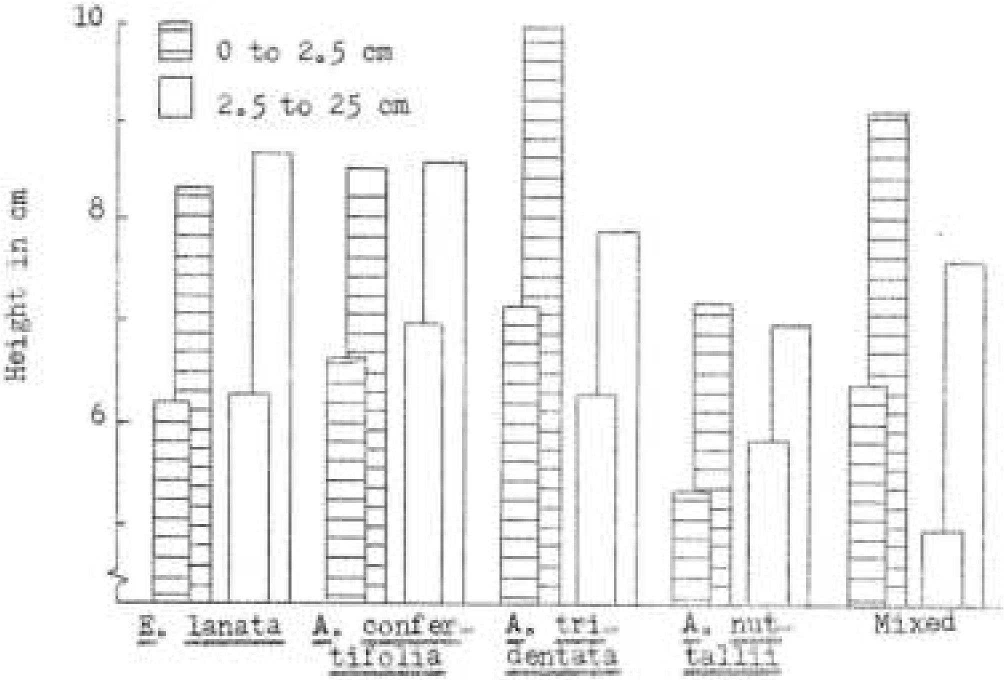


Figure 12. Mean height of A. confertifolia seedlings grown in pots in five different soils and two depths, at 30 and 50 days after seeding.

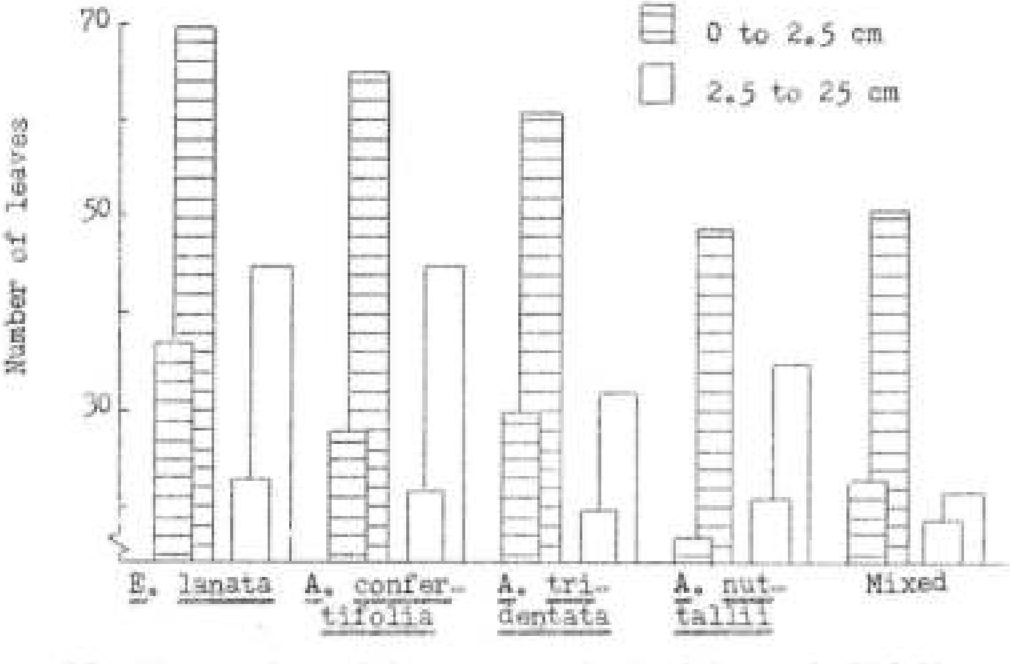


Figure 13. Mean number of leaves per plant of A. confertifolia grown in pots in five different soils and two depths, at 30 and 50 days after seeding.

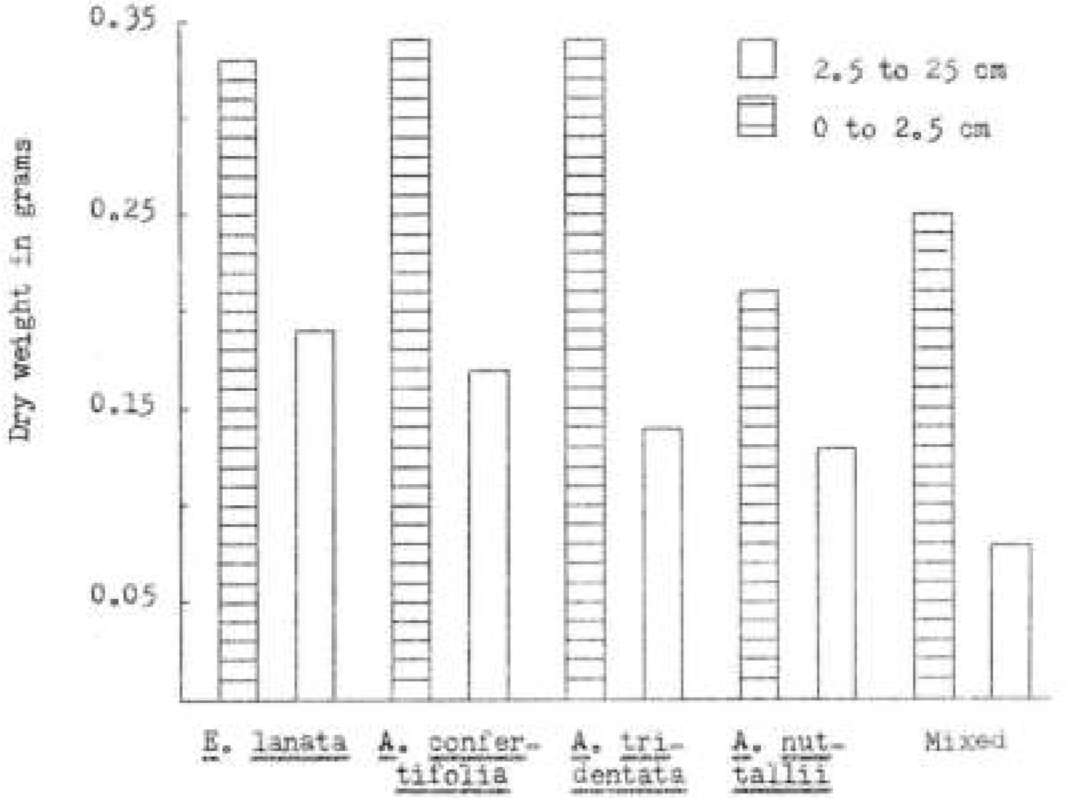


Figure 14. Mean dry weight per plant of A. confertifolia grown in pots in five different soils and two depths, at 50 days after seeding.

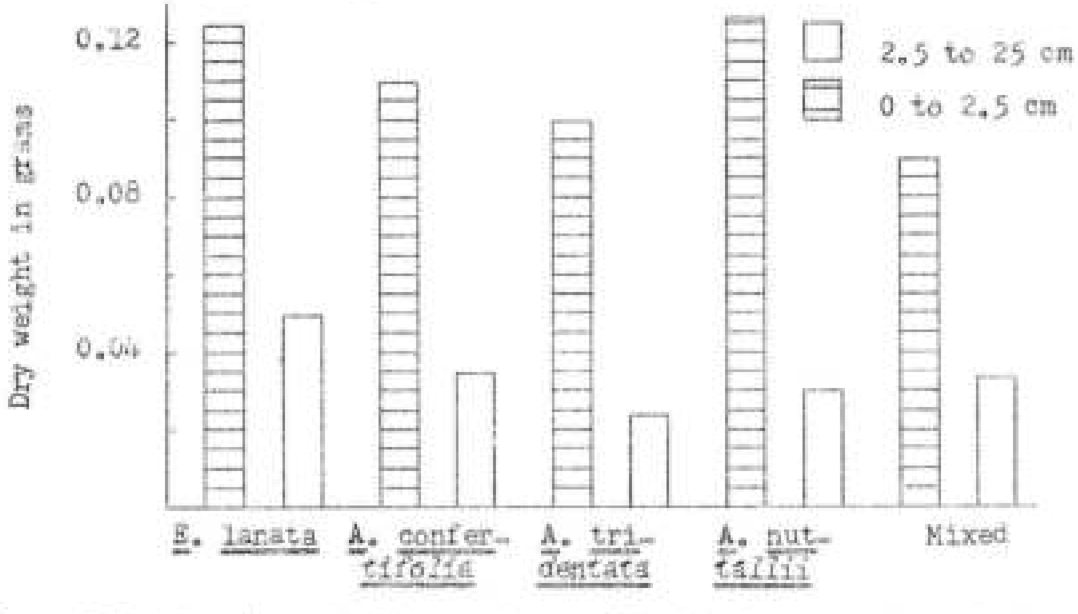


Figure 15. Mean dry weight per plant of E. lanata grown in pots in five different soils and two depths, at 110 days after seeding.

under any of the five plant communities. The smaller plants were always those growing on soils from the deeper layer.

The greatest number of leaves was produced when these plants were grown in the surface soil from the E. lanata, A. confertifolia, and Artemisia tridentata communities where an average of 70, 65, and 61 leaves per plant were produced, respectively, after 50 days of growth. From the soil of the mixed stand there were, on the average, only 51 leaves and 49 leaves per plant on the soil from under the pure stand of A. nuttallii.

The seedlings of shadscale produced less leaves when growing in soils from the lower layer. Under these circumstances, the largest number was produced when growing in the soil from under the E. lanata and A. confertifolia stands. Growing plants in the soils from under the A. nuttallii, Artemisia tridentata, and the mixed stands produced a progressively lower number of leaves.

The influence of soil on seedling growth can perhaps be better evaluated by comparing the final dry weight of the plants. After 75 days the plants with larger sizes were those growing in the top soil from the Artemisia tridentata, Atriplex confertifolia, and Eurotia lanata stands. The mixed stand and the Atriplex nuttallii soil induced less growth of the seedlings.

When growing in soils from the deeper layer, shadscale plants produced larger amounts of dry matter on the winterfat soil, and progressively reduced production of biomass on the Atriplex confertifolia, sagebrush, nuttall saltbush, and mixed stand soils.

The height of the seedlings was not a good indicator since it only reflects a small proportion of the different number of leaves and dry weight. Plants often had a similar height such as the seedlings growing in the E. lanata soil where the average height at 50 days was 8.3 and 8.7 cm on the soil from the surface and deeper layer, respectively. However, the number of leaves per plant was 70 and 45, while the weight per plant measured a few days later was 0.334 grams and 0.191 respectively. Similar results occurred in many of the other treatments.

The results of this study show that there is a clear influence of soil in the growth of these plants. Different soils induce Atriplex confertifolia seedlings to grow at a different rate. Since the soil and the plants were placed under uniform conditions, the difference in seedling growth can be attributed to the edaphic influence.

Shadscale seedlings grew well in all the soils studied. This is proof that there is not any limiting factor in the soil which causes the plant to be excluded from certain areas only because of the particular soil. None of the soils studied proved to have any factor in quantities beyond that of the tolerance limits of the species. The seedlings of shadscale could grow perfectly well and develop on the nuttall saltbush soil, in the winterfat, or in the sagebrush soil of the surrounding communities when interspecific competition was eliminated.

There has to be another explanation for the absence of this species. This explanation cannot be based on a simple application of the Law of Limiting Factors or in the Law of Tolerance on the individual plants of shadscale.

It is also obvious that there is possibly a large effect of the vegetation on soil and of soil on the vegetation. The upper 2.5

cm of soil has strikingly different characteristics than the lower layer. The difference between these two layers of soil in each plant community is by far larger than the differences in soil from one stand to the other. This can be proved comparing the integrated value of soil as measured by the growth of shadscale. The best integrator of the environment is the vegetation itself (Clements, 1920, 1928; Sampson, 1939; Tansley and Chipp, 1926).

The surface layer of soil in all of these five stands is extremely variable. It can be observed, even with the naked eye, that there are large differences in microrelief, even in a few decimeters of distance from litter cover, organic matter, soil structure, compaction, amount of surface cracks, etc. This heterogeneity within the stand, or alpha heterogeneity which is mostly induced by the vegetation itself, could be even more important than the heterogeneity between nearby stands dominated by different species.

The soil by itself cannot be used as the sole explanation of the distribution of the species in the salt desert shrub vegetation type. Besides this, Atriplex confertifolia grew better on soils other than in its own. The seedlings of this plant could germinate perfectly well and grow on other soils from nearby communities. Their absence is not induced by the soil alone in a limiting factor sense.

Another study was made with E. lanata seedlings. The same soils and environmental conditions were used (Appendix table 23, Figures 15 on page 91, 16 on page 95, and 17 on page 96).

The height of the plants was a good indicator of their size. The same basic differences in the size of the plants were observed

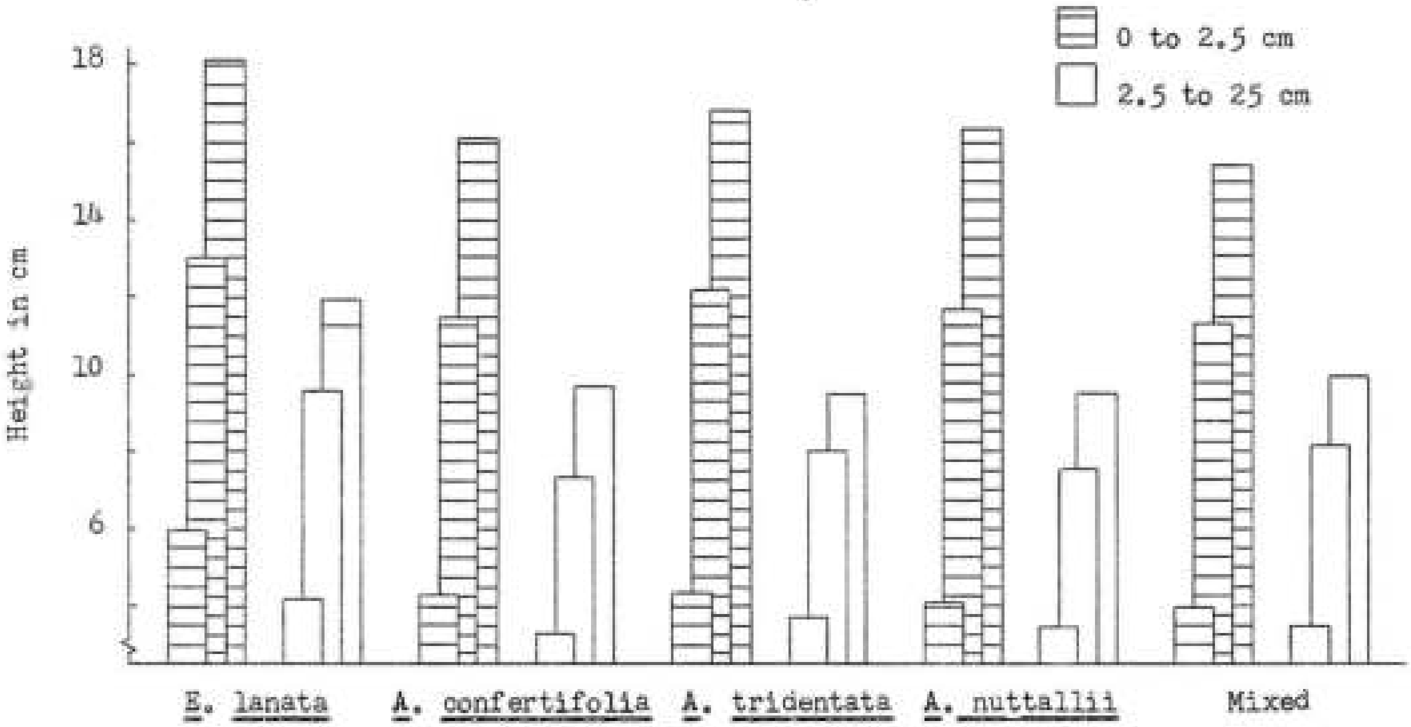


Figure 16. Mean height of *E. lanata* plants grown in pots in five different soils and two depths, at 40, 70, and 110 days after seeded.

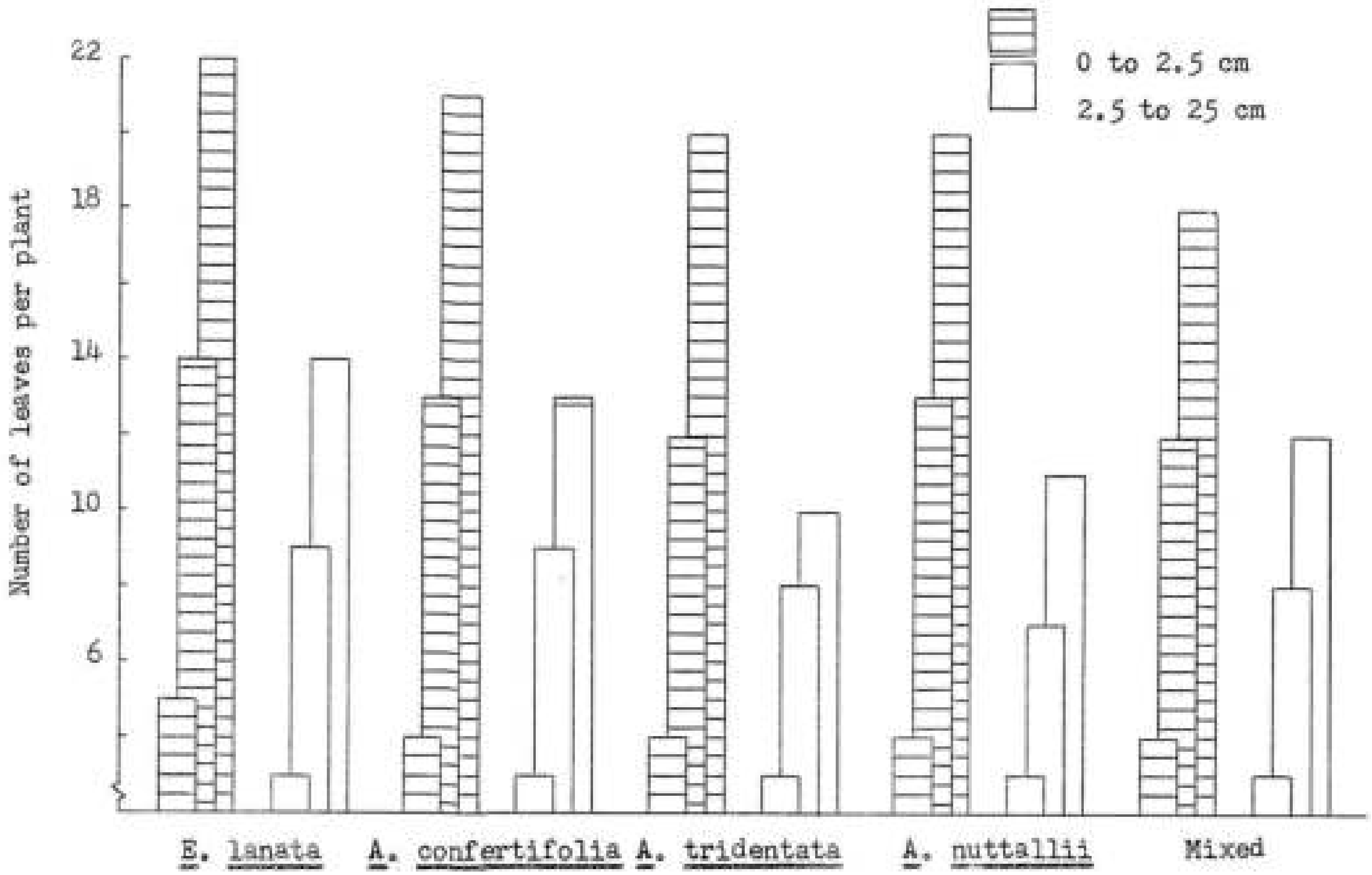


Figure 17. Mean number of leaves per plant of *E. lanata* grown in pots in five different soils and two depths, at 40, 70, and 110 days after seeded.

at 40, 70, and 110 days. However, at later dates their differences were larger and showed more clearly the effect of soil over a longer period of time.

Winterfat plants reached a taller height when growing in the pots with soils from the upper layers, no matter from what stand the sample was taken. Thus the most important factor is from what part of the soil profile the sample was taken and not from under what plant community. The largest size was reached when growing on *E. lanata* soil and the lowest on the mixed stand.

The growth on soils from the deeper layer was less than on the surface ones. The largest values were obtained on those soils where the same species grew. The differences between stands are, however, very small.

The number of leaves grown per plant indicates also that seedlings grew better on the top soil. At 110 days of age there were an average of 20 leaves per seedling growing on the top soil. The largest value was in *E. lanata* soils with 22 leaves, and the lowest in the mixed stand soil with 18. The other seedlings all had 20 or 21 leaves per plant. On the lower layer soils, the seedlings had only an average of 12 leaves, and a range from 14 to 10 leaves per plant. The seedlings growing on the *Artemisia tridentata* soil had the lowest number of leaves, while those growing on *E. lanata* and *A. confertifolia* soil had the largest.

The weight per plant kept the same basic relationship, that is, larger values on the upper soils then on the lower ones. The largest weights were found for those seedlings growing in the surface soil from under *E. lanata* and *A. nuttallii*, while the lowest for those in A. tridentata and the mixed stand soils.

The dry weight of the seedlings growing in the deeper soil samples was between one-half and one-fourth of those found from plants growing in the soil from the same stand, but from the surface layer. Thus, the influence of vegetation and environment on soil is of considerable importance for later growth of the plants themselves.

The influence of soils on seedling growth and development of winterfat is similar to that of shadscale. Plants grew well in all the soils no matter what stand or the depth from where the samples were taken. Thus for this plant, there is not a limitation of the soil per se which could restrict its distribution to certain areas in the salt desert shrub vegetation type. The distribution of this species is not restricted by edaphic tolerances under the actual soil conditions existing in the area where the soil samples were taken.

The soil is important in interpreting the distribution of the species, but obviously it is not the only environmental factor influencing the vegetation. If soil was the only controlling factor, the species would be more abundantly found in an area larger than it is actually found. The plant grew as well, or even better, in other soils than in the one that is actually found. Interference and competition are also important and perhaps are the causes which in a direct way have a greater influence in the distribution of the species in the salt desert shrub vegetation type.

In appendix table 24, the results of a similar experiment on E. lanata are reported. It is simply a repetition of the previous experiment in order to check some of the results and to better understand the influence of soil on the vegetation itself. The values reported show basically similar results, and thus the conclusions which can be drawn are the same. There is, however, one measurement which was done here and not in the previous study; this is the percentage of plants in flower. Since the previous experiment was shorter, the plants did not reach the flowering stage.

In this study, the influence of soil on the rate of growth and development was demonstrated. Most of the plants growing in pots from the upper soil from all of the five communities studied were in flower at 125 days. However, none of the plants growing in the deeper soil flowered in this period.

Speed of growth could be one of the limitations in the establishment of the individual. Under desert conditions the growth season is short. The seedlings die if they do not find favorable conditions during the limited growing season. This limitation means time. However, since the length of the growing season is fixed by the climatic characteristics of the environment where they live, it can only be slightly modified by the vegetation. Thus, the main mechanism to counteract the limited length of the growing season is the developmental rate of the seedlings. The seedlings which develop faster can reach the beginning of the unfavorable season at a more advanced stage of development, and thus have a greater chance of survival.

Besides the probable effect on the survival of the individuals themselves, there is also an effect on the reproduction of the population. The production of flowers and seeds at an earlier age is also related with a larger germination rate of the population. A larger germination rate, if the other factors remain constant, means a greater survival value for the population.

Considering the results of seedling development of both species together, some general conclusions can be reached. The first and most obvious is that the nature of the substrate has important influences in seedling development. Both seedlings were directly affected in their growth when different soils were used. The differences were shown in the height of the plants, number of leaves, total length of stems, dry weight, age of flowering, and rate of development.

Despite the fact that seedlings reacted differently to different soils, the results by no means can be used as an indication that the restricted distribution of the species in the area is regulated directly by the soil. If the plant is used as the best indicator of the integrated effect of the environment acting holocoenotically upon it, the soil would not be the cause of the restricted distribution of seedlings.

The soil influence itself, as it was shown here, would permit a much broader distribution of both species. If their distribution is broader, the potential area occupied by each species would be larger and in many places overlapping. Under these circumstances, since the same area cannot be occupied by pure stands of two different species, by competition, one of the species has to eliminate the other.

This is what really happens. The soil influences shadscale or winterfat in two different ways, because both species are different genetically, morphologically, and ecologically. Since according to

Gause's Rule, no two species can occupy exactly the same niche, and in most of the area the niche that both species could occupy is the same, then one species has to exclude the other.

If both species can successfully survive as individual plants in the area in dispute, competition has to be at the population level. The population of shadscale or that of winterfat which can most successfully occupy the area when submitted to the interference of the other species is the one which would remain permanently in the area.

The answer to the question of why one species is found in one area and not in the other cannot be based in the edaphic differences nor in the general climate of the area, which are both between the limits of tolerance for both species. Sometimes, the species is not even found rooted in the soil which is more favorable for it, but in others less favorable. The answer has to be found in interference.

The direct influence of soil in the distribution of the species is on the competitive ability under the determined edaphic conditions. The ability of the species to compete is directly influenced by soil, as well as other environmental factors such as ecotype, breeding system, season and intensity of use, and many others. Thus to find a simple and direct explanation based exclusively on soil seems now incomplete and unsatisfactory. Later in this chapter a more detailed explanation of an hypothesis explaining the causes of the distribution of the species in the area will be made.

Seedling Growth and Production Under Natural Conditions

The total density of seedlings alive at particular times of the year when the determinations were made is an indication of how favorable environmental conditions were. During the 1966 season, the mean density of seedlings of all the shrubby species alive in all the stands increased as the season advanced. This increase reached the maximum value during the period of May 7 to 14 when mean density was 29.8 seedlings per ten square meters (Table 3, Figures 18 and 19). This value progressively decreased as the season advanced, being only 10.4 seedlings per ten square meters one month later on June 15, and 6.4 two months later, on August 19.

The mean of all the transects and its variability throughout the growing season reflects, better than any other measurement, the influence of climatic conditions on the germination and mortality of seedlings under conditions such as are present in nature. To understand the differences in soils and microenvironment, in general, the differences in density of seedlings in the various stands included in this study would be more helpful.

During the same growing season, in 1966, no seedlings were found at any date in the ungrazed stand of Eurotia lanata, as well as in the mixed stand of E. lanata - A. confertifolia, or in the pure stand of this last species.

The grazed stand of winterfat showed a density of zero plants per ten square meters prior to April 23, while at that date the

Table 3. Number of live seedlings of *E. lanata* and *A. confertifolia* per ten square meters in various stands and at various dates during the 1966 season.

Stand and treatment	April			May			June					August
	4	23	30	7	14	21	1	9	15	23	28	19
Ungrazed *E. lanata*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Grazed *E. lanata*	0.0	4.0	5.3	5.3	5.3	6.7	6.7	6.7	6.7	5.3	4.0	4.0
Ungrazed ecotone	26.7	40.0	45.3	45.3	45.3	32.0	29.3	21.3	21.3	18.7	16.0	10.7
Grazed ecotone	12.0	29.3	56.0	57.3	57.3	48.0	48.0	40.0	34.7	34.7	33.3	24.0
Mixed *E. lanata*-*A. confertifolia*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Grazed *A. confertifolia*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Inside exclosure	12.3	20.0	22.6	22.6	22.6	16.0	14.6	10.6	10.6	9.3	8.0	5.3
Outside exclosure	6.0	16.6	30.6	31.3	31.3	27.3	27.3	23.3	20.7	20.0	18.6	14.0
Mean all stands	6.4	12.2	27.7	29.8	29.8	14.4	14.0	11.3	10.4	9.8	8.9	6.4

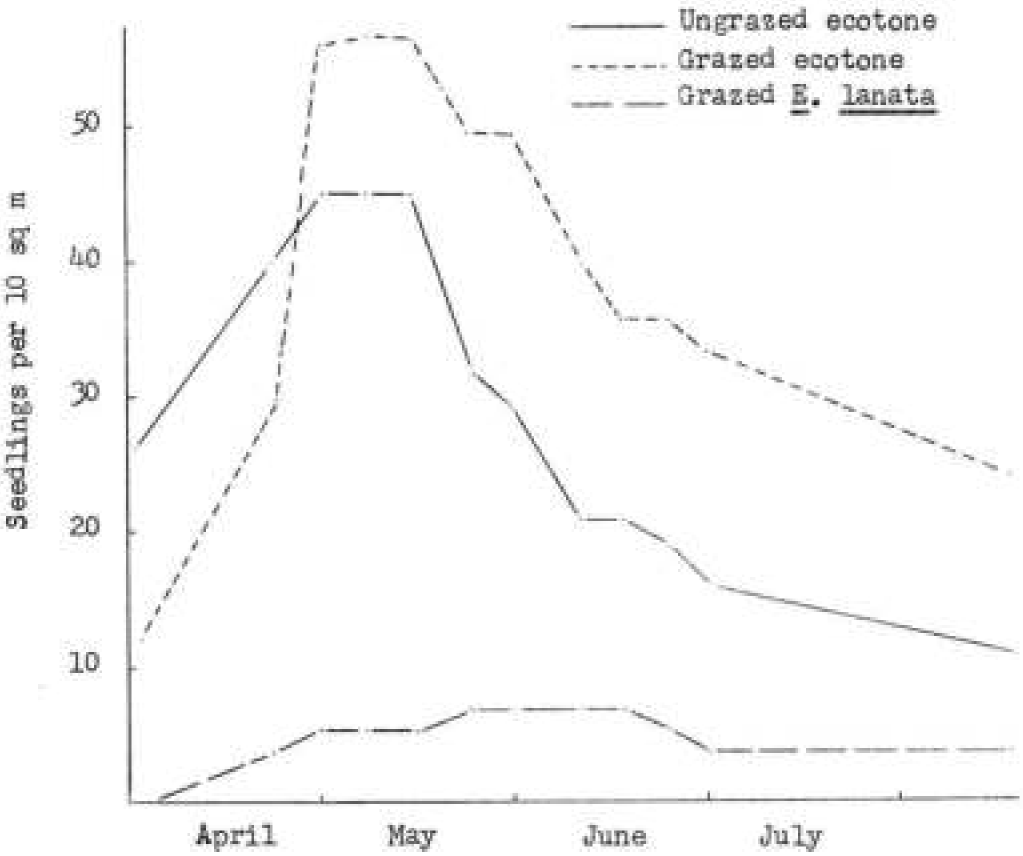


Figure 18. Mean density of seedlings of all shrubby species alive during the 1966 season at different dates in every stand.

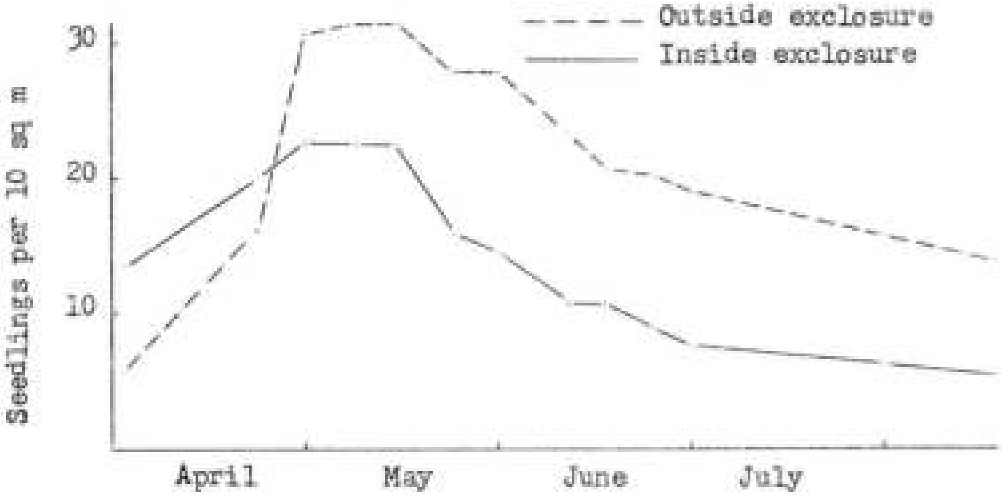


Figure 19. Mean density of seedlings of all shrubby species alive during the 1966 season at different dates, outside and inside the exclosure.

density was 4, and increased up to 6.7 plants per ten square meters on May 21. By the end of the growing season, when the plants became dormant, only 4.0 seedlings per unit area were still alive.

By far the largest number of seedlings occurred in the ecotones, both grazed and ungrazed. The grazed ecotone had as many as 57.3 seedlings per ten square meters on May 7 and 14, while the density on the ungrazed ecotonal area was only 45.3. Density gradually decreased until the end of the growing season in August when they entered the dormant period. The values recorded are 10.7 seedlings per ten square meters on the grazed area and 24.0 on the ungrazed ecotone.

The influence of grazing on the density of seedlings remaining alive can best be analyzed by comparison of the results from the transects located inside the exclosure with the equivalents located outside. The results presented in the table indicate that the maximum density of live seedlings was larger on the grazed area both in the first half of May when it reached the largest value, as well as at the end of the growing season. On the grazed area at the beginning of the dormant season in August, the density was 14.0 seedlings per ten square meters while on the exclosure, density was only 5.3.

The density of living seedlings is really a component to two factors. The first is the number of seedlings germinated and emerged and the other, the number of seedlings dead. The difference between these two components represents the number of seedlings alive at any date during the growing season.

The number of seedlings which emerged in relation to the location and time of year is presented in appendix tables 25 and 26, and Figures 20 and 21. The mean value of all locations and dates indicates that no seedlings emerged before April 30.

An average of 6.9 seedlings per ten square meters were germinated before April 4, while 8.0 new seedlings per ten square meters were found between that date and April 23. The maximum appearance of new seedlings occurred in the last week of April when 10.4 seedlings per ten square meters were germinated. Later only occasional new seedlings were observed, while during June, July, and the other remaining months of the year, no emergence at all was observed.

The effect of prior grazing was of large positive influence for seedlings. The grazed area produced as many as 28.6 new seedlings per ten square meters during the last week of April, and 18.6 from April 4 to April 23, while the exclosure produced only 5.3 and 2.6 per ten square meters for these dates, respectively. However, before April 4, the average production of new seedlings was 6.0 per ten square meters outside the exclosure and 14.6 inside.

Most of the seedlings were produced in the ecotones. The grazed ecotone produced the largest number 12.0, 33.3, and 54.6 per ten square meters on April 4, 23, and 30 respectively, while the ungrazed ecotone produced only 29.3, 10.7, and 5.3 seedlings per ten square meters. Later in the season, the production of new seedlings was very small or nil. The grazed stand of pure E. lanata also produced some seedlings but few in comparison to the ecotones. The other areas, that is the ungrazed stand of pure E. lanata, the mixed stand of the two species and the grazed stand of pure A. confertifolia, did not produce any seedlings in the plots observed.

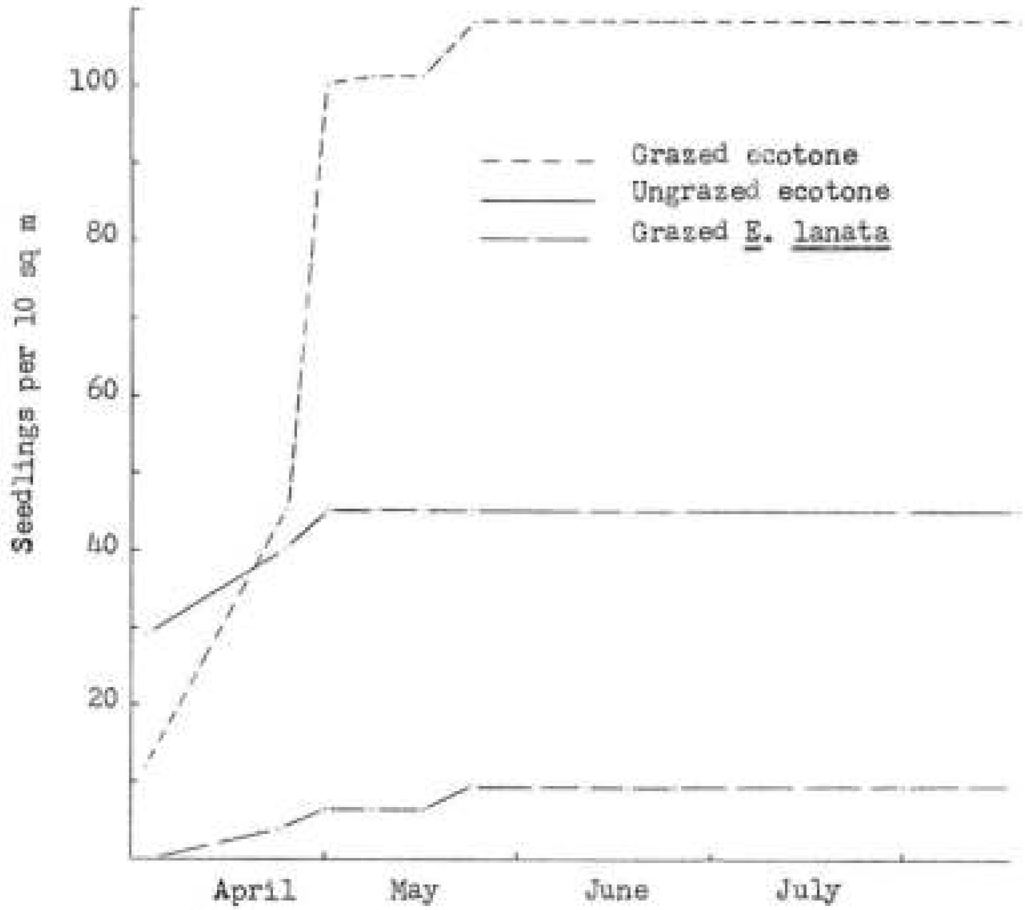


Figure 20. Mean accumulative emergent seedlings of all shrubby species in every stand at several dates during the 1968 season.

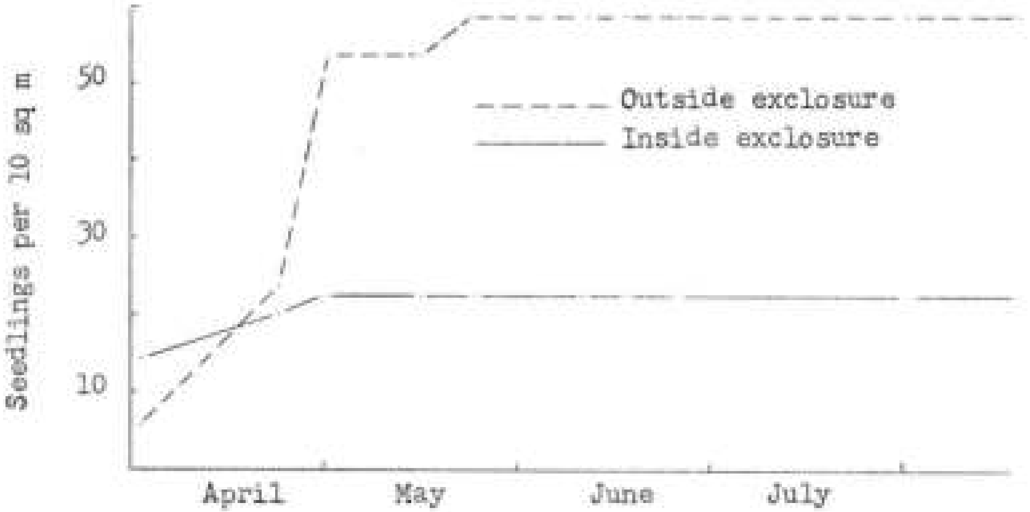


Figure 21. Mean accumulative seedlings of all shrubby species emerged inside and outside the exclosure during the 1966 season.

The death of seedlings occurred mostly between May 21 and June 9. Very few seedlings were reported dead before that date while larger amounts disappeared during the later part of the growing season (Appendix tables 27 and 28, Figures 22 and 23). The largest number of deaths occurred on the grazed ecotone, while slightly fewer deaths occurred on the ungrazed ecotone. However, the proportion of seedling deaths in relation to the total amount germinated was larger in the ungrazed ecotone.

The largest number dead occurred on the area located outside the exclosure, while slightly smaller numbers occurred inside. However, on the grazed area the amount germinating was much larger.

The results of the 1966 season clearly indicate that the conditions for seed germination and emergence were favorable only during the first part of the growing season, that is during the month of April or earlier. At that time, the temperature of the air is lower, thus, there is not an excessive amount of evapotranspiration. Soil moisture content is higher than at other times of the year because of its accumulation in the soil during the winter months and because of low evapotranspiration and occasional rains.

Moisture conditions are generally better for growth, as well as for germination and emergence early in the growing season. Because of this, seedling deaths were also less. Most of the seedlings which emerged during the 1966 growing season survived during the first part of the growing season. The mortality was highest at the beginning of the dry season in June and end of May, and slightly reduced after that date.

The single most important value is the density of live seedlings.

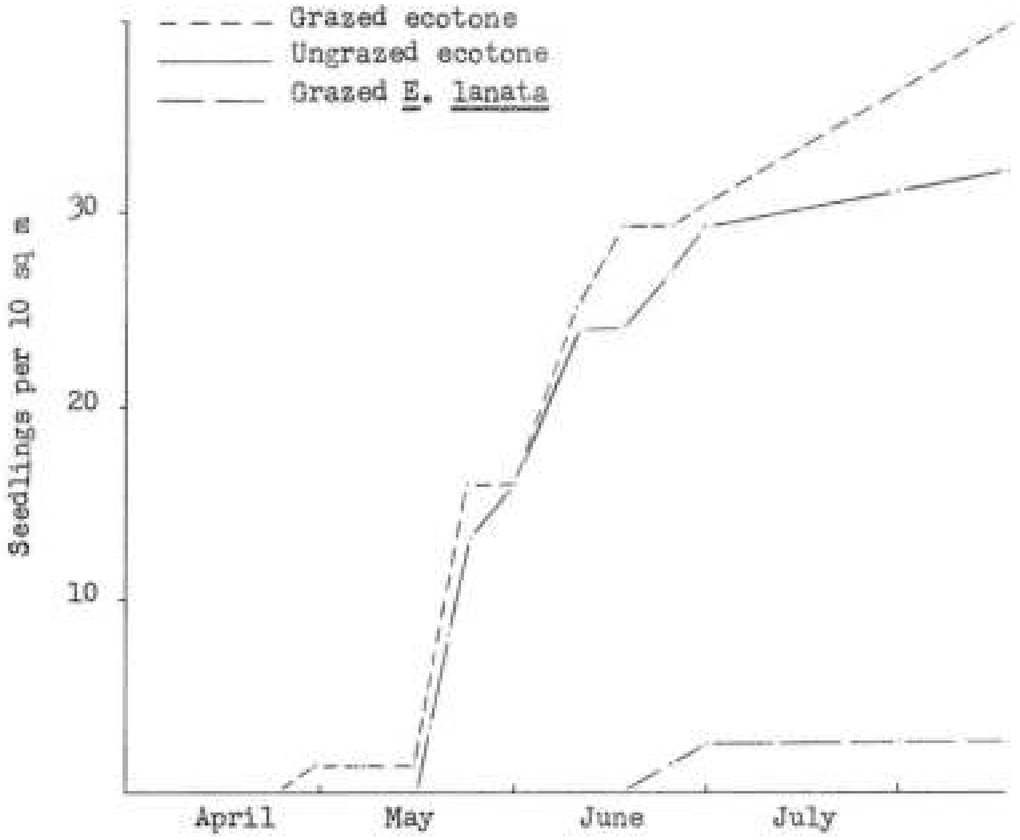


Figure 22. Mean accumulative dead seedlings of all shrubby species in every stand at several dates during the 1966 season.

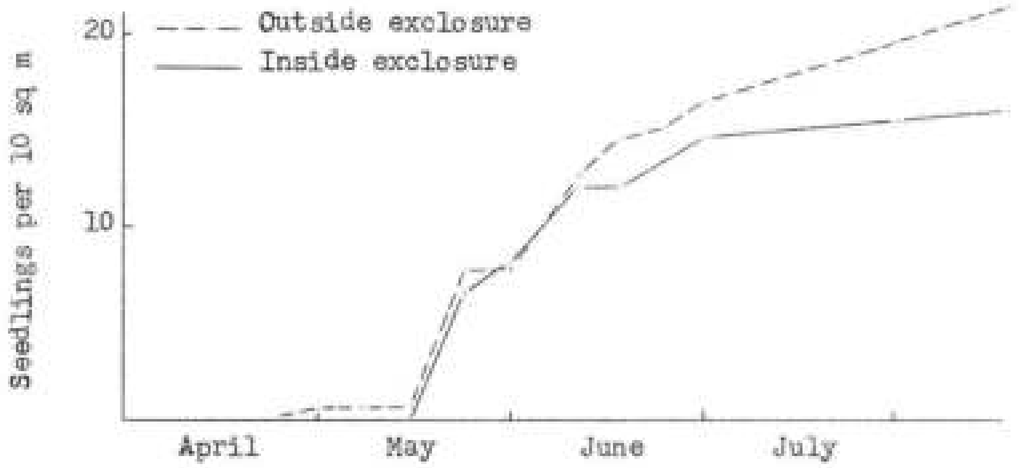


Figure 23. Mean accumulative dead seedlings of all shrubby species inside and outside the exclosure at several dates during the 1966 season.

It integrates the various environmental influences studied on the seedlings and its variability throughout the year. The results, in general, clearly point out that certain stands or environments were more favorable to sustain a larger density of seedlings. These are the ecotones. The pure stand of shadscale and the mixed stand of the two species showed completely unfavorable conditions for seedling emergence during that season.

The 1966 season was better for A. confertifolia than for E. lanata seedling emergence if the total number of seedlings of each species is compared (Appendix table 29, Figures 24 and 25). However if the density of seedlings surviving at the end of the growing season is compared, it was almost as good for winterfat as for the other. The density at the beginning of the dormant season was 4.7 seedlings per ten square meters for winterfat, while only 5.3 for shadscale.

The slight difference in final density was achieved after a large difference in density throughout the earlier part of the growing season. Shadscale had as many as 23.5 seedlings per ten square meters during the first half of May. However, because of their large mortality during the second half of May and all of June, the density decreased rapidly. Winterfat, on the other hand, had a low density during May and thereafter. The highest value achieved was 5.9 seedlings per ten square meters on April 30 through May 14. After that, surviving seedling density gradually decreased until the end of the growing season.

Shadscale had a larger production of seedlings during the season but this was also compensated for with more deaths. Winterfat

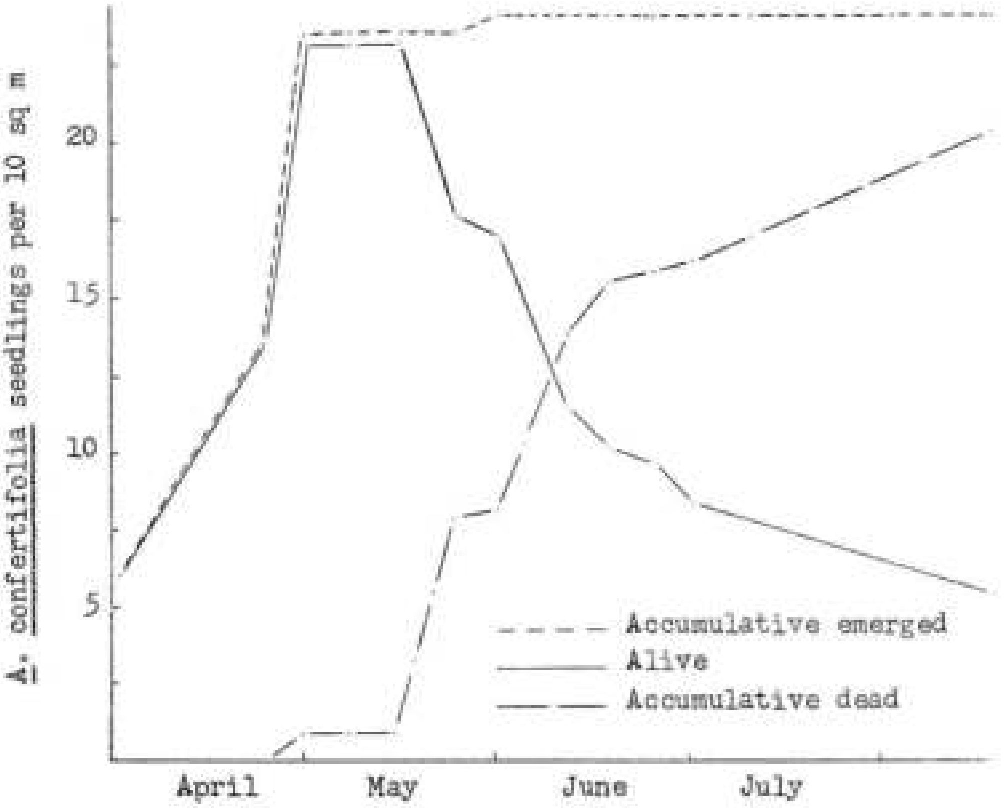


Figure 24. Mean density of live seedlings, accumulative number of emerged and dead seedlings in all stands containing A. confertifolia during the 1966 season.

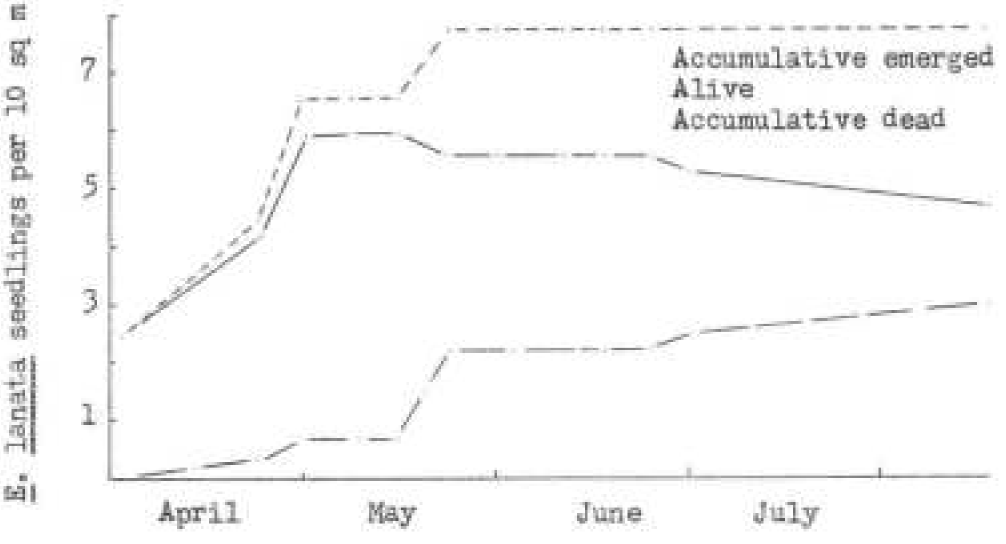


Figure 25. Mean density of seedlings alive, accumulative number of seedlings emerged and dead in all stands containing E. lanata during the 1966 season.

had proportionately a much smaller production of seedlings, but their death was insignificant in proportion to the other species. Thus, the final value, that of the density of seedlings alive at the end of the growing season, was about the same for both species.

Winterfat seedlings produced a different kind of reaction than shadscale to the climatic, edaphic, and vegetational environment. Both species gave a differential magnitude of response to the various environments. This could be useful in interpreting the causes of their distribution in restricted areas within the salt desert shrub vegetation type.

The 1967 season was in mnay respects different than the previous one. The main distinction is perhaps that during this year only two seedlings of E. lanata were recorded in all the transects, and one of them survived only one week while the other survived until the end of the season (Table 4 and Figures 26 and 27).

The first part of the season was closely similar to the climatic average. Seedling emergence was concentrated mostly during the month of April or before and until the beginning of May. Then strikingly different environmental conditions occurred. The rains were intensive and a record germination period occurred, thus increasing the seedling density.

The mean seedling density of all the stands was 0.0 seedlings per ten square meters by March 25, increased to 1.8 by April 7 and 15, and lowered to 0.2 seedlings per ten square meters by April 22. After that density increased rapidly to 2.4 by May 3, and to the highest point by May 10 on which 6.3 seedlings per ten square meters were observed. After this, there was a general decrease during most

Table 4. Density of live *E. lanata* and *A. confertifolia* seedlings per ten square meters in various stands and at various dates during the 1967 season.

Stand and treatment	March	April			May				June		July	August
	25	7	15	22	3	10	17	24	5	21	19	18
Ungrazed *E. lanata*	0.0	0.0	0.0	0.0	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9
Grazed *E. lanata*	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ungrazed ecotone	0.0	8.0	8.0	0.0	8.0	8.0	8.0	13.3	13.3	13.3	13.3	13.3
Grazed ecotone	0.0	2.7	2.7	0.0	5.3	5.3	5.3	5.3	4.0	4.0	2.7	2.7
Mixed *E. lanata*-*A. confertifolia*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Grazed *A. confertifolia*	0.0	0.0	0.0	0.0	0.0	26.7	10.7	10.7	10.7	8.0	5.3	5.3
Inside exclosure	0.0	4.0	4.0	0.0	4.4	4.4	4.4	7.1	7.1	7.1	7.1	7.1
Outside exclosure	0.0	1.3	1.3	0.6	2.7	2.7	2.7	2.7	2.0	2.0	1.3	1.3
Mean all stands	0.0	1.8	1.8	0.2	2.4	6.3	4.1	5.0	4.8	4.4	3.7	3.7

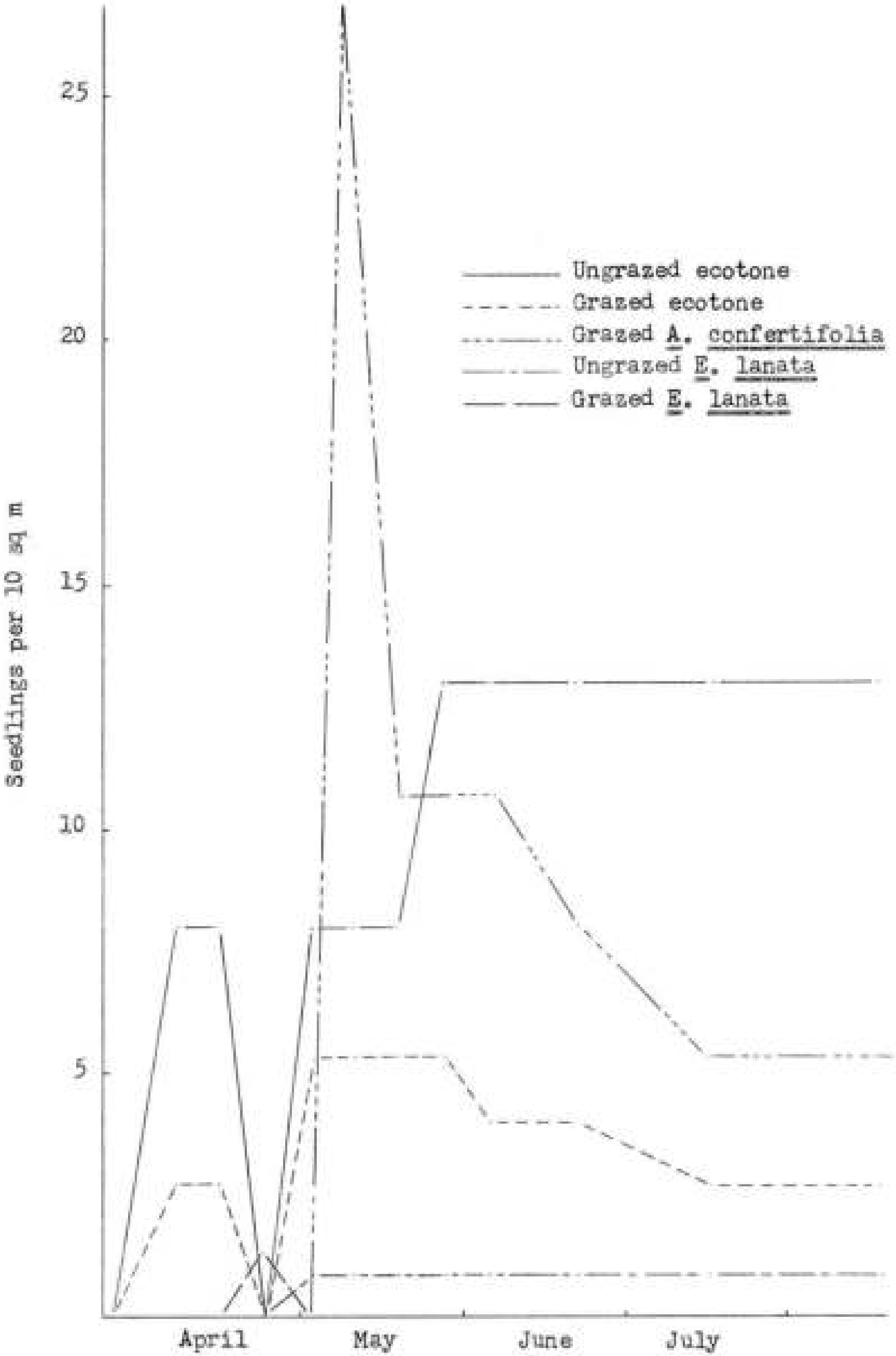


Figure 26. Mean density of seedlings of all shrubby species alive during the 1967 season at different dates in every stand.

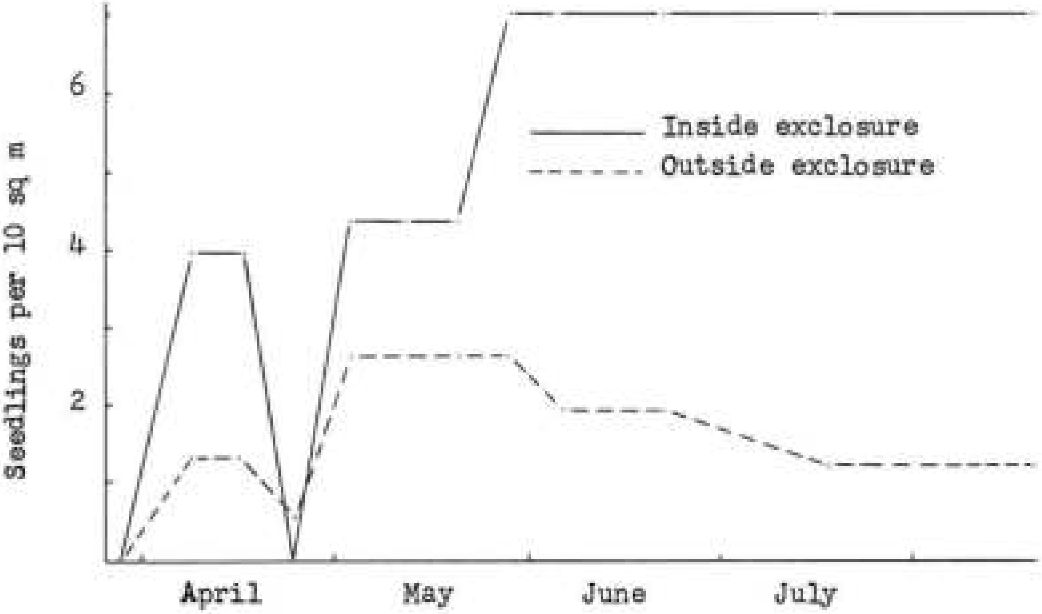


Figure 27. Mean density of seedlings of all shrubby species alive during the 1967 season at different dates outside and inside the exclosure.

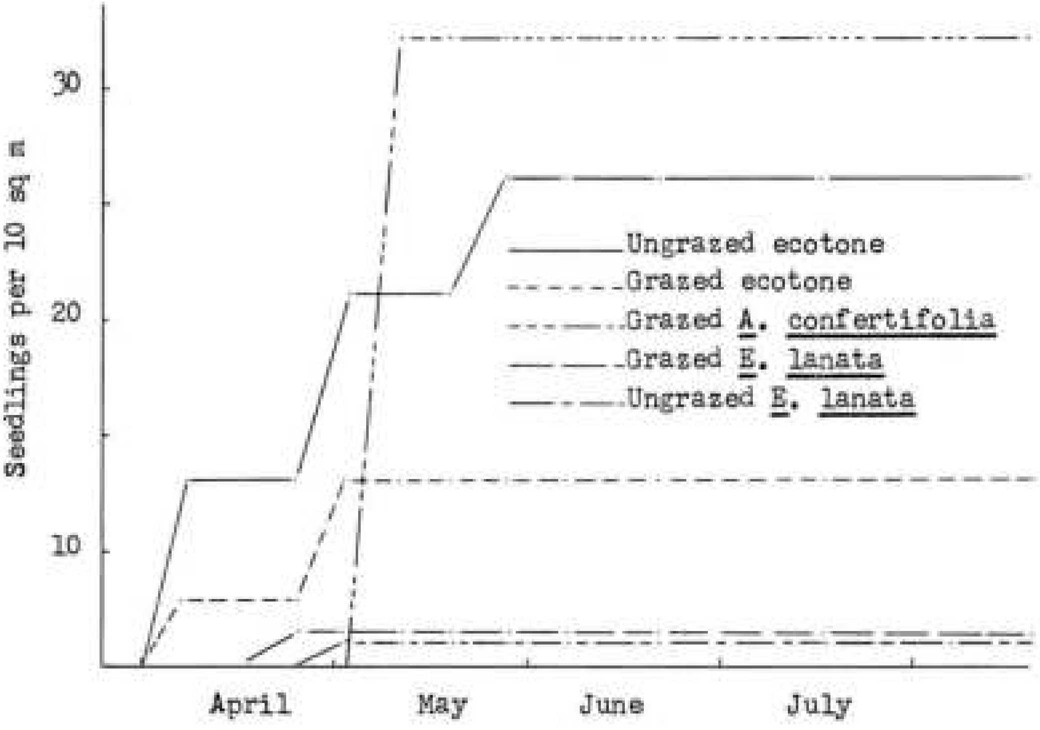


Figure 28. Mean accumulative seedlings of all shrubby species emerged in every stand at several dates during the 1967 season.

of the remaining growing season until the end of observations on August 18 when there remained only 3.7 seedlings per ten square meters.

The density of seedlings remaining alive during the 1967 season was lower than both the previous years and the following one. In the average for all the stands, the maximum density was around May 10, 1967 and was only one-fifth of the 1966 and one-ninth of the following year, which was 57.0 seedlings alive per ten square meters. However, by the end of the season the differences were largely reduced in proportion. The density during the 1967 season was only two-thirds of the density of the previous year, and one-fourth of the following one. Thus, the final values for the three consecutive years were 6.4, 3.7, and 11.7 seedlings per ten square meters. These differences are slight in comparison to what occurred during the most favorable part of the growing season. This seems to indicate that despite the large climatological differences occurring from year to year, which induce large variability in the seed germination and seedling emergence from year to year, there are other influences which counteract, at least in part, some of these variabilities.

In good seasons when there was a large density of seedlings because of large germination occurring at the beginning of the season until the first half of May, the mortality was greater. The opposite occurred in bad years when the density of germinants was low, and their mortality during the last part of the season was also lower and the final densities of the year did not differ much from year to year.

The ungrazed stand of E. lanata produced the only seedling of this species which remained alive during the active growing season. However it died later during its apparent dormancy. Seedling production was extremely low under these conditions. This seedling emerged under special microhabitat conditions; a protective environment formed by a small cavity where the temperature and moisture relations, as well as seed dissemination and germination could have been more favorable than in other microhabitats (Appendix tables 30 and 31, Figures 28 and 29).

The grazed stand of E. lanata also was not very prolific in seedling emergence in 1967. Only one seedling of this species emerged in the plots and it survived less than a week.

The ungrazed ecotone had the highest density of seedlings throughout most of the season. At the beginning of April 7, a density of 8.0 seedlings per ten square meters was recorded, while on March 25 none was present. This density remained constant during most of the season. On May 24, it increased to 13.3 seedlings per ten square meters and remained as such until the beginning of the dormant period.

The density on the grazed ecotone was smaller than in the exclosure but reached as much as 5.3 seedlings per ten square meters during the month of May, and later gradually reduced until the end of the growing season when density was 2.7 seedlings per ten square meters. No seedlings emerged in the mixed stand transects during the 1967 season (Appendix tables 31 and 32, Figures 30 and 31).

The greatest difference between the 1967 season and the other two years occurred in the grazed stand of A. confertifolia. Until

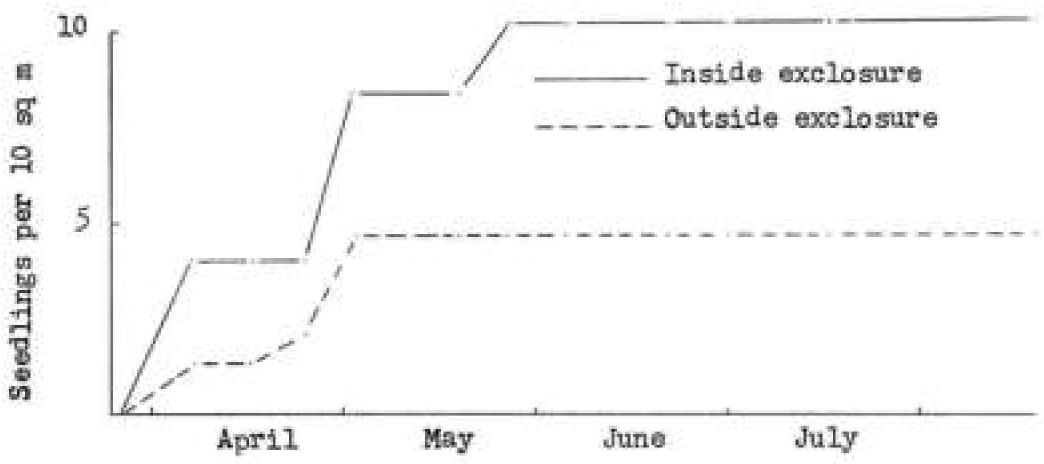


Figure 29. Mean accumulative seedlings of all shrubby species emerged inside and outside the exclosure at several dates during the 1967 season.

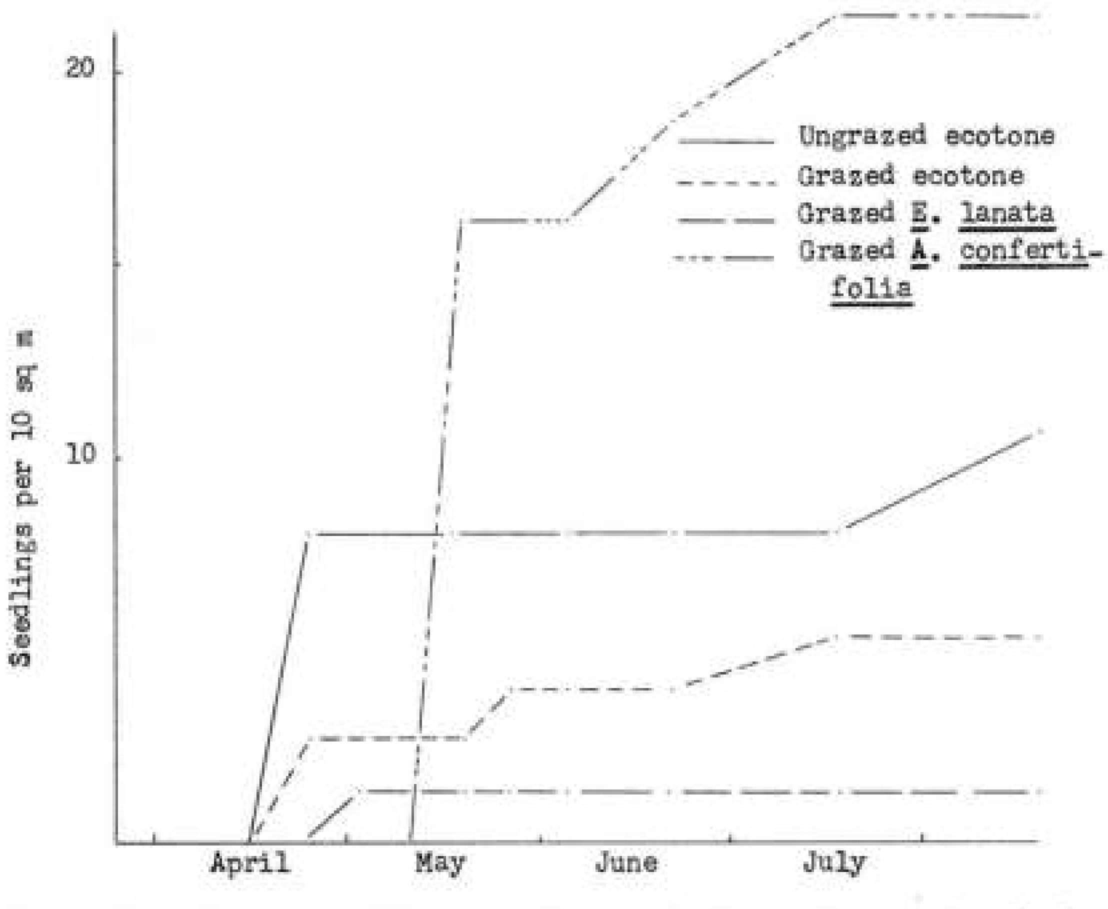


Figure 30. Mean accumulative seedlings of all shrubby species dead in every stand at several dates during the 1967 season.

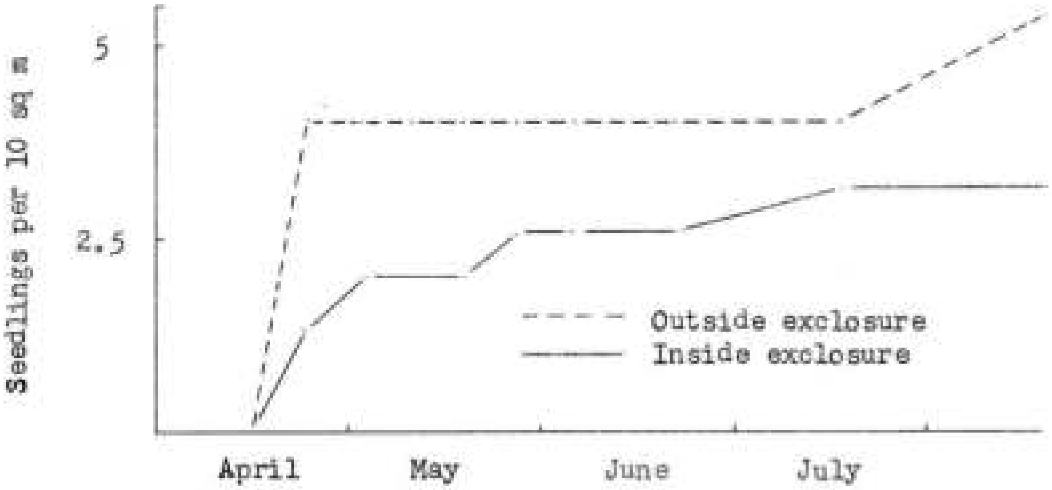


Figure 31. Mean accumulative seedlings of all shrubby species dead inside and outside the exclosure at several dates during the 1967 season.

the beginning of May, the density was zero. However, on May 10, after a large increase in the amount of rainfall received, an increase in seedling density was recorded. By May 10, the density was 26.7 per ten square meters but rapidly decreased to 10.7 one week later, and to 5.3 per ten square meters by the end of the season.

The 1967 season was excellent for A. confertifolia seedlings in this location for it was the only season when seedlings survived as well as germinated. Germination occurred in two completely different germination sites. One was in some soil cracks characteristic of the surface soil on this stand. The other was in places where there was no crack but some slight influence of dead organic matter from other adult plants of the same species was noted. Here the surface soil presented a better structure. The seedlings which emerged from the soil cracks started to die immediately after the surface soil moisture was depleted, and at the end of the growing season were all dead. The only live seedlings at the end of the season were those which emerged on the other kind of microhabitat (Figures 38 on page 126, 43 on page 131, and 44 on page 131).

The reproductive value of cracks as an influence on the germination and emergence rate of the population of shadscale is now dubious. Cracks are perhaps important because they act mostly as traps and thus the seed concentration and the possibilities of germination are greater. However, the environmental conditions for seedling growth and survival are unfavorable and so reduce their effective reproductive value.

The influence of grazing during this season resulted in a lower density of seedlings than inside the exclosure. The main reason is that the ecotone inside the exclosure produced large numbers of seedlings and thus, the general average of the exclosure was raised. However it does not seem proper to generalize a positive influence of the exclosure (Figures 32 and 33).

The species comparison during the 1967 season does not add very much new information to what has already been said. Since the production of winterfat seedlings was almost nil, all what has been said applies mostly to shadscale (Appendix table 34, Figures 34 and 35).

The germination and emergence of shadscale occurred during two distinct periods. The first corresponded to the normal period, that is during the latter part of March and early April. A second germination period occurred during the first half of May. This is probably not common and was, as a matter of fact, the only time that

Figure 32. Grazed E. lanata (south) transect. The taller shrubs are A. tridentata.

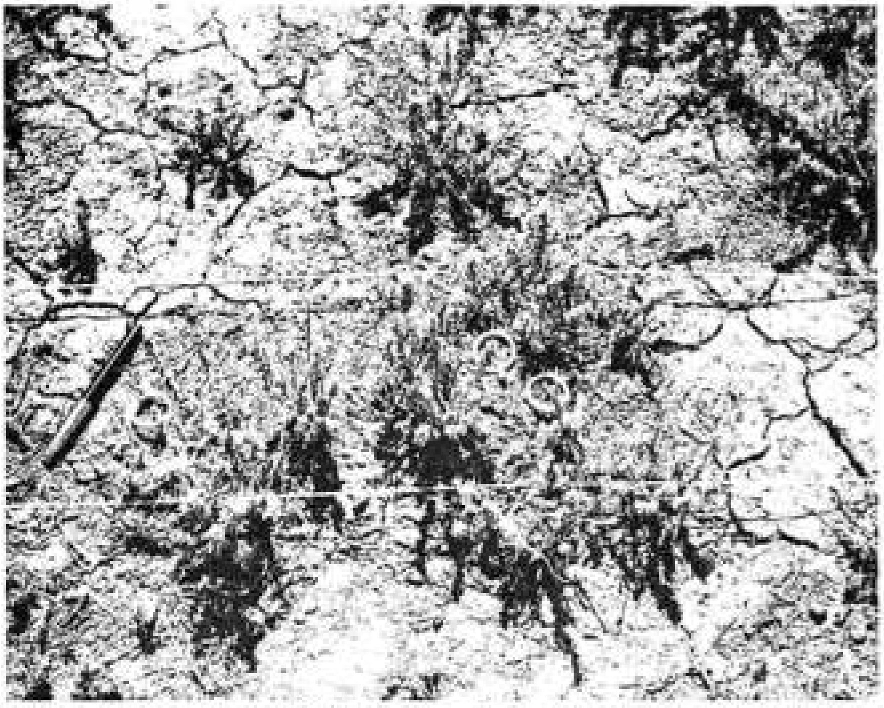


Figure 33. Close view of the grazed E. lanata (south) transects. The adult plants are winterfat while the rings indicate the location of two A. tridentata seedlings and one of E. lanata.

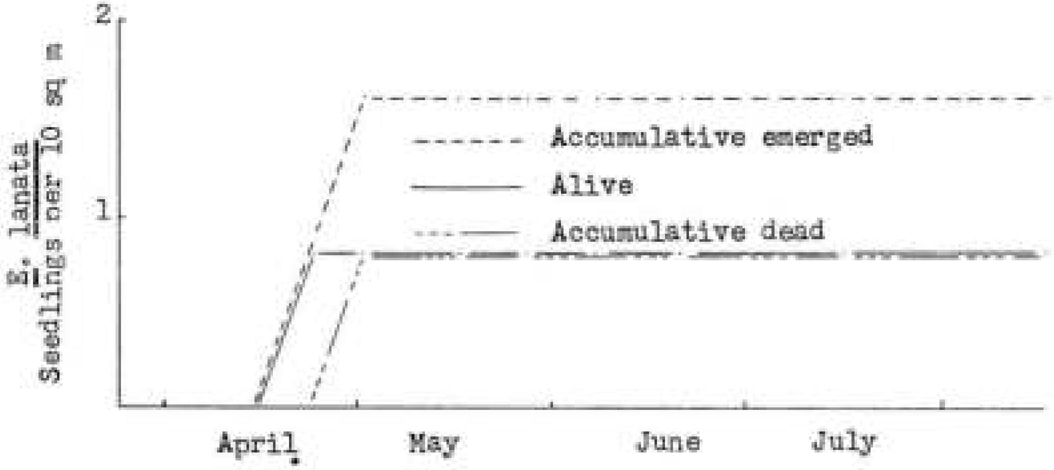


Figure 34. Mean density of live winterfat seedlings, accumulative number of emerged and dead seedlings during the 1967 season in all stands containing E. lanata.

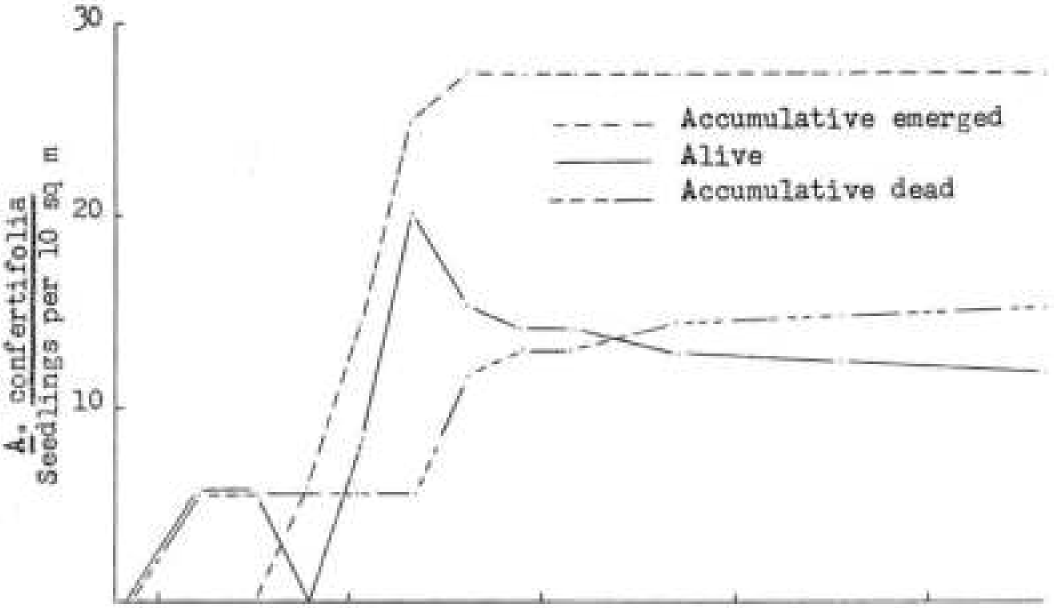


Figure 35. Mean density of live shadscale seedlings, accumulative number of emerged and dead seedlings during the 1967 season in all stands containing A. confertifolia.

something like this occurred during the study period.

The abundant germination and emergence of A. confertifolia seedlings can be easily related with the supranormal rains which occurred at that time. This extra moisture could be related with the research results previously reported by Vest (1952). He found that the seeds of this species don't germinate because of a large concentration of a germination inhibitor in the bracteoles. The substance, which is water soluble, could be washed away by abundant precipitation.

The removal of the inhibitor by the excessive rains and the favorable environmental conditions for germination and emergence induced the large increase in density which occurred at this time of the year. The surface soil was moist and temperatures were moderate, thus the chance for germination was greater if there were enough seeds in the soil ready to germinate in an uninhibited conditions.

Winterfat seeds do not have this inhibitory mechanism which has been reported for A. confertifolia. The germination of winterfat seeds occurs whenever the environmental conditions surrounding the seeds are favorable for germination. The main controlling factors are water potential, temperature, and salinity (Springfield, 1968; Workman and West, 1967, in press).

The environmental conditions for germination of winterfat were favorable during the first part of the 1967 season until the middle of May. The reason there was no germination then has to be blamed upon the lack of seed. This explanation cannot be supported with experimental results from the field, but general observations on seed production during the previous season indicated that it was extremely low or none occurred at all.

The reduced germination of E. lanata was caused by the shortage of seed and not by unfavorable germination conditions. Seedling production could be influenced more by seed production from the previous year than by the conditions existing for germination itself (Figures 36, 37, 38, 39, 40, and 41).

The 1968 season was good for seedling production (Table 5, Figures 42, 43, 44, and 45). The mean density of live seedlings calculated from information of all the stands studied indicates that the largest value occurred at the beginning of the growing season on March 19. On that date the mean density was 57.0 seedlings per ten square meters.

The emergence of seedlings during this growing season began in early March (Appendix tables 35 and 36). However, they were not individualized and tagged because their radicles were not yet attached to the soil. This season had two main differences from the others. One is the maximum seedling density during the season, as well as the actual density at the end of the growing season, was larger than those of the previous years. The other difference is the maximum density which occurred in the middle of March or even perhaps earlier, while in the previous years, it occurred in the first half of May.

The mean density in all stands at the end of March was reduced from 57.0 to 52.1 seedlings per ten square meters. The gradual reduction in density occurred during the rest of the growing season. By the end of April, it was only 36.9 seedlings per ten square

Figure 36. General view of the grazed ecotone transect. The small plants are *E. lanata* while the largest one is *A. confertifolia*.

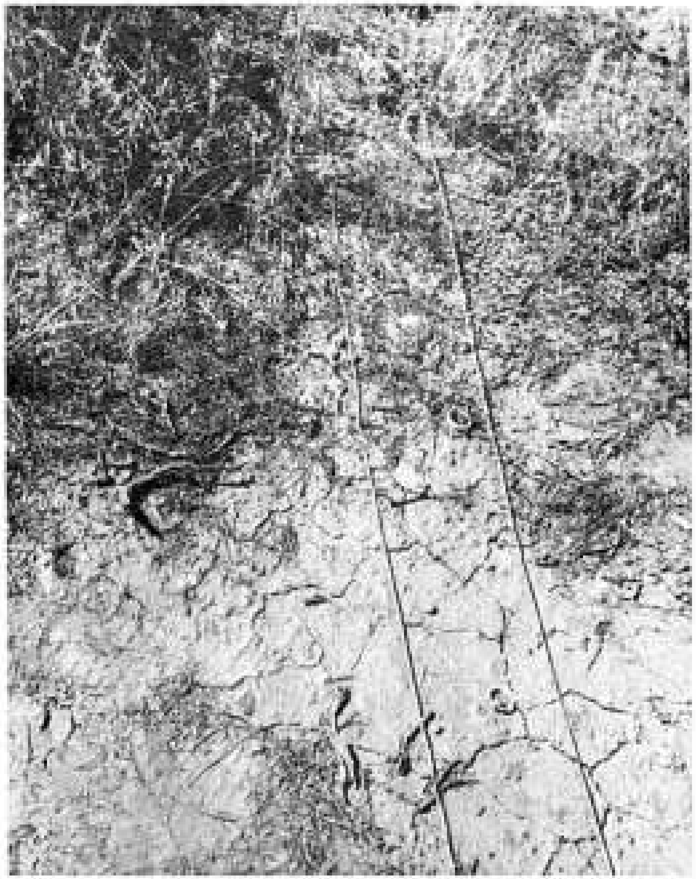


Figure 37. General view of a seedling transect located in the mixed *E. lanata* - *A. confertifolia* stand.

Figure 38. A. confertifolia seedling growing in the grazed stand of the same species. The seedling is in the second growing season.

Figure 39. E. lanata seedling growing in the ungrazed ecotone. The seedling is in its fourth growing season.

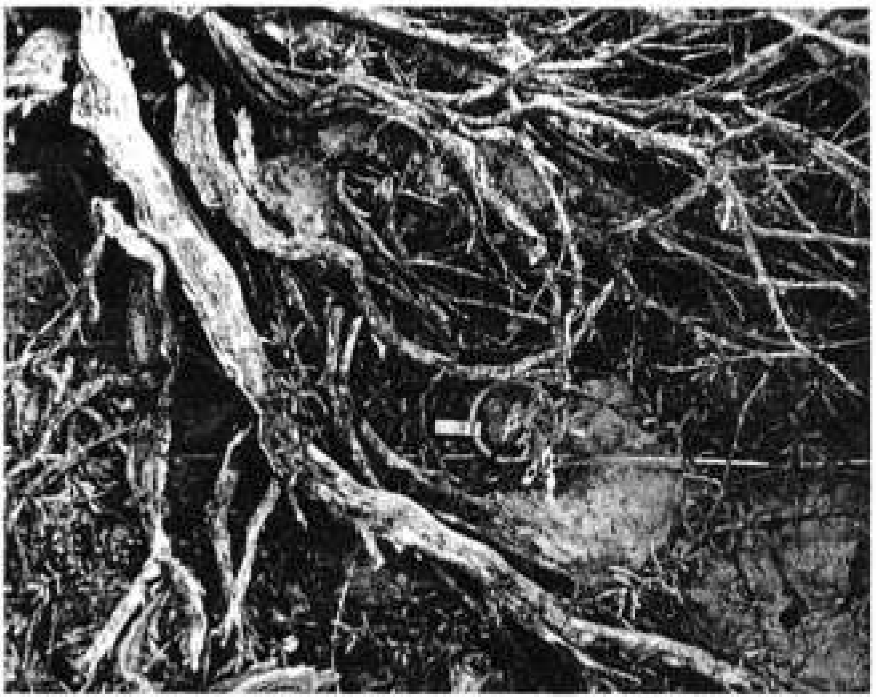


Figure 40. Location of a A. confertifolia seedling on the second season of growth, in a transect located in the grazed stand of the same species.

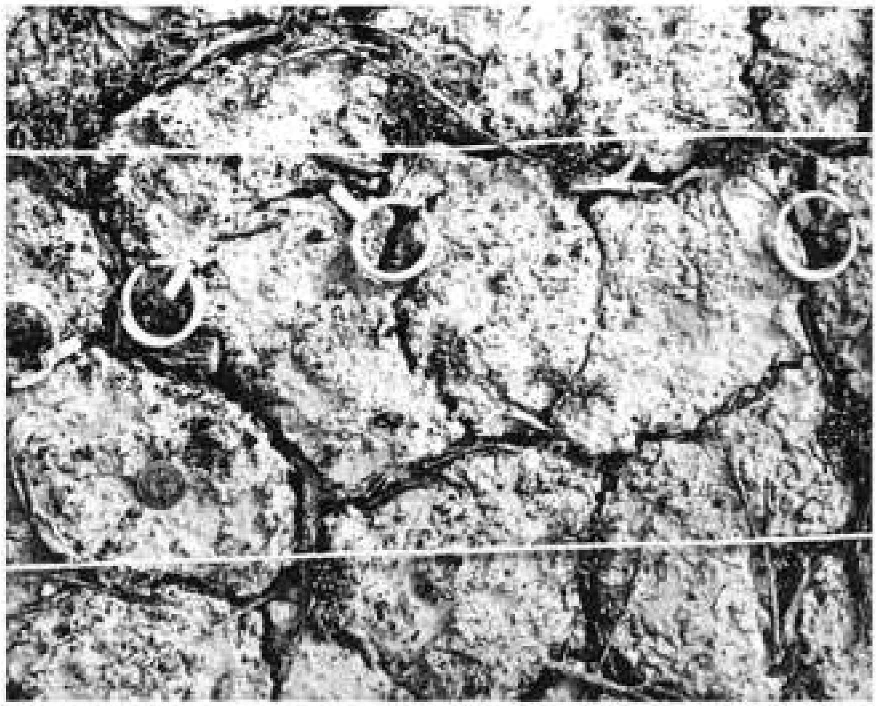


Figure 41. Close view of sector of the grazed A. confertifolia seedling transect. The rings indicate the location of some of the seedlings born in 1967. The seedlings shown in the picture are of Halogeton glomeratus.

Table 5. Number of live seedlings of *E. lanata* and *A. confertifolia* per ten square meters in various stands and at various dates during the 1968 season.

Stand and treatment	March		April				May				June	
	19	30	6	13	20	28	4	11	19	25	13	19
Ungrazed *E. lanata*	53.3	41.7	28.4	26.7	24.0	22.2	17.8	17.8	16.9	16.9	16.0	16.0
Grazed *E. lanata*	70.7	68.0	57.3	46.6	57.3	56.0	45.6	48.0	46.6	46.6	44.0	37.3
Ungrazed ecotone	69.3	50.7	32.0	29.3	26.7	24.0	24.0	21.3	21.3	18.7	18.7	18.7
Grazed ecotone	118.7	118.7	116.0	112.0	98.7	89.3	78.6	73.3	72.0	72.0	66.6	62.6
Mixed *E. lanata*-*A. confertifolia*	40.0	33.8	35.5	34.7	32.9	30.2	25.8	25.8	25.8	25.8	25.8	19.5
Grazed *A. confertifolia*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Inside exclosure	61.3	46.2	30.2	28.0	25.3	23.1	20.9	19.5	19.1	17.8	16.9	16.9
Outside exclosure	94.7	93.3	86.6	79.3	78.0	72.6	62.1	60.6	59.3	59.3	55.3	50.0
Mean all stands	57.0	52.1	44.9	41.6	39.3	36.9	32.0	31.0	30.1	30.0	28.5	25.7

Table 5. Continued

Stand and treatment	July	August		Sept.
	26	7	29	24
Ungrazed *E. lanata*	12.4	10.0	7.1	7.1
Grazed *E. lanata*	34.7	22.6	22.6	22.6
Ungrazed ecotone	8.0	8.0	2.7	2.7
Grazed ecotone	52.0	48.0	34.6	33.3
Mixed *E. lanata*-*A. confertifolia*	9.8	7.1	5.3	4.5
Grazed *A. confertifolia*	0.0	0.0	0.0	0.0
Inside exclosure	10.2	9.0	4.9	4.9
Outside exclosure	43.3	35.3	28.6	27.9
Mean all stands	19.5	15.9	12.0	11.7

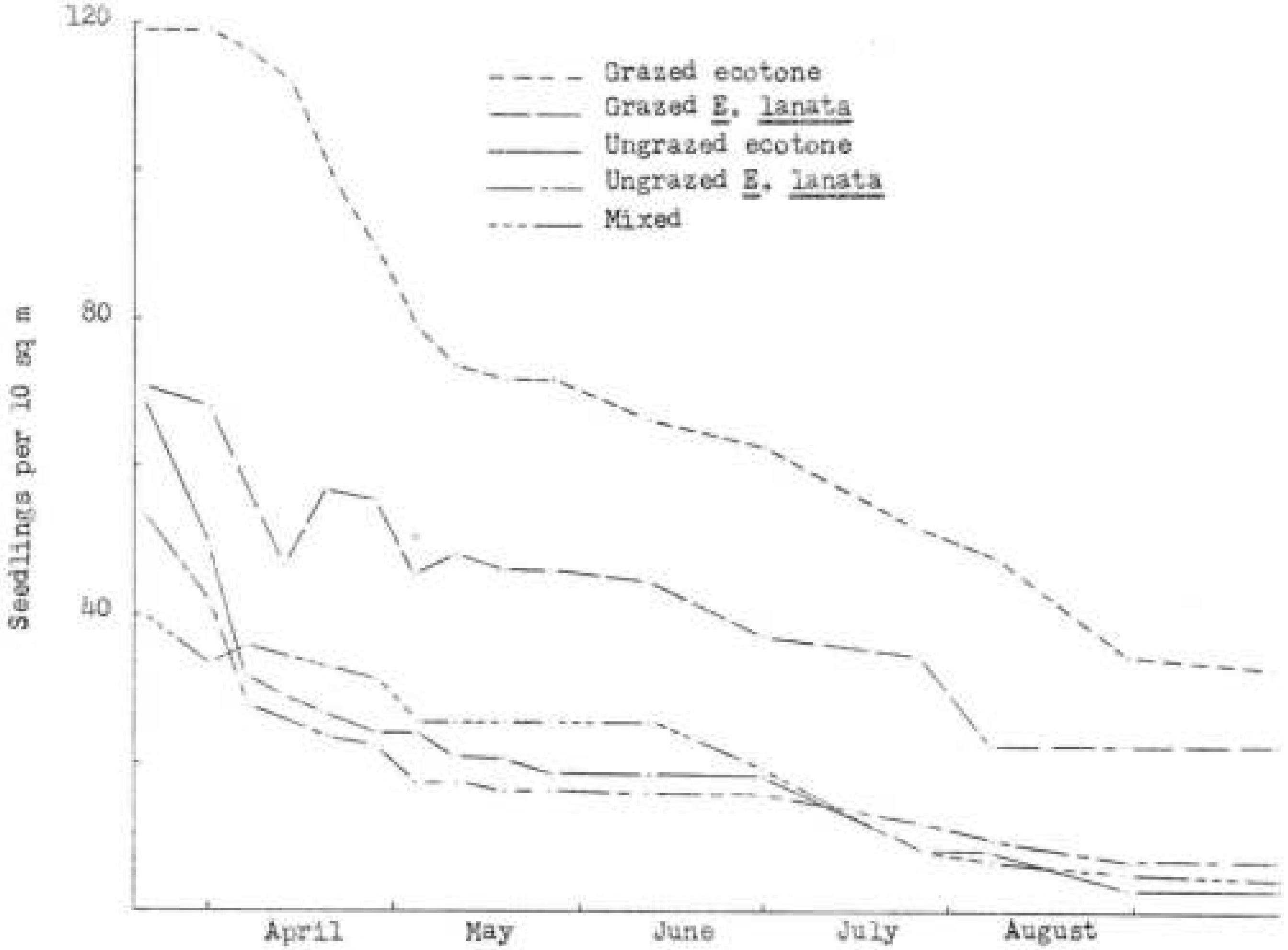


Figure 42. Mean density of live seedlings of all shrubby species at several dates during the 1968 season.

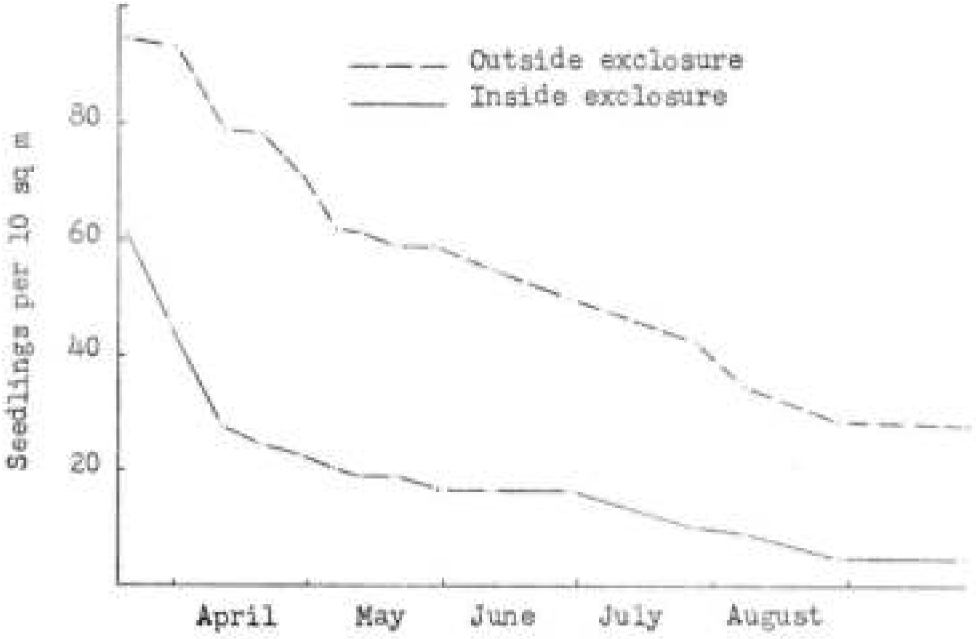


Figure 43. Mean density of live seedlings of all shrubby species inside and outside the exclosure at several dates during the 1968 season.

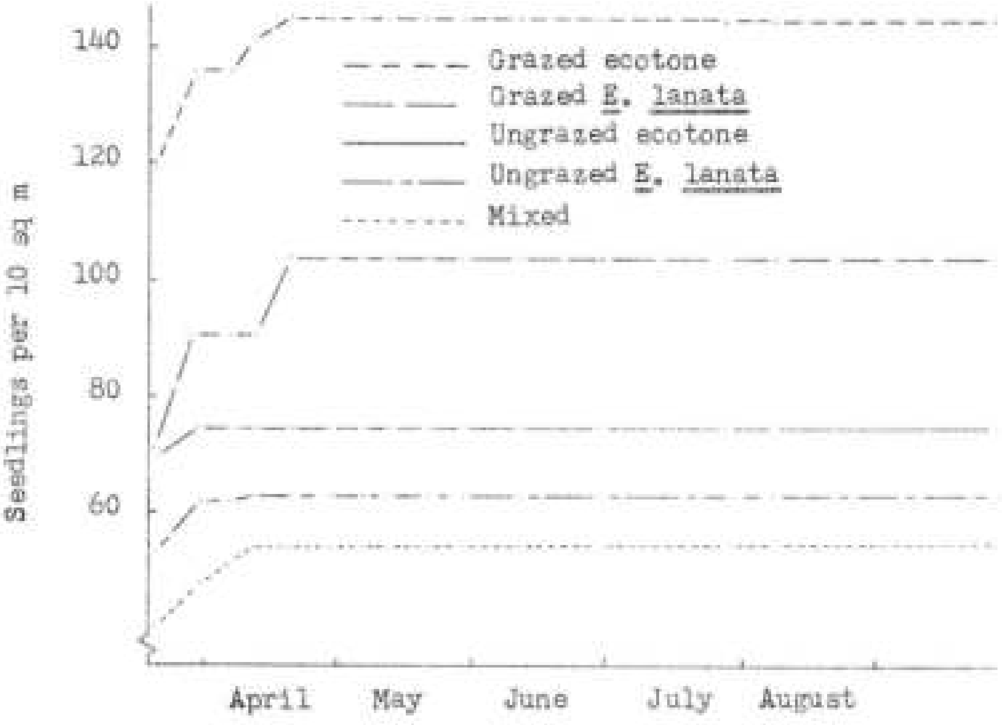


Figure 44. Mean accumulative emerged seedlings of all shrubby species in every stand at several dates during the 1968 season.

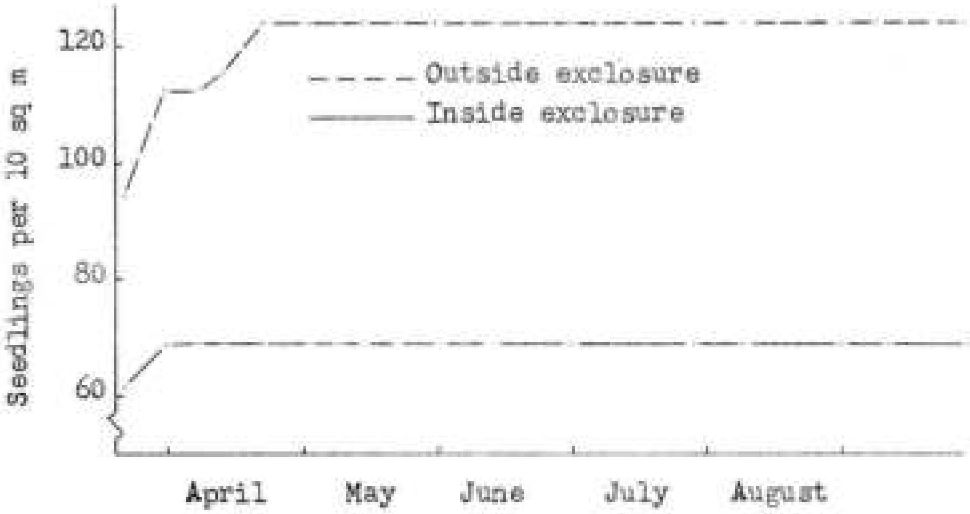


Figure 45. Mean accumulative emerged seedlings of all shrubby species inside and outside the exclosure at several dates during the 1968 season.

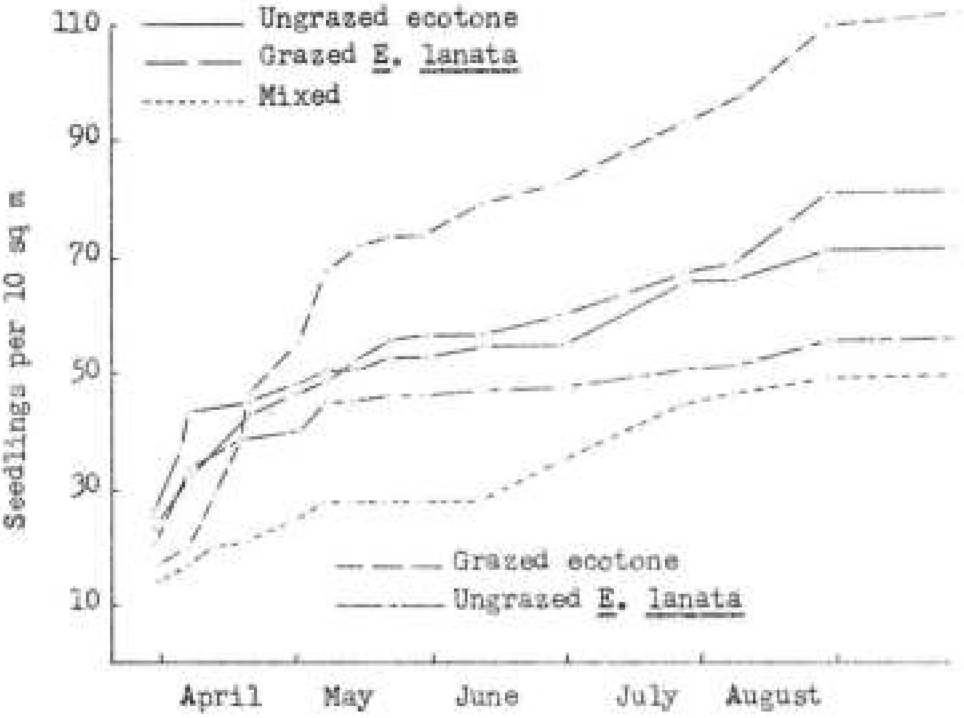


Figure 46. Mean accumulative seedlings of all shrubby species dead in every stand at several dates during the 1968 season.

meters, 30.0 at the end of May, 25.7 at the end of June, and 19.5 seedlings per ten square meters one month later. On August 29 the density was 12.0, while one month later it was 11.7 seedlings per ten square meters. A very small reduction occurred at the end of the growing season (Appendix tables 37 and 38, Figures 46 and 47).

The number of seedlings alive at a particular date is a consequence of two processes acting independently and in opposite directions. One is the rate of germination and emergence and the other is the rate of mortality. In the 1967 season these two processes reached their optimum value in May. The reason for this is there was some mortality during that time of the year, but in general it was minimal and emergence rate surpassed it until after the first half of that month. After that time, the rate of mortality of seedlings did not increase appreciably but the rate of emergence sharply reduced to zero or near so.

During the last season the two processes also operated in a similar way, but the dates were different. Seedling emergence occurred mostly during the month of March. After that the amounts were almost negligible until April 20 when the last recorded seedling emerged. The rest of the year no new seedlings appeared. Seedling deaths were highest during late March and early April. The rest of the year did not vary too much except at the end of the growing season from July to September when it increased to some degree. On a monthly basis the lowest absolute mortality occurred during the month of June, while the highest occurred in March, April, July, and August.

Considering the results of seedling production in relation to

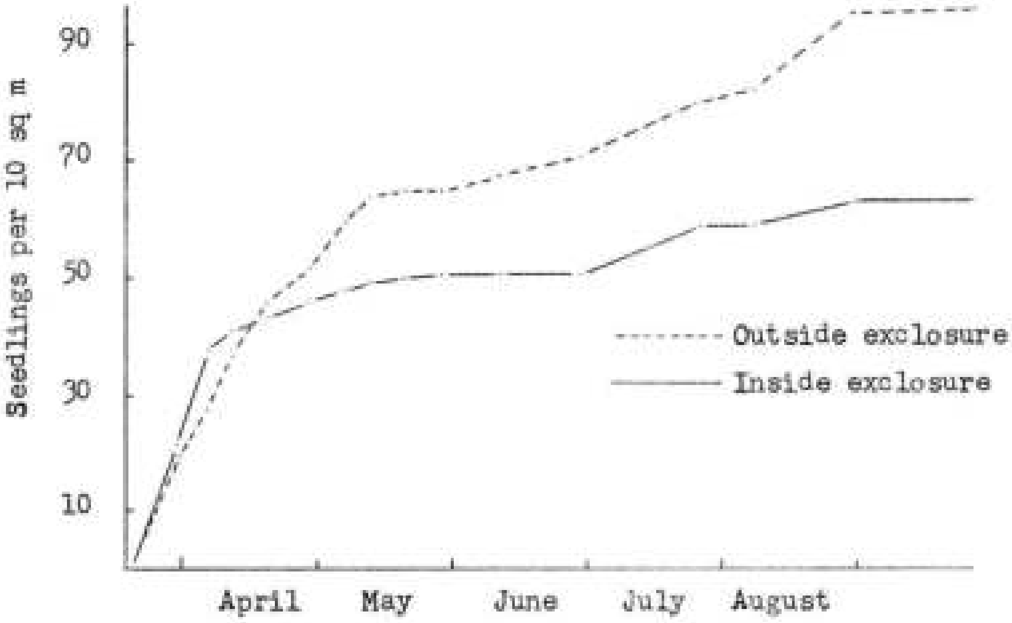


Figure 47. Mean accumulative seedlings of all shrubby species dead inside and outside the exclosure at several dates during the 1968 season.

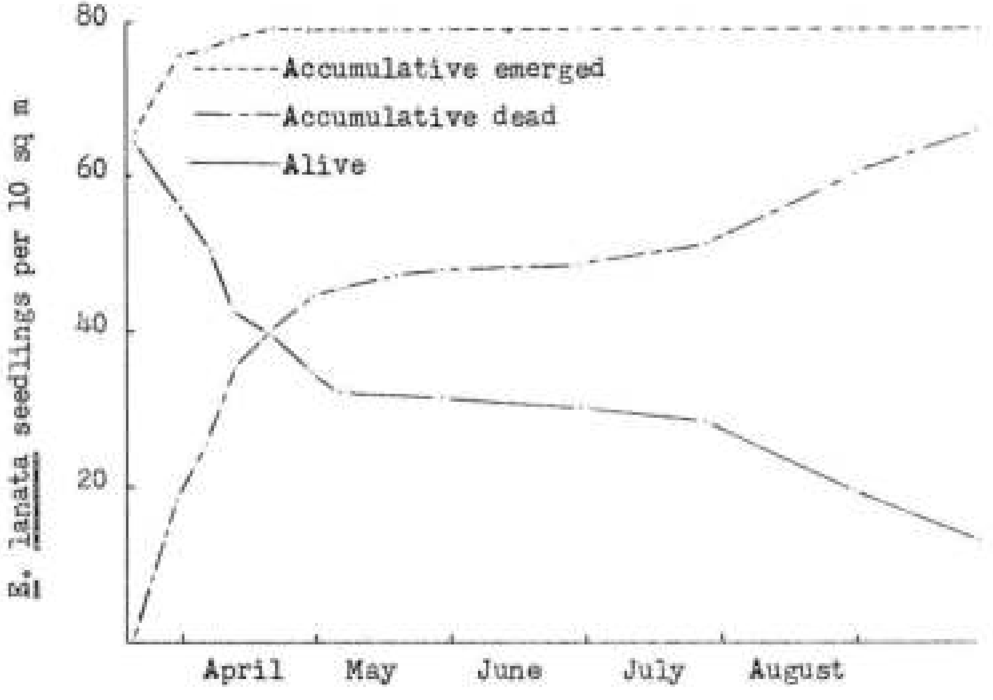


Figure 48. Mean density of winterfat seedlings alive, accumulative number of seedlings emerged and dead in all stands containing *E. lanata* during the 1968 season.

the stand, the results show that during the 1968 season the best conditions occurred on the grazed ecotone. The density of seedlings alive on March 19 was 118.7 per ten square meters. This is the highest value recorded for all the seasons and locations. By the end of the season the density was 33.3 seedlings per ten square meters. This means slightly less than one of every three seedlings survived during the year.

The ungrazed ecotone also produced a large density of seedlings at the beginning of the season. From a maximum value of 69.3 per ten square meters, the density of seedlings gradually decreased until the end of the season when it reached a low of 2.7 seedlings per ten square meters. This means that one of every 26 seedlings survived. The conditions for germination and emergence were favorable if the maximum density and the number of seedlings emerged per unit area are considered. However, the survival conditions were unfavorable if the rate of mortality is considered.

The grazed stand of E. lanata provided satisfactory conditions for seedling emergence. The maximum density of seedlings was high, 70.7 per ten square meters on March 19. The decrease in density during the growing season was small. September was reached with only a reduction of slightly less than one-third of the seedling population. Twenty-two and six-tenths seedlings per ten square meters is more than enough to maintain the density of the population of E. lanata in equilibrium (Figures 44 on page 131, and 45 on page 132).

The ungrazed stand of E. lanata produced lower maximum densities of seedlings at the beginning of the growing season. The data indicate that the density of seedlings was appreciably smaller than on the grazed stand. Besides this, the seedling survival was also proportionally smaller than in the grazed stand. Only one of every 8 seedlings alive at the beginning of the season survived (Figures 46 on page 132 and 47 on page 134).

Two striking differences occurred between the grazed and ungrazed areas. The maximum density of seedlings was always higher on the grazed area than in the ungrazed. The other difference was that the rate of reduction of the density throughout the growing season was larger on the excluded area than in the grazed one. Thus, grazing induced beneficial results in seedling production by increasing the seedling density and reducing mortality. The exclosure was probably a closed community.

The grazed stand of A. confertifolia did not produce seedlings during the 1968 season. The mixed stand of the two species had a maximum density of 40 seedlings per ten square meters. This was the first time that seedlings were recorded in this area. Despite the fact that some seedlings emerged, the reduction in density was tremendous because of mortality so high that at the end of the growing season, only a few were still alive. The results reported from this area are harder to analyze because this is the only stand of perennial shrubs which also have a large density of early germinating annuals comprised mostly of Bromus tectorum. Seed production, germination, and mortality of the shrubby species could be mostly affected by the annuals and not by their own populations. Because of the design of the study itself, there is insufficient information on the annuals and their effects on the perennial shrub seedlings (Figures 49 and 50).

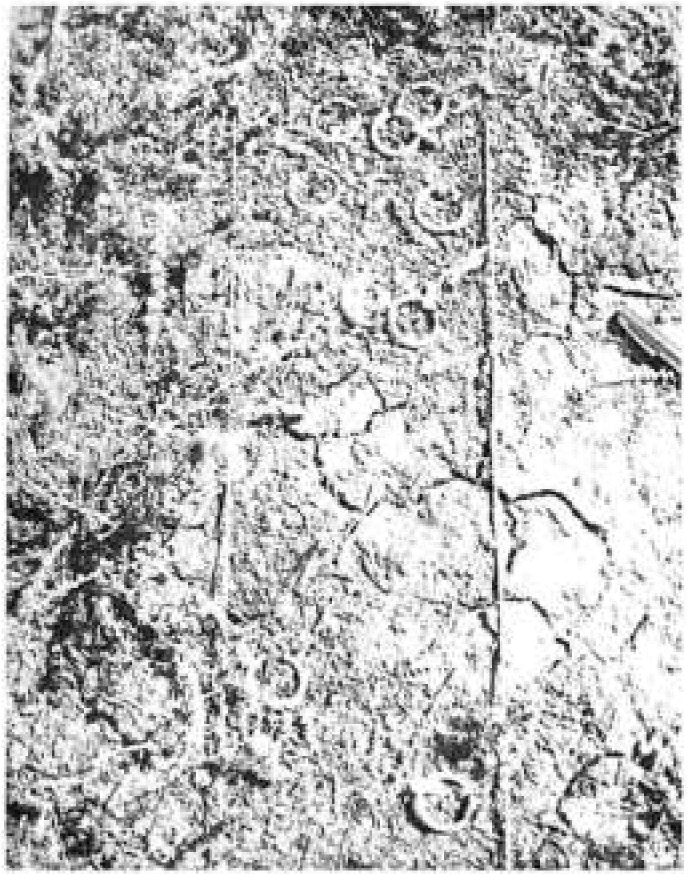


Figure 49. Close up view of a segment of the grazed ecotone (north) seedling transect. The seedlings are both winterfat and shadscale.

Figure 50. General view of the grazed *A. confertifolia* seedling transect. *In the front* of the picture, the location of some seedlings of 1967 can be observed.

From the information provided by this study, it is obvious that the interspecific competition between these seedlings and the annuals is mainly responsible for the reduction in density of the perennials as it has also been reported by Holmgren (1956).

Seedling emergence occurred only during the very first part of the growing season. If moisture is the main regulator of germination, these results are explainable according to Springfield's study (1968b). Greater germination of seeds should be found when the soil moisture content is higher. This is what actually occurred. Conditions for germination were favorable earlier when the water potential was greater. Thus, all the seeds that were ready to germinate did so in March or early April. Later in April and May there were also favorable environmental conditions for germination but the viable seeds had already germinated. Because of lack of seeds later in the season, and not because of inadequate environmental conditions, no germination occurred at that time of year.

Winterfat seeds which don't have any inherent mechanism to delay germination have to germinate when the first opportunity of favorable environmental conditions presents itself. Shadscale seeds also germinate when the environmental conditions are favorable, provided that the internal cause inhibiting seed germination has been removed. Since this process is caused by a physical factor which dissolves and moves away the substance responsible for it, time is required until new seeds are ready to germinate.

If this line of reasoning applies to what actually occurs under natural conditions, then winterfat should have germination concentrated on certain dates when the environmental surroundings for the seeds are more favorable. Germination in groups on certain dates occurs with large variability from year to year since seed production also varies annually.

Shadscale has a more sophisticated mechanism to regulate germination and so it should have less variability from year to year. Since seed inhibition may last for several years, no matter what the seed production the previous season, there should be enough of a supply of seeds produced in previous years that can germinate. However since most of the wetting and removal of the inhibitor occurs during the early and not inactive part of the year, seed germination of A. confertifolia is also concentrated during the early part of the season. The most important influence of the inhibitory mechanism for delaying germination is its influence in providing viable seeds for germination every year, and thus reducing the annual variability in seedling production. If it were not for this mechanism, seedling density variability from year to year would be much greater.

The 1968 season was, in general, characterized by high production of E. lanata seedlings. Following the same line of reasoning, it should be expected that during the previous season large numbers of seeds of this species were produced. Thus, a large number of seedlings should appear later in the next season (Table 1 on page 60 , Figure 8 on page 62).

The maximum density of winterfat for all the stands was 65.7 seedlings per ten square meters. This figure contrasts to the seed production which was 1554 seeds per the same unit of area in the mixed stand, 898 in the grazed stand, and 491 in the exclosure.

This is an average of 981 seeds for the three areas; thus, for every 15 seeds only one produced a seedling.

A similar comparison could be made using the seed production during the previous season and the number of seedlings surviving at the end of the following growing season. Under these circumstances, for every 6 seedlings produced, only one survived at the end of the following season. The difference between seed production and survival is due to two factors. One indicates what proportion of the seeds produced per unit area is later going to germinate and emerge, while the other indicates of those that germinated, what proportion survived.

The germination of seeds and the emergence and survival of seedlings is not only a function of their physiology, but it is related to the characteristics of the physical environment where they live. There are also other important ecological influences such as the predator-prey relationship which could occur both at the seed or at the seedling stage of development.

Around the few scattered plants of big sagebrush, in the pure stand of winterfat, there were large densities of seedlings of this species (Table 6). This was observed in many places in the pure winterfat stand where isolated plants or groups of plants of A. tridentata were growing. However, this phenomenon was recorded in only one transect dominated by winterfat but with a few individuals of big sagebrush around it, which produced large amounts of seeds the previous year. The seedlings of this species differed from those of winterfat in their emergence date. Most of them were recorded at a later date, that is around April 20, whereas they began dying by May 4. The rate of death was low but increased as the season

Table 6. Mean number of seedlings of E. lanata, A. confertifolia, and A. tridentata per ten square meters, in all locations at several dates during the 1968 season.

Seedlings	March		April				May				June	
	19	30	6	13	20	28	4	11	19	25	13	29
E. lanata												
Alive	64.7	57.4	51.1	47.5	43.4	40.0	34.8	33.2	32.7	32.2	31.0	28.1
New emerged	64.7	10.9	1.4	1.7	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Accumulative emerged	64.7	75.6	77.0	78.7	79.7	79.7	79.7	79.7	79.7	79.7	79.7	79.7
Dead	0.0	18.2	7.7	5.3	5.1	3.4	5.1	1.7	0.5	0.5	1.2	2.9
Accumulative dead	0.0	18.2	25.9	31.2	36.3	39.7	44.8	46.5	47.0	47.5	48.7	51.6
A. confertifolia												
Alive	1.4	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
New emerged	1.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Accumulative emerged	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4
Dead	0.0	0.7	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Accumulative dead	0.0	0.7	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4
A. tridentata												
Alive	0.0	8.0	8.0	8.0	32.0	32.0	29.3	29.3	29.3	29.3	29.3	29.3
New emerged	0.0	8.0	0.0	0.0	24.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Accumulative emerged	0.0	8.0	8.0	8.0	32.0	32.0	32.0	32.0	32.0	32.0	32.0	32.0
Dead	0.0	0.0	0.0	0.0	0.0	0.0	2.7	0.0	0.0	0.0	0.0	0.0
Accumulative dead	0.0	0.0	0.0	0.0	0.0	0.0	2.7	2.7	2.7	2.7	2.7	2.7

Table 6. Continued

Seedlings	July	August		September
	26	7	29	4
E. lanata				
Alive	21.1	19.4	13.6	13.1
New emerged	0.0	0.0	0.0	0.0
Accumulative emerged	79.7	79.7	79.7	79.7
Dead	7.0	1.7	5.8	0.5
Accumulative dead	58.6	60.3	66.1	66.6
A. confertifolia				
Alive	0.0	0.0	0.0	0.0
New emerged	0.0	0.0	0.0	0.0
Accumulative emerged	1.4	1.4	1.4	1.4
Dead	0.0	0.0	0.0	0.0
Accumulative dead	1.4	1.4	1.4	1.4
A. tridentata				
Alive	21.3	16.0	8.0	8.0
New emerged	0.0	0.0	0.0	0.0
Accumulative emerged	32.0	32.0	32.0	32.0
Dead	0.0	5.3	10.7	0.0
Accumulative dead	10.7	16.0	26.7	26.7

advanced. Mortality was greatest during the month of August.

The death rate of winterfat was high during April and until the early part of May. After that it remained at a fairly constant rate until the end of the season. Shadscale, because of the small number of seedlings, did not show a clear pattern of mortality. However, mortality occurred only during the first part of the growing season in April. After that the density was zero.

Besides the variability in seedling production from year to year and throughout the growing season, there is also the heterogeneity of the horizontal distribution of the seedlings. Table 7 and Figure 51 present some results in this respect.

The upper part of the table indicates the percentages of ground covered by litter. In the grazed Eurotia lanata stand, 6 percent of the surface was covered by thick litter. Considering that only a small percentage of ground was covered by this category of litter, if the distribution of seedlings is at random, a similar percentage of seedlings should occur in this microhabitat. Nevertheless, this is not the case because 30.9 percent of the seedlings were found there. Twelve percent of the land was covered by abundant litter; however, 28.5 percent of the seedlings were found under that kind of cover (Figures 53, 54, and 55).

The percentage of land covered by a fair amount of litter was 12 percent, while 23.8 of the seedlings occurred there, while the percentages covered by little, very little, traces of litter, and bare ground were larger than the percentages of seedlings emerged under those conditions. The respective values of seedlings emerged under these conditions were 9.5, 7.1, 0.0, and 0.0 percent.

Table 7. Percentage of ground cover by litter density classes in six different stands, and location of seedlings in the stand according to the litter density.

Stand	Litter Cover						
	Thick	Abundant	Fair	Little	Very little	Traces	Bare
	Ground covered by litter, percent						
Grazed *E. lanata*	6	12	12	13	12	11	34
Ungrazed *E. lanata*	3	10	13	14	10	9	41
Grazed ecotone	4	7	15	14	12	10	38
Ungrazed ecotone	6	8	14	14	10	8	40
Mixed	28	14	12	9	8	11	18
Grazed *A. confertifolia*	14	12	10	8	5	8	43
	Location of seedlings, percent						
Grazed *E. lanata*	30.9	28.5	23.8	9.5	7.1	0.0	0.0
Ungrazed *E. lanata*	35.0	28.0	23.0	10.0	0.0	0.0	4.0
Grazed ecotone	47.2	22.2	20.8	8.3	1.4	0.0	0.0
Ungrazed ecotone	50.0	30.0	10.0	10.0	0.0	0.0	0.0
Mixed	27.3	27.3	24.2	12.1	6.1	0.0	3.0
Grazed *A. confertifolia*	0.0	40.0	20.0	20.0	0.0	0.0	20.0

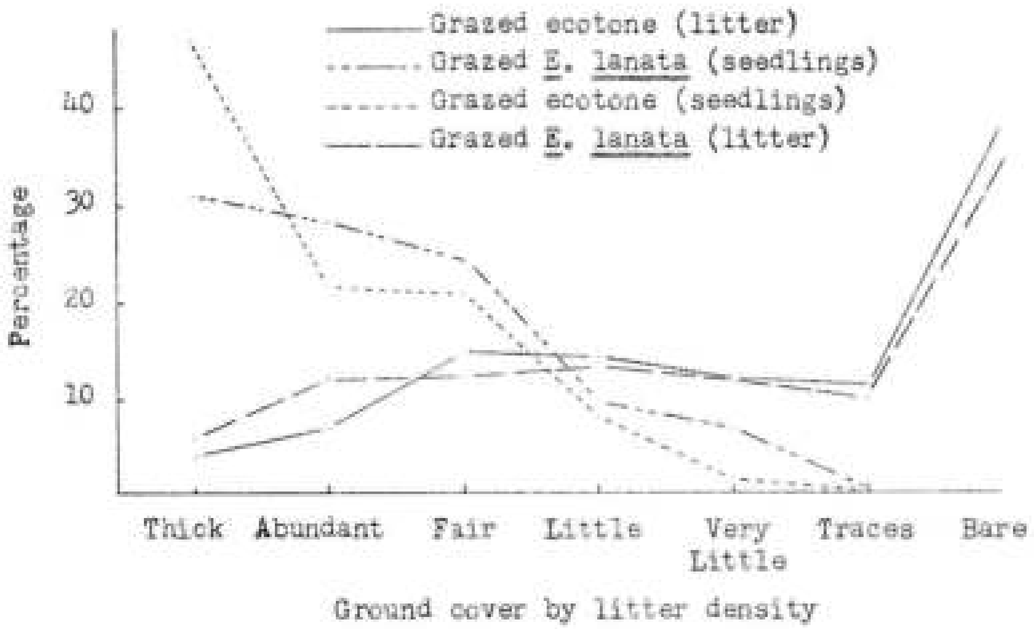


Figure 51. Percentage of ground covered by various classes of litter density on two different stands, and location of seedlings in the stand according to the litter density.

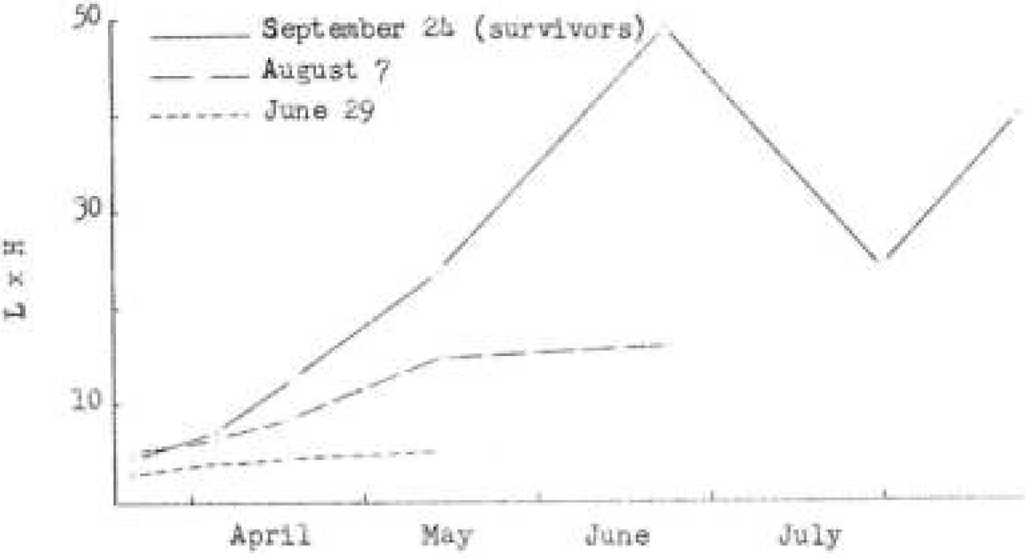


Figure 52. Mean size (number of leaves times maximum height in cm, L x H) of *E. lanata* seedlings emerged in 1968, in the grazed stand of the same species and grouped according to the date of their death.

Figure 53. Representation of a 2.2 m segment of two transects located on the grazed stand of *Eurotia lanata* and on the ecotone on the grazed area. The right figure represents the south transect and the left one, the north transect. The areas in between the two central continuous lines represent the 15 cm wide transects themselves, and at both sides, areas 20 cm wide surrounding them. The crown cover of the adult plants of *E. lanata*, *A. confertifolia*, and *A. tridentata* is indicated in both figures. Also, the area around the plants where the microtopography has been modified by their influence. In the transects themselves, the location of the seedlings and the ground cover by litter is also indicated.

● *E. lanata*
◯ *A. tridentata*
◍ *A. confertifolia*
⊖ Perennial grass

○ Seedling location
▨ Abundant or thick litter cover
▩ Fair litter cover
⊘ Little litter cover

⊜ Bare ground
----- Microrelief limit
——— Transect limit

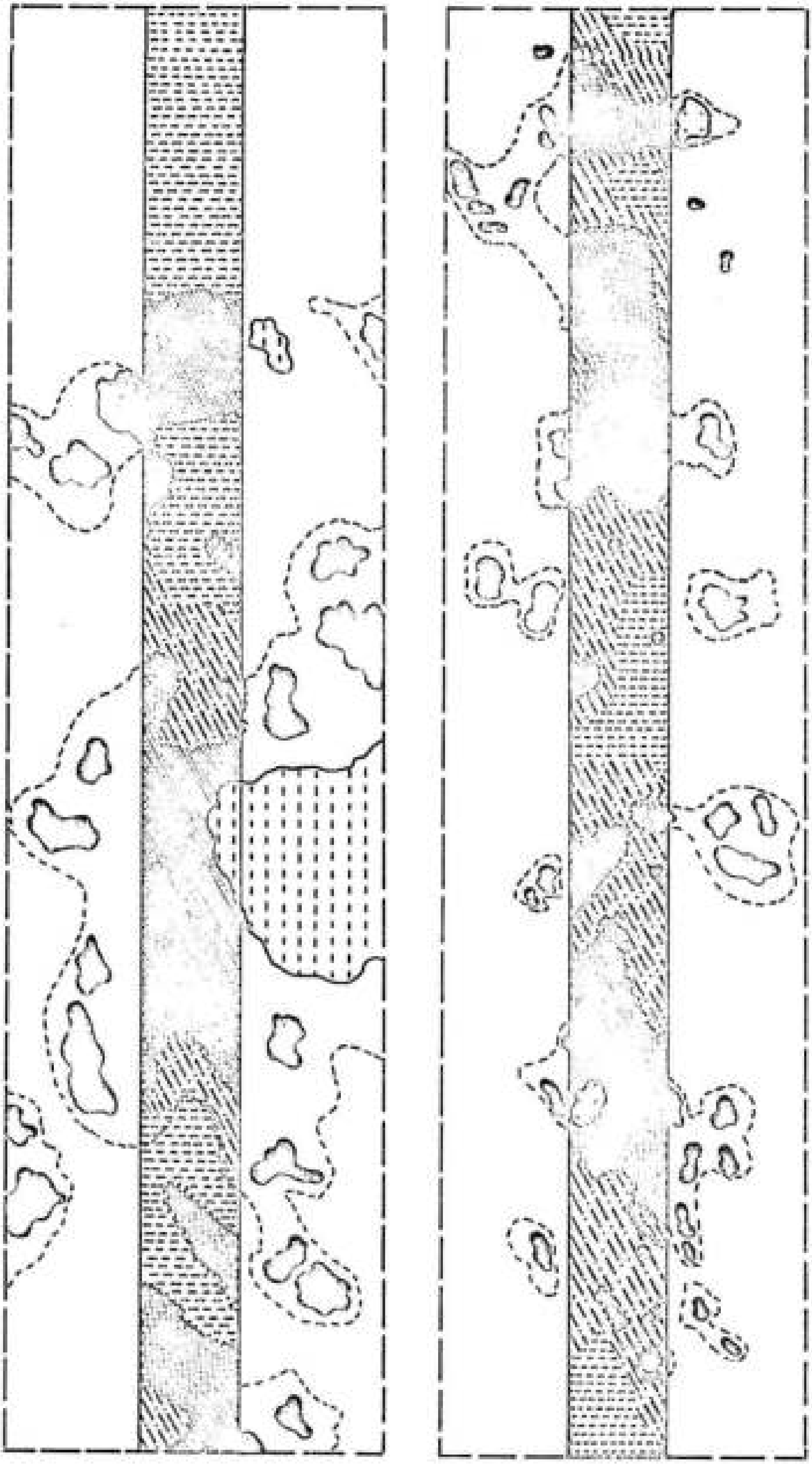


Figure 5b. Representation of two 2.20 segments of the transects located in the west side of the exclosure (ungrazed ecotone). The areas in between the two central continuous lines represent the 15 cm wide transect themselves, and at both sides the areas of 20 cm wide surrounding them. The crown cover of the adult plants of *E. lanata*, *A. confertifolia*, *S. hystrix*, and A. *tridentata* is indicated in the figures. Also the area around where the microtopography has been modified by their influence. In the transects themselves, the locations of the seedlings and the ground cover by litter is also indicated.

● *E. lanata* ○ Seedling location ◌ Bare ground

○ *A. tridentata* ▨ Abundant or thick litter cover ----- Microrelief limit

⦶ *A. confertifolia* ▦ Fair litter cover —— Transect limit

⊖ Perennial grass ⊘ Little litter cover

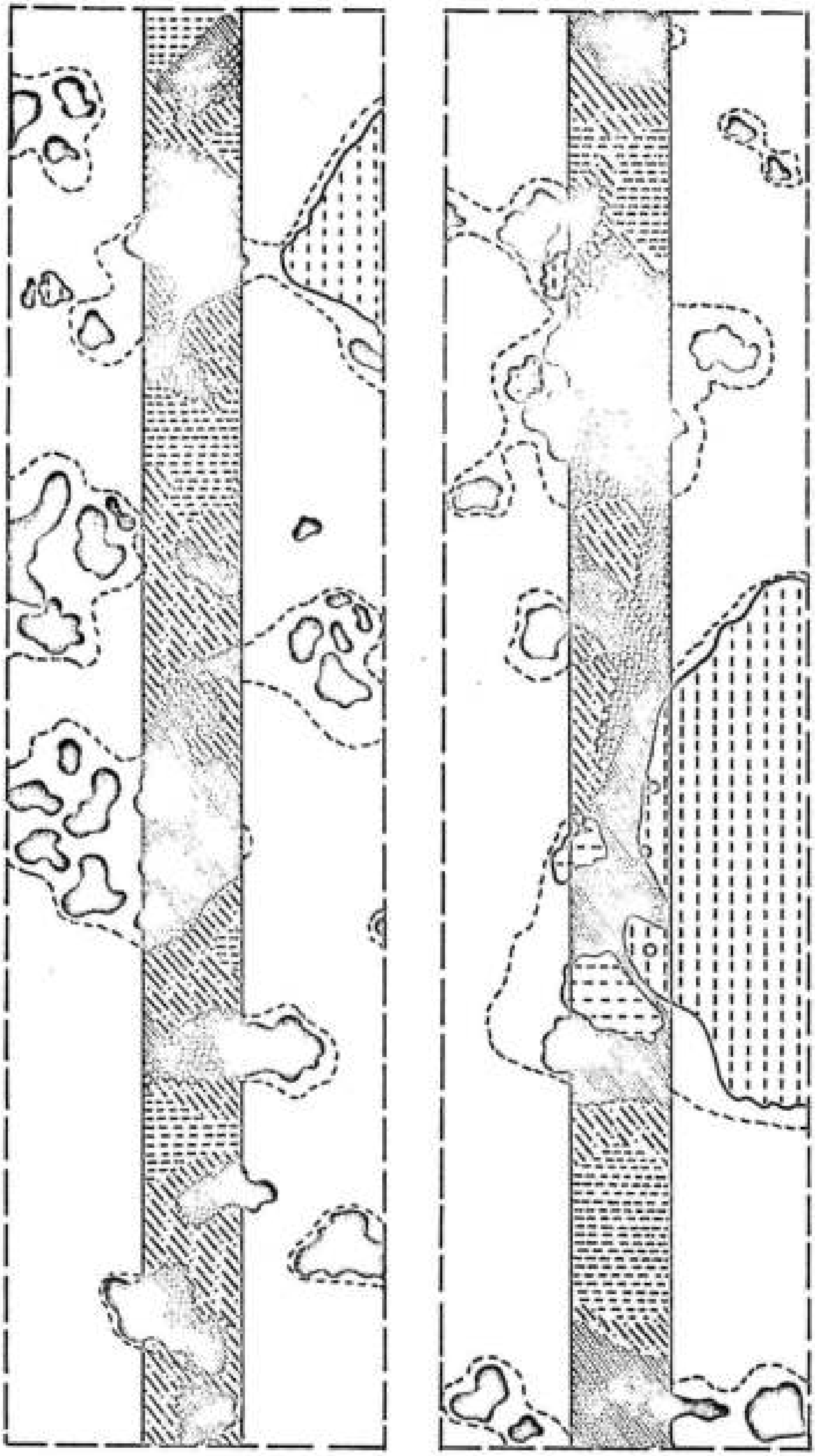


Figure 55. Representation of a 2.20 m segment of the transect located in the grazed stand of *A. confertifolia*. The area in between the two central continuous lines represents the 15 cm wide transect itself and at both sides, areas of 20 cm wide surrounding them. The crown cover of the adult plants of *S. systrix* and *A. confertifolia* is indicated in the figure. Also the area around the plants where the microtopography has been modified by their influences. In the transects themselves, the locations of the seedlings and the crown cover by litter is also indicated.

⦶ A. confertifolia

⊖ Perennial grass

○ Seedling location

◌ Bare ground

—— Transect limit

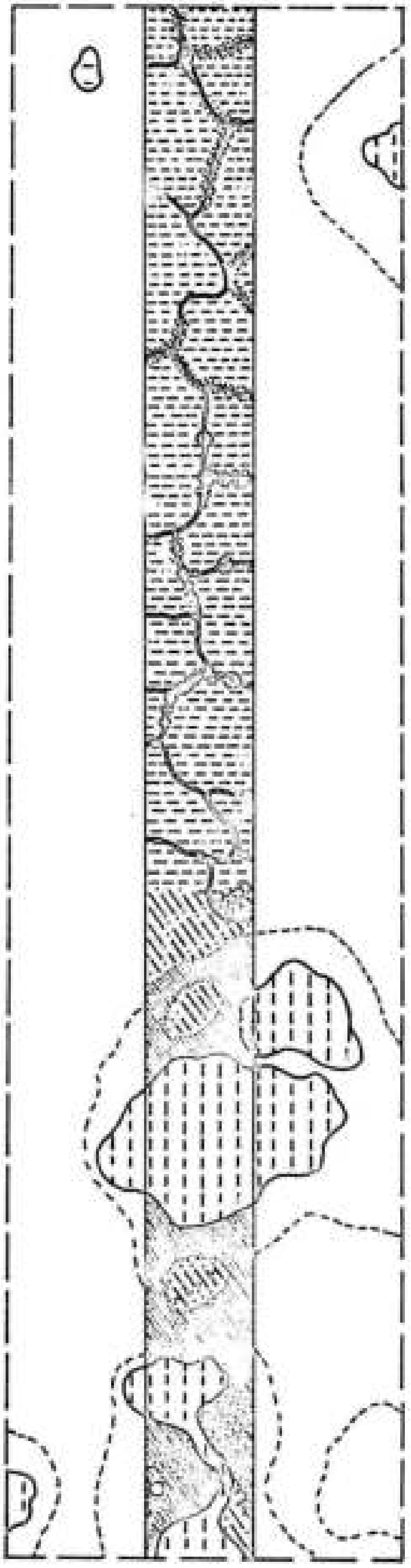
▩ Abundant and thick cover

▦ Fair litter cover

▧ Little litter cover

----- Microrelief limit

━━ Soil crack



The ground cover percentage contributed by thick litter was less in the ungrazed stand than on the grazed. Here thick litter cover was only 3 percent, whereas 35.0 percent of the seedlings were found associated with this kind of ground cover. Twenty-eight percent of the seedlings were located under abundant litter cover while only 10 percent of the land was covered by it. Thirteen percent of the land was covered by fair amounts of litter but 23 percent of the seedlings were located in association with this feature. Ten percent of the seedlings were found associated with little litter cover while 14 percent of the surface was covered by that kind of litter. Beyond that cover, only 4 percent of the seedlings emerged on bare ground and zero percent of seedlings emerged on locales with traces of litter.

Similar results to those already described were found in both grazed and ungrazed ecotone areas. The percentage of seedlings which emerged under thick litter cover was the largest, despite the fact that the actual ground cover by it was only 4 percent on the grazed ecotone and 6 percent on the ungrazed. This means that at the first area the seedlings had a 12 times greater chance to emerge where the litter was thick then the chance they would have had if their distribution would have been at random at the soil surface.

The percentage of seedling emergence decreases as the density of litter decreases. Thus, at the four locations already discussed a mean of 22.2 percent of the seedlings emerged in abundant litter, 20.8 on fair, 8.3 in little, and only 1.4 in very little litter. The respective percentages of ground cover with traces and 38 percent was classed as bare ground.

Eight percent of the ground was covered by abundant litter in the ungrazed ecotone area while 30 percent of the seedlings emerged in that kind of ground cover. The percentage of ground covered by fair and little litter was 14 percent, while only 10 percent of the seedlings were found there. No seedlings at all emerged in the other 58 percent of the land where the ground was covered by very little, traces of litter, or bare ground.

The results presented up to this point all follow a similar pattern; the percentage of bare ground represents the largest single value. It covered between 34 and 40 percent of the surface in all these four stands. Despite this fact, usually none of the seedlings emerged there.

As the litter density covering the ground increased, the chances of seedling emergence increased. An average of 9.5 percent of the ground was covered by traces of litter with none of the seedlings being established under these conditions; 13.5 percent of the ground with fair litter cover had 19.4 of the seedling establishment associated with it. The largest percentages of seedlings occurred in the abundant and thick litter cover classes which represent 9.2 and 4.5 percent of the area, respectively. However, the mean percentage of seedlings was 27.1 and 40.7 percent, respectively.

The results are very clear in indicating that on those microhabitats where there is the largest density of litter cover, there is the greatest chance of seedling emergence. Nevertheless, the results do not indicate the real cause of this difference. It could be that the litter itself, its influence on certain soil characteristics, or on the germination site positively increases the chances of germination of seeds. This could be explained based on the germination reported in other papers such as Springfield (1968), Workman and West (1967, in press), and Vest (1952) where moisture relations in the soil, temperature, salinity, and other factors could in a direct or indirect way influence the germination percentage.

Besides this, the density of litter is also related with the proximity to plants. This could influence the microhabitat where emergence occurs and thus shading, snow accumulation, surface soil temperature, etc. could be modified, and thus have a direct influence on seedling emergence. The date of seed germination could also be modified by the microenvironmental influence of proximity of adult plants as well as soil surface cover. In other parts of this study it was demonstrated that the percentage of seed germination was greater when seeds were placed on soils samples taken from the upper layer than on those of the deeper layer. This indicates that the characteristics of the substratum where seeds are germinated have direct influences on germination. In spite of the fact that it is not known which of the biological, physical, or chemical properties of the soil are responsible for the enhanced germination, it is obvious that greater emergence occurred on those substrata containing greater percentages of organic matter.

Another possible explanation for the non-random distribution of seedlings in the stands is that perhaps the dissemination of seeds in the area is not at random. It is logical to expect most of the seeds and branches with the ataached seeds to fall by gravity under the crown of the plant where there is also a larger concentration of litter. If this is the case, there is then a greater chance of having seeds in those areas where there is also a larger concentration of litter (Figures 56 and 57).

The survival value of the seeds could also vary according to the place where the seed is stored from the moment it is produced until its germination. The amount of litter could also be related with the amount of protective sites. Thus a smaller number of seeds would be eaten by predators or destroyed by other agents.

There is finally the possibility that these results are a consequence of several causes acting together. Seed density, percentage germination, and the protective influence is greater on those microhabitats where there is the largest density of litter, and is least favorable where the surface of the ground is bare.

Seedling emergence in the mixed stand was somewhat different than on those already discussed. In this stand, intraspecific competition of the shrubby species is presumably the same as before, but besides this, there is the interspecific competition from the annual plant, <u>Bromus</u> <u>tectorum</u> which is only conspicuous in wet years and produces large amounts of litter. Thus, many areas which would be bare ground or traces are in fact covered by cheatgrass. Quantitatively the results are different in the sense that the litter influence is less obvious than in the other stands. However, they follow approximately the same line of influence but with less distinction than the previously discussed areas. That is, as the density of the litter on the ground decreases, the chances of germination and emergence of seedlings decrease.

In the grazed stand of <u>A</u>. <u>confertifolia</u> no seedling was found in the thick litter cover. This is expected because of the characteristics of this plant. A high density means a deep layer of

Figure 56. Close up of a segment of the grazed ecotone(north) transect. The seedlings inside the rings are of E. lanata. Most of the ground is covered by litter and E. lanata fruits.

Figure 57. Close up of a seedling born in a bare spot of the grazed ecotone (north). The seedling inside the ring is E. lanata and the others outside are annual weeds.

litter which impedes the emergence of the seedling. Large amounts of dead organic matter on the surface of the shadscale stand had negative effects on seedling emergence. It is also possible that the salt content of the decaying organic matter may influence the germination and emergence of their seedlings. Abundant, fair, or little litter cover produced positive effects on the seedling density, however.

There is one value from the pure shadscale stand that is obviously different than those found on the other stands. The percentage of seedlings on the bare ground was 20.0. The explanation of this difference lies in the fact that all those seedlings were located in soil cracks. These cracks are characteristically found in the surface soils under the shadscale stand; they are prominent and open during the dry part of the year. They act both as a seed and dead organic matter trap as well as providing a germination site for the seeds. The germination site was most favorable and provided a higher density of seedlings. Nevertheless, the environment was not favorable for continued growth as was demonstrated a few weeks later when all the seedlings which started in cracks died.

The Table 8 and Figures 52 on page 145, 58 on page 160 , 59 on page 160 , and 60 on page 161 indicate the mean size of seedlings of the 1968 season at several dates according to the death date. On the grazed stand of E. lanata the seedlings which survived until the end of the growing season were larger than those which died earlier. This difference was observed from the beginning of the growing season.

The mean size was obtained by multiplying the height of the

Table 8. Size of the seedlings emerged during the 1968 season at several dates, and grouped according to the date of death. The dates of death were August 7, June 29, and May 4. Another category was formed by those surviving beyond September 24 of the season they emerged. H means height (cm), L means number of leaves, and HL means height (cm) times number of leaves.

Date dead or last recorded	April 20			May 4			May 19		
	H	L	HL	H	L	HL	H	L	HL
Artemisia tridentata (grazed *E. lanata* stand)									
September 24	0.40	4.00	1.60	0.53	4.00	2.12	1.10	6.67	7.33
August 7	0.46	3.00	1.38	0.50	4.67	2.33	0.90	6.67	6.00
June 29	0.27	2.00	0.54	0.27	2.00	0.54	0.40	5.33	2.13
Eurotia lanata (grazed *E. lanata* stand)									
September 24	1.00	4.43	4.43	1.15	6.43	7.39	1.55	8.29	12.85
August 7	0.95	5.50	5.22	1.12	6.33	7.09	8.54	15.47	15.70
June 29	0.75	4.00	3.00	0.85	5.00	4.25	0.90	5.00	4.50
May 4	1.07	5.33	5.70						
Eurotia lanata (ungrazed *E. lanata* stand)									
September 24	1.01	4.00	4.04	1.00	5.70	5.70	1.25	6.75	8.44
August 7	0.75	3.00	2.25	0.85	4.00	3.40	0.95	5.50	5.22
May 4	0.86	3.60	3.01						
Eurotia lanata (grazed ecotone stand)									
September 24	1.08	4.32	4.66	1.10	7.04	7.74	1.48	8.56	12.67
August 7	0.60	2.40	4.00	0.66	3.52	3.53	0.87	5.22	6.00
June 29	0.80	2.13	2.67	0.87	3.48	4.00	0.97	5.33	5.17
Eurotia lanata (mixed stand)									
September 24	1.06	4.80	5.00	1.08	8.00	8.64	1.46	9.60	14.02
August 7	0.85	4.00	3.40	0.95	6.00	5.70	1.25	8.00	10.00
June 29	0.75	3.33	2.50	0.78	3.33	2.60	0.78	5.14	4.01

Table 8. Continued

Date dead or last recorded	June 13			July 26			August 29			September 24		
	H	L	HL	H	L	HL	H	L	HL	H	L	HL
				Artemisia tridentata (grazed *E. lanata* stand)								
September 24	1.60	9.33	14.93	1.97	9.33	18.38	1.33	13.00	17.29	1.93	20.67	39.89
August 7	1.17	10.67	12.48	1.40	11.67	16.33						
June 29	0.83	6.00	4.98									
				Eurotia lanata (grazed *E. lanata* stand)								
September 24	2.09	11.57	24.18	2.06	43.54	48.94	2.00	12.36	24.72	2.24	17.79	39.85
August 7	1.60	9.67	15.47	1.57	10.00	15.70						
June 29	0.80	6.50	5.20									
				Eurotia lanata (ungrazed *E. lanata* stand)								
September 24	1.47	9.50	13.96	1.26	8.00	10.08	1.31	9.12	11.95	1.65	12.75	21.04
August 7	1.10	9.00	9.90	0.85	8.00	6.80						
				Eurotia lanata (grazed ecotone stand)								
September 24	2.12	11.64	24.68	1.91	11.52	22.00	1.95	12.00	23.40	2.05	14.76	30.26
August 7	1.10	6.67	7.34	1.10	7.33	8.06						
June 29	1.10	6.67	7.34									
				Eurotia lanata (mixed stand)								
September 24	2.02	13.20	26.66	1.96	12.40	24.30	1.76	11.60	20.42	2.10	20.80	43.68
August 7	1.35	10.00	13.50	1.20	9.00	10.80						
June 29	0.90	7.14	6.43									

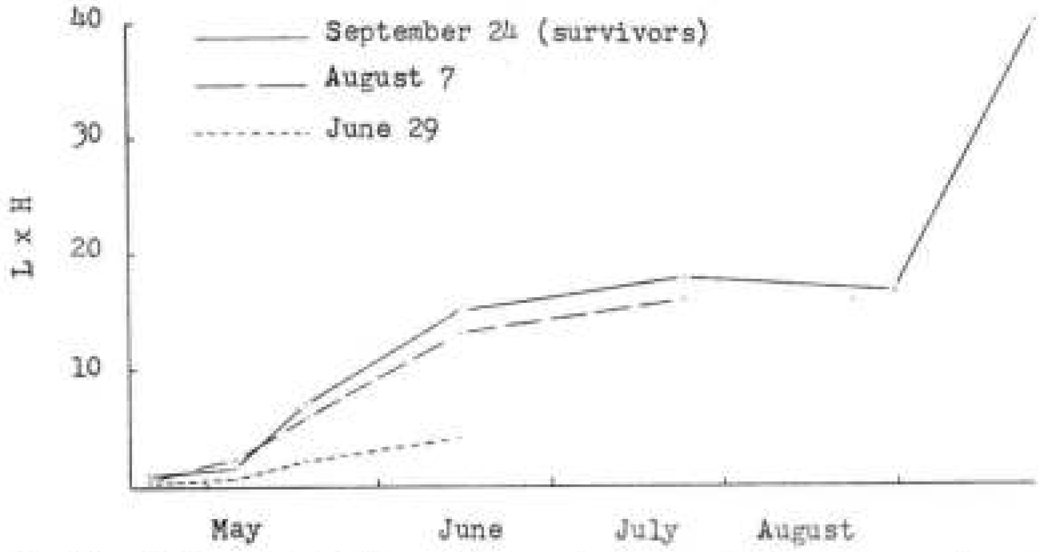


Figure 58. Mean size of Artemisia tridentata seedlings emerged during 1968 and grouped according to the date of death.

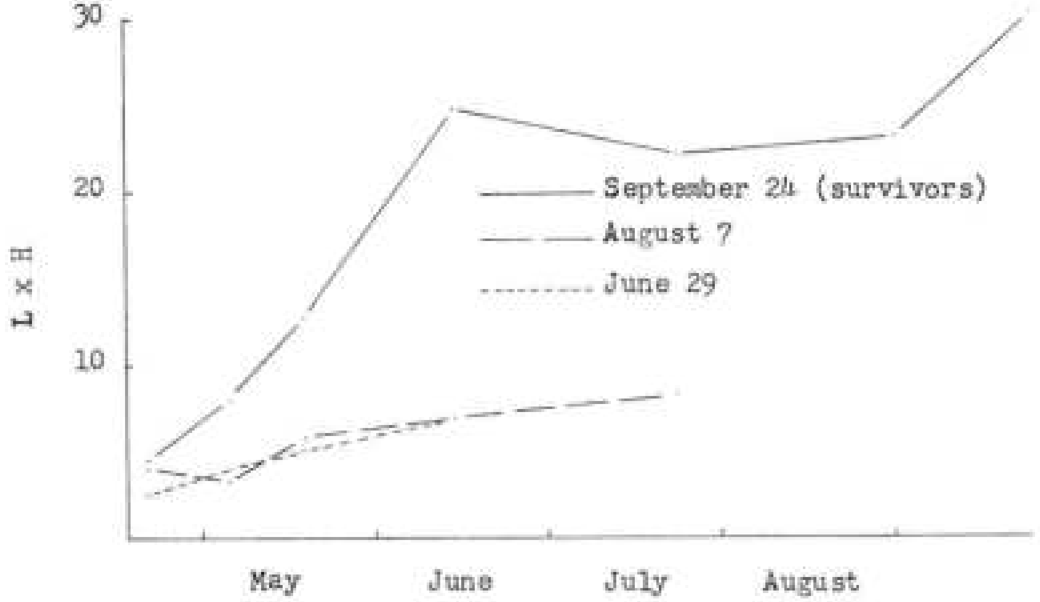


Figure 59. Mean size of E. lanata seedlings emerged in 1968 in the grazed ecotone stand and grouped according to the date of death.

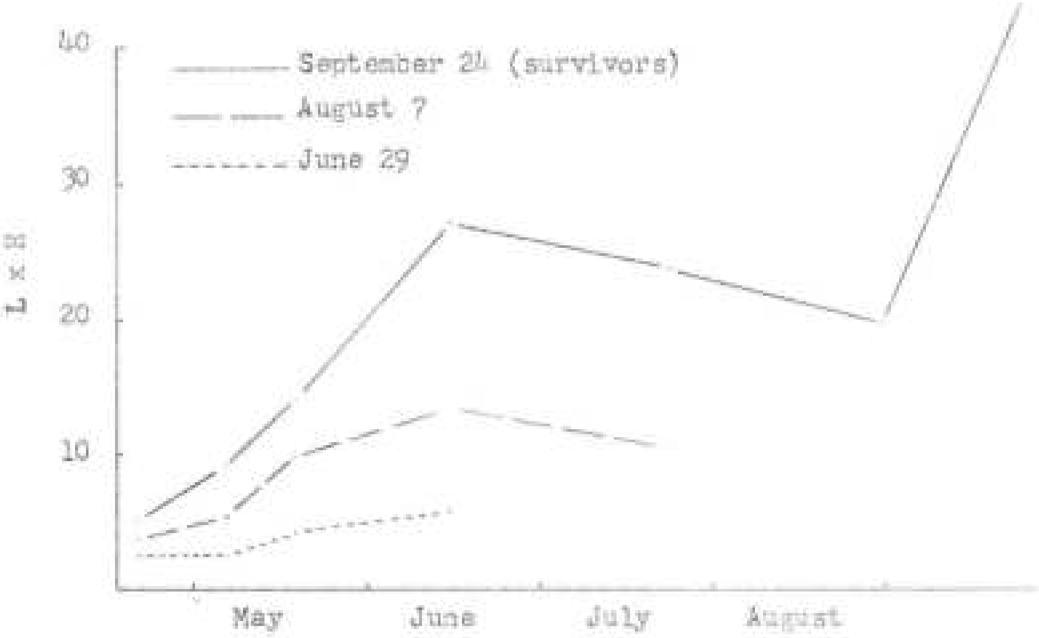


Figure 60. Mean size of E. lanata seedlings emerged in 1968 in the mixed stand and grouped according to the date of death.

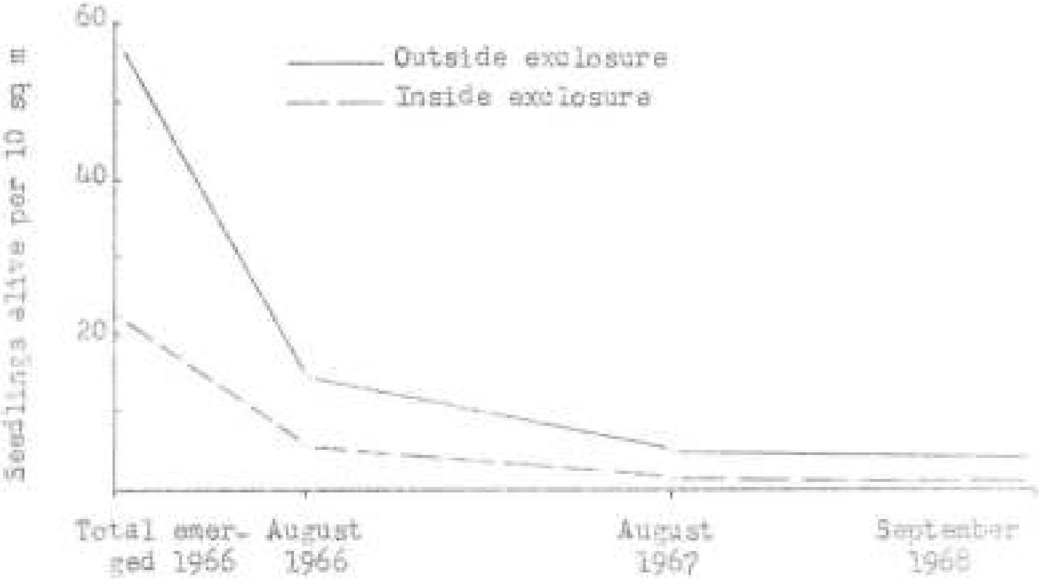


Figure 61. Density shrinkage of the 1966 seedling cohort inside and outside the exclosure.

seedling in cm times the number of leaves (H x L). On May 4, the index was 7.39 for those surviving all the season, while only 7.09 for those which died on August 7, and 4.25 for those which died on June 29. On May 19, the size indexes were respectively 12.85, 8.54, and 4.50. On June 13, the differences were even larger, 24.18, 15.47, and 5.20.

Similar patterns of size variations were found in the other stands of E. lanata, the grazed and ungrazed ecotone and in the mixed stand, as well as for Artemisia tridentata seedlings. The comparison was not made for A. confertifolia since during the 1968 season seedling production of this species was too small.

The seedlings surviving the longest were larger than those dying at a younger age. The size expression of differential mortality appears early in the season, much in advance of their actual death.

The causes of seedling mortality are of great importance in understanding the perpetuation and dynamics of the community itself. If the size of seedlings is one indicator of the probability of mortality, it is important to know why seedlings have different sizes.

There are probably two main lines of explanation. One is that seedlings are different in size because the seeds from which they come were different, and thus influenced them in such a way that it induced different growth. Tueller (1966) has demonstrated that E. lanata can produce different sizes of seeds when grown in different conditions, and that seed size could induce differential growth of seedlings. Besides, the same plant may produce seeds of different sizes. Perhaps the growth and survival of the seedlings are, at least partially, functions of their seed size.

The other possibility is that seedling size is mostly a function of the microhabitat where they grow. It was demonstrated earlier in this study that seedling size was affected to a large extent by the nature of the substrate. This influence is great and measureable even in a few weeks. Besides the substrate itself there could also be some other microclimatic and competitive relations which could affect the rate of growth and thus, their survival.

Whether inherent characteristics of the seed itself or a direct influence of the microhabitat or both are involved in differential survival is not known. The design of this study does not permit clarification of the factors responsible for the differential growth and survival. The importance of the results presented here is to demonstrate the seedling mortality as a function of their size. Further studies will have to demonstrate in a quantitative manner which are the factors and in what magnitude they influence seedling development.

The mean size of the seedlings expressed in number of leaves, height of the plant, or the product of the two parameters does not show any general relation with litter cover. It is not clear if the amount of litter is correlated in some way with the rate of growth and size attained by the seedlings. It could, however, be important in modifying the edaphic and microclimatic environment where the seedling lives and so influence their growth. However, under the natural conditions where this study was conducted there are many other influences besides litter that could largely confound the results.

Among these main causes is the inter- and intra-specific interference between the seedlings and the adult shrubby plants. Interference could be a function of distance to other plants. The concentration of litter on the surface is not uniform and in general follows a similar pattern to that of vegetation. The closer the seedling to the adult plant, the greater the total density, but also, the greater the interference. Thus, if there is a positive effect of litter on seedling growth, it could be expected to be counteracted by competition.

The seedlings which emerged on bare ground were usually located further from other plants and so competition should be less. However it is not known if litter has a beneficial effect on growth by simple comparison of the seedlings from areas with different litter cover. Other independent factors are also simultaneously acting upon the seedling, thus increasing or decreasing the effect of the litter itself.

The variation of seedling density after the first growing season can best be analyzed on Table 9 and Figures 61 (page 161), 62, and 63. The data represent the cohort shrinkage since 1964.

At the end of 1966, only a few seedlings of those which emerged in 1964 were still alive; they were on the ungrazed ecotone. The results indicate that by the end of 1968, that is the fifth growing season, the seedling density was the same as that during the third growing season. In the other stands no seedling from this cohort was still alive. Because of the small size of the sample represented, the greater density in the ungrazed ecotone stand is not necessarily an indication of the greatest survival under those conditions, nor

Table 9. Density of seedlings of all perennial shrubs expressed in number of plants per ten square meters from the 1964 to the 1968 cohorts.

Stand and treatment	1964 Cohort			1965 Cohort			1966 Cohort			
	Alive End 1966	Alive End 1967	Alive End 1968	Alive End 1966	Alive End 1967	Alive End 1968	Total Emerged 1966	Alive End 1966	Alive End 1967	Alive End 1968
Ungrazed *E. lanata*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Grazed *E. lanata*	0.0	0.0	0.0	0.0	0.0	0.0	9.4	4.0	1.3	1.3
Ungrazed ecotone	2.7	2.7	2.7	2.7	2.7	2.7	45.3	10.7	2.7	2.7
Grazed ecotone	0.0	0.0	0.0	1.3	1.3	1.3	107.9	24.0	8.0	6.7
Mixed	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Grazed *A. confertifolia*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Inside exclosure	0.7	0.7	0.7	0.7	0.7	0.7	22.6	5.3	0.7	0.7
Outside exclosure	0.0	0.0	0.0	0.4	0.4	0.4	58.6	14.0	4.7	4.0
E. lanata	----	----	----	0.3	0.3	0.3	7.7	4.7	2.1	1.5
A. confertifolia	0.5	0.5	0.5	0.2	0.2	0.2	25.6	5.3	1.1	1.1
A. tridentata	----	----	----	----	----	----	----	----	----	----

Table 9. Continued

Stand and treatment	Total Emerged 1967	Alive End 1967	Alive End 1968	Total Emerged 1968	Alive End 1968
Ungrazed *E. lanata*	0.9	0.9	0.0	63.1	7.1
Grazed *E. lanata*	1.3	0.0	0.0	104.0	22.6
Ungrazed ecotone	21.3	13.3	5.3	74.3	2.7
Grazed ecotone	8.0	2.7	1.3	145.3	33.3
Mixed	0.0	0.0	0.0	54.2	4.5
Grazed *A. confertifolia*	26.7	5.3	5.3	0.0	0.0
Inside exclosure	11.1	7.1	2.6	65.9	6.0
Outside exclosure	4.6	1.3	0.6	124.6	27.9
E. lanata	1.6	0.8	0.0	79.9	13.1
A. confertifolia	27.2	12.0	4.3	1.4	0.0
A. tridentata	-----	-----	-----	32.0	8.0

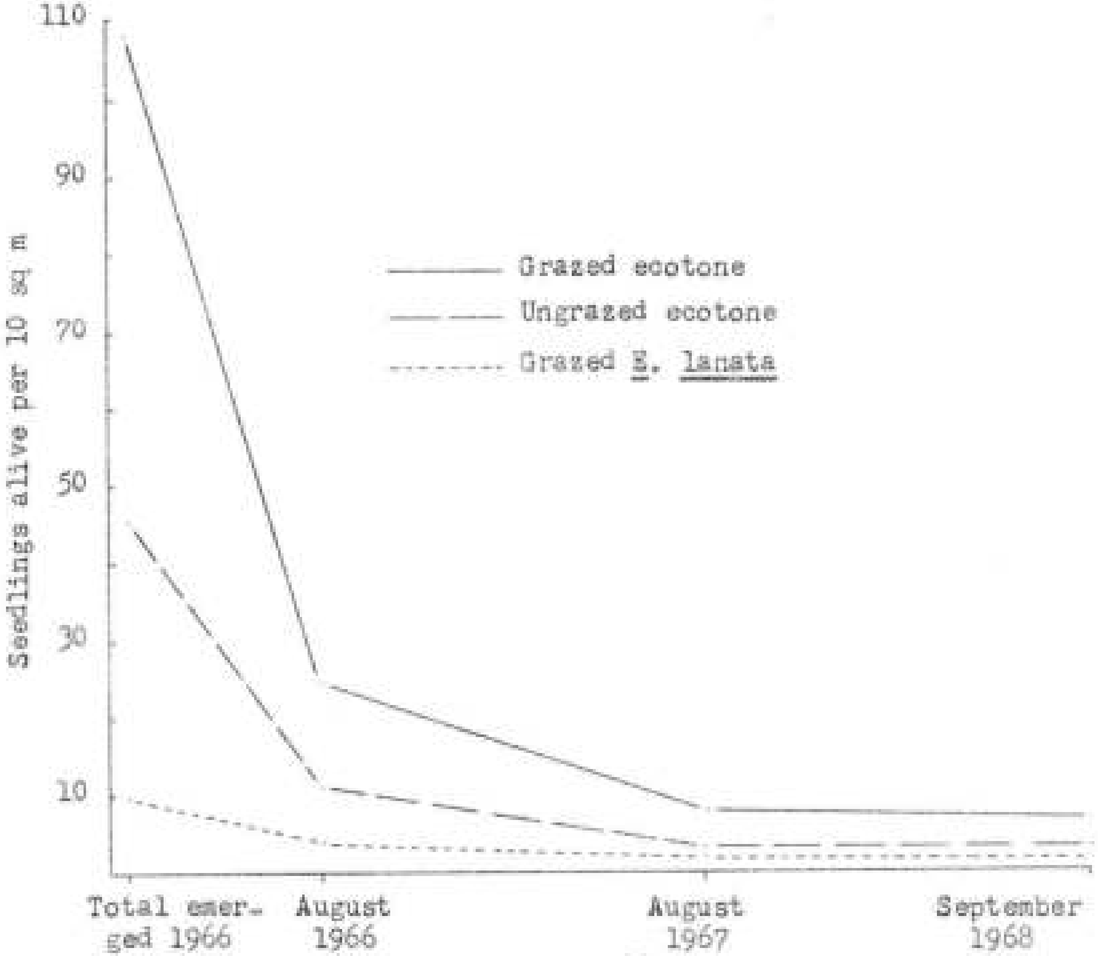


Figure 62. Density shrinkage of the 1966 seedling cohort of shrubby species in all stands where emergence occurred.

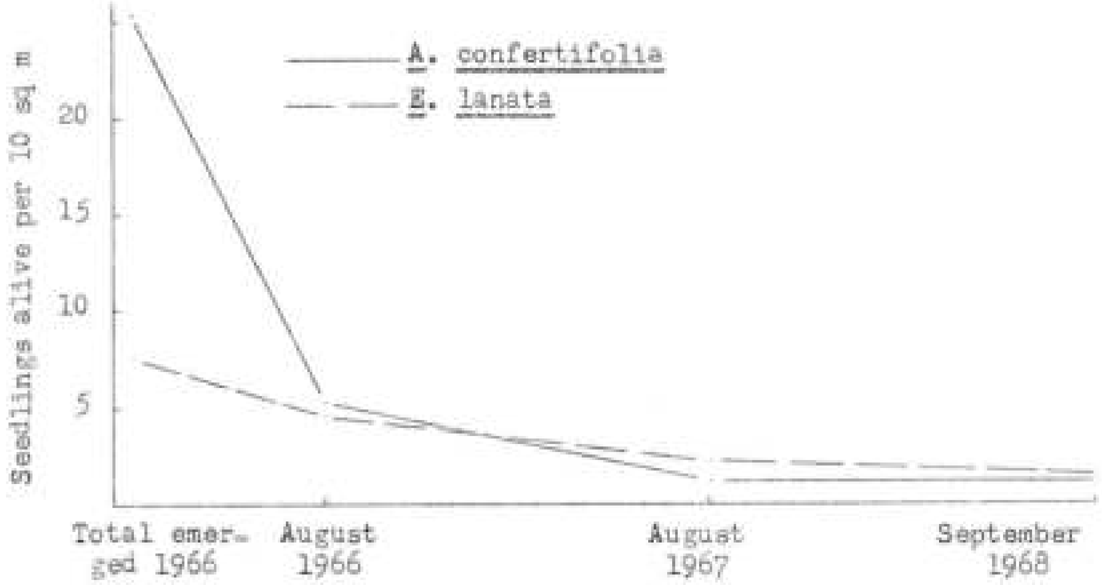


Figure 63. Density shrinkage of the 1966 seedling cohort of *E. lanata* and *A. confertifolia*.

a greater seedling emergence.

In a similar way the results are not indicative of the influence of grazing on seedling survival. The greater density in the exclosure does not necessarily represent greater survival due to non-grazing. The number of seedlings and the sampling area were too small to have significant differences.

The results of the 1965 cohort are in many respects comparable to those from the previous year. By the end of the second growing season in 1966, 2.7 seedlings per ten square meters were still alive in the ungrazed ecotone of E. lanata, and 1.3 in the grazed ecotone. In the other stands, the density was zero. Because of the size of the sample and number of seedlings recorded, no valid comparison could be made.

The most important conclusion that can be reached from the study of cohort shrinkage is that from the third to the fifth years, the reduction in density is minimum, in this case zero. These values can be compared with those already presented in this paper where it was demonstrated that the reduction is greatest during the first growing season.

The original cohort of seedlings emerged during the 1966 season in the grazed stand of E. lanata was 9.4 per ten square meters. By the end of the same season only 4.0 seedlings per ten square meters were still alive. One year later the density was 1.3 plants per ten square meters and did not change by the end of the third year.

The ungrazed ecotone had a density of total emerged seedlings during the 1966 season of 45.3 per ten square meters, but only

10.7 were alive by the end of the season. During the second and third years, the density was 2.7. The total number of seedlings which emerged during the season was four and a half times greater than those remaining at the end of the season. But from the first to second year, this reduction was of slightly smaller proportional magnitude. However, from the second to the third year there was no change at all.

The grazed ecotone produced the largest density of seedlings, 107.9 per ten square meters, but only 24.0 were alive by the end of the season. At the end of the second season, only 8.0 seedlings per ten square meters were still alive while 6.7 existed at the end of the third growing season. This is a 75 percent reduction during the first season, and from the first to the second. However, from the second to the third only slight shrinkage occurred.

Grazing influences were evaluated by comparing the areas inside and outside the exclosure. The excluded vegetation showed a mean density of seedlings emerged of 22.6 per ten square meters, while only 5.3 remained by the end of the growing season. This means a shrinkage to one-fourth of the original. On the equivalent grazed area, the shrinkage was similar but the densities were higher; 58.6 seedlings were reduced to 14.0 by the end of the season.

During the second season, the reduction in density in the excluded area was down to 0.7 seedlings per ten square meters and remained the same one year later. In the grazed area this reduction in density was down to 4.7 on the second year and to 4.9 in the third. Thus, the cohort shrinkage during the second and third years was proportionally greater in the exclosure than in the equivalent grazed area. It was down to one-seventh and one-fourth, respectively.

The cohort shrinkage should be analyzed keeping in mind that the seedling survival was probably affected by the above average precipitation received during the 1967 and 1968 seasons. Besides this, when comparing the ungrazed areas with those utilized by livestock, it should also be remembered that during the last two years, no livestock grazing occurred outside the exclosure.

A species comparison of the 1966 seedling population shrinkage shows that __A. confertifolia__ suffered a proportionally greater reduction than __E. lanata__. The original density of shadscale was 25.6 seedlings per ten square meters and was reduced to 5.3 by the end of the first season, and 1.1 on the second and third year. However the density of winterfat was less at the beginning but by the third year, a larger proportion of plants remained alive. Winterfat started with 7.7 plants per ten square meters and respectively reduced its density to 4.7, 2.1, and 1.5 over the same period.

The 1967 cohort shows similar patterns of shrinkage. However because of the reduced number of emergent seedlings in certain areas, the samples studied may not adequately represent the seedling population in each particular stand. In the ungrazed stand of __E. lanata__ as well as in the grazed stand, the size of the sample was too small. Only one seedling was found in each area; thus, no valid conclusion can be reached in this respect.

The ungrazed, as well as the grazed ecotone, had greater numbers of seedlings. From an original density of 21.3 seedlings per ten square meters on the ungrazed area, only 13.3 remained alive by the end of the first growing season, and 5.3 by the end of the second in 1968. In the grazed ecotone the reduction was from an original 8.0 seedlings per ten square meters to 2.7 in the first season, and 1.3 in the second. This is a shrinkage in a two-year period of 4 to 1 on the ungrazed ecotone and from 6 to 1 in the grazed stand.

The pure stand of A. confertifolia had a considerable reduction in density during the first year. From a total density of 26.7 seedlings per ten square meters, it was reduced to 5.3 at the end of the same season and remained the same during the following season.

The cohort shrinkage effect can best be analyzed by comparing the seedling density inside the exclosure with that of the equivalent area outside. The decrease in density of the grazed area was proportionately larger than on the ungrazed area. The reduction was down to one-fourth and one-seventh respectively.

Comparative study of the results presented here dealing with five cohorts indicates that some general conclusion can be drawn.

The first and most obvious conclusion is that the largest shrinkage in density occurred during the first growing season. The absolute number of seedlings dying, as well as the proportion of survivors in relation to the total number of seedlings emerged, both indicate that the largest mortality occurred during the first growing season.

The high first season mortality could be a result of four different processes. One is the timing when seedlings emerge in relation to weather. If weather conditions occurring at their emergence and immediately after are favorable for survival, the shrinkage would be less. Timing of germination can be slightly modified by managing the vegetation. It is possible to induce edaphic and microclimatic changes in the microhabitat which could in one way or another affect the germination date of seedlings. The temperature of the soil, water relations especially for the surface layer, soil structure and aeration, and salinity concentration can all be managed by manipulating vegetation.

The results obtained in this part of the study indicate that germination dates of seedlings was subject to large variation from year to year. If the weather conditions existing when the seedlings germinate and emerge are less favorable for their survival, supposedly, the cohort shrinkage would be greater.

Another main reason why there is such a large mortality is that many seedlings germinated and emerged on a less favorable microhabitat. These plants have a greater chance to die than the ones which germinate in a more favorable environment. The results presented in this study are not conclusive in what is a favorable or unfavorable environment for the seedlings. However, it is possible to think that the outstanding differences which exist on the microhabitats should in one way or another differentially influence their survival. Since the location of seedlings is mostly a function of seed dispersal and germination site, their survival can be greatly affected if the microhabitat where they germinate is not favorable.

Mechanical damage by insects or other agents could influence to some degree the seedling density. However the results obtained in this study indicate that less than 20 percent of the seedlings recorded were mechanically damaged by insects, other animals, or other physical damage. The remaining ones just appeared dried but intact. The real cause of death of most seedlings is not known.

There could be some hereditary physiological trait of the seedlings inducing an early death. However it seems that this is not the case. In most of the seedling studies conducted in the greenhouse with seedlings from these species, the mortality was nil or almost so. Seedlings did not die when the environmental conditions were favorable for their growth.

If the mortality cause is not physiological or mechanical, then it is possible to think that it is mostly ecological. If this is the case, most of the seedlings should die because of emergence date or microhabitat. But the question is now to determine what is the optimum and what are the limits to germination dates and, finally what are the magnitudes of the different environmental factors favorable for seedling survival?

The rate of mortality of the surviving population was slightly reduced during the second season and more so in the third year. During the fourth and fifth years, the mortality was almost zero.

During the first two years, and especially the first growing season, the seedling has to adjust to the environment. If the conditions are favorable, they survive; otherwise, they die and disappear. After that adjustment period the seedlings have to grow and in doing this, they have to compete for the limited resources existing in the environment. The growth of the seedling at this time is a function of the availability of resources in the environment as well as the competitive and interference abilities of the seedling.

Appendix table 39 indicates that mean size of seedlings is a function of their age. It is obvious that for young seedlings, growth is mostly a function of age. However for older ones, such as those 3 to 5 years old, size is mostly a characteristic of the seedling itself and its competitive ability in relation to the available resources.

The large differences in size measured for individuals of the same age is an indication that other factors are more important than time. This is the ecological relation of the seedling itself with its surrounding physical and biological environment. Under laboratory conditions the growth of seedlings in absence of competition from the other shrubby species, and without serious environmental limitations, showed the growth of both species in a few weeks was greater than the growth in the field in several years. The greatest growth limitation for seedlings is ecological and not physiological. The potential growth of the plant is many times greater than that actually found under natural conditions in the field.

Water Relations

The results of soil moisture relations studies in the grazed stands of *E. lanata*, *A. confertifolia*, and the mixed one will be presented in two parts. First will be presented the results on moisture relations in the surface soil from 0 to 15 cm and later will be presented the results of water relations in the deeper layers of soil from 30 to 150 cm.

The moisture percentage by weight in the upper 2.5 cm and its variation throughout the year is presented in appendix table 40 and Figure 64. The values calculated indicate that, in general, the higher moisture percentages were obtained early in the growing season

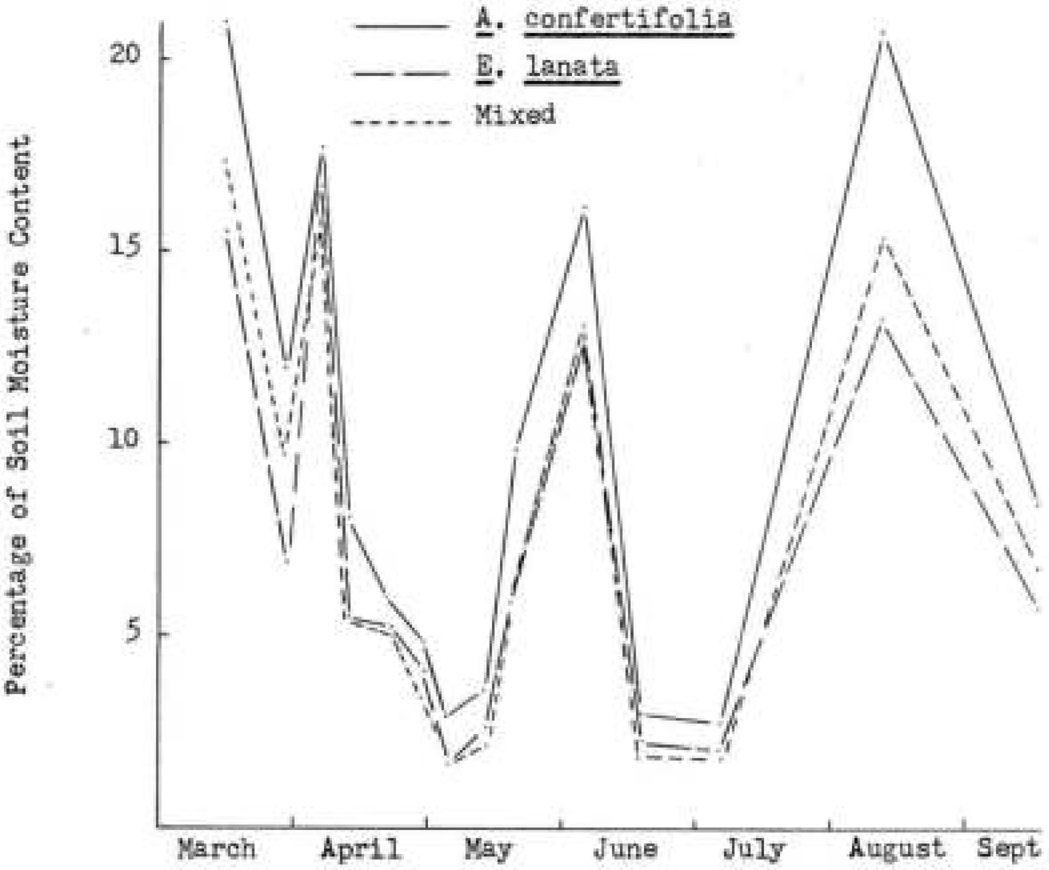


Figure 64. Moisture percentages of the upper 2.5 cm of soil at several dates during the 1968 season for the three stands.

in March and early April. However there is extreme variability from one sampling date to the next.

Under the E. lanata stand on March 2, the soil was saturated because of a previous rain and by March 18, it was near field capacity with 15.5 percent moisture. By the end of the month, the moisture percentage was 7.0, which indicates a matric potential below the permanent wilting percentage. One week later on April 6, the moisture content was 16.7 percent, which corresponds with a matric potential around field capacity again.

Later, the moisture content in the upper 2.5 cm of the soil profile rooting the Eurotia lanata stand was usually below 5 percent.

However, occasionally such as on June 6 and August 13, the matric potential raised to values around field capacity due to occasional rains. However, due to the high temperatures prevailing at that time of the year, the desicating power of the atmosphere is great and the soil soon loses its moisture.

The soil moisture percentages under the mixed stand are similar to those of the winterfat stand. Early in the season the moisture percentage as well as the matric potential were greater. On March 2 the soil was saturated, while on March 18 and 30, the percentages were respectively 17.4 and 9.8. On April 6, soil moisture content again raised to 15.9 percent which is near field capacity. During the remaining part of the growing season the matric potential was usually around the wilting percentage with the exception of a temporary increase due to occasional rains.

The surface soil layer under the Atriplex confertifolia stand had greater moisture percentages than the other two stands at any time during the growing season. However, because the moisture retention curve calculated for this soil is different, the matric potential calculated was always less than that of the other two stands. With the exception of nearly all of March and early April, most of the growing season, the matric potential was below the permanent wilting point. Another exception is during the month of August when, because of the intensive and frequent precipitation, the surface soil remained wet at least part of the month.

The moisture percentage and the matric potential in the upper 2.5 to 7.5 cm of soil followed a similar pattern of variation throughout the growing season to that of the surface soil (Appendix table 41). However, here the percentage of moisture content as well as the matric potential values were larger than the equivalent ones determined on the same date but for the surface soil. This means that the matric potential was above the permanent wilting percentage, and thus, the available water lasted for a longer period in the soil.

The values calculated indicate that there is extreme variability between sampling dates in the upper 15 cm layer (Table 10). The highest percentage of soil moisture by volume in the winterfat stand occurred on April 6, while during the month of March the context was slightly less, 12.6 and 11.5 percent in contrast with the maximum of 15.2 percent. During the remaining part of April and until May 10, there was a gradual decrease in moisture content until it reached a minimum of 5.6 percent. This means that the moisture retaining force decreased from a maximum of -66 Joules per kilogram to -1500 on May 3, and thereafter, it remained as such for the rest of the season. The only exception was for the observations of May 17 when the percentage of moisture increased to 12.3 and the matric potential to -200, and on August 13 and September 1 when it was -540 and -900 Joules per kilogram.

For the mixed stand, the percentages of moisture content by volume as well as the matric potential were extremely similar to those calculated for the upper 15 cm layer of soil in the _E. lanata_ stand.

Soils associated with the _Atriplex confertifolia_ stand possessed different soil moisture characteristics from the other two soils examined. Despite the fact that the percentages of moisture content

Table 10. Moisture percentage by weight and matric potential in Joules per kilogram of the upper 15 cm of soil on three stands and at several dates during 1968.

Moisture	March		April			May			June	July	August	Sept.	
	23	29	6	12	27	3	17	24	20	26	13	1	19
						E. lanata							
Percentage	12.6	11.5	15.2	11.4	9.4	8.2	12.3	8.4	7.4	2.7	10.2	9.3	6.6
Potential	- 190	- 270	- 66	- 210	- 860	-1500	- 200	-1500	-1500	-1500	- 540	- 900	-1500
						Mixed							
Percentage	12.9	10.7	15.0	11.4	9.0	6.4	12.7	9.1	6.3	2.7	10.6	8.9	7.6
Potential	- 125	- 280	- 80	- 210	- 860	-1500	- 130	- 810	-1500	-1500	- 300	- 920	-1500
						A. confertifolia							
Percentage	15.4	14.8	18.8	16.5	12.5	10.9	19.5	14.7	9.1	4.5	14.2	12.5	8.6
Potential	-1500	-1500	- 620	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500

were always higher for this stand than for the other two, the matric potentials were always less because of soil moisture release characteristics. In only one measurement, on April 6, the value determined was above the permanent wilting percentage. Minus 620 Joules per kilogram was determined on that date in comparison with the -66 and -80 which were the measurements at the same depth and date from the other two stands. Later on April 20, when the other two stands had -210 Joules per kilogram, the shadscale stand had a value of -1500 (Figures 65 and 66).

Soils rooting shadscale consistently showed lower matric potential values than either of the other two stands, both in the surface 0 to 15 cm layer of soil or at greater depths. An explanation of why the matric potential of the upper layer was much less than those calculated for the other two stands is related to the water holding capacity of each of these soils. The surface layer, since it receives a larger amount of solár energy, is capable of losing a larger proportion of moisture by evaporation. Since the water holding capacity of the shadscale soil is greater, the solar energy received makes it lose a larger proportion of the moisture stored since a larger percentage is stored in the upper centimeters. When the soil is recharged with moisture from precipitation, the water infiltrates into the soil but its movement reaches the deeper layers in the coarser soils since the water holding capacity is less. Thus, finer soil with greater water holding capacity means greater losses from the upper few centimeters of soil and lower matric potential for plant growth.

In interpreting these results there is, however, one main

Figure 65. Neutron probe and scaler used to determine soil moisture from 30 to 150 cm depths. The vegetation corresponds to the one existing in the area around the neutron tubes in the grazed A. confertifolia stand.

Figure 66. General view of the grazed stand of E. lanata and the location of the neutron tubes.

question. This is, what is the actual permanent wilting percentage and the available moisture in the soil where these plants are growing. It seems from the results obtained in this study that the wilting point is not -1500 Joules per kilogram as it is generally accepted for most mesophyte species. Winterfat and shadscale grew perfectly well during most of the growing season with moisture below -1500 Joules per kilogram. This means that they have to be adapted for growth and reproduction under total moisture potential below that value.

The soil moisture content under the E. lanata stand in the 30 cm layer was 15.9 percent on the last week of April, 1967, when the measurements started (Appendix tables 42 and 43, Figures 67, 68, and 69). One week later, it was 15.8 percent and decreased slightly until May 16 when it was 14.1 percent. After that there was a sharp decrease in the moisture percentage by volume to only 8.8 on May 23 and to 9.2 percent on June 9.

After the late May and early June dry period, intensive rains occurred in Curlew Valley and moisture penetrated the soil in an unusual way. The moisture percentage raised to 22.4 on June 23 and rapidly dried to 11.3 percent by July 3. This intensive drying period continued the rest of the summer, especially during July and August. By July 13 the moisture percentage was 8.0, and one month later was only 2.5 percent.

The evapotranspiration rate from this upper layer of soil from the winterfat stand decreased later in the summer. It decreased only because there was little water left. From August 23 to November 4, the moisture percentage decreased from 1.5 to 1.0 percent.

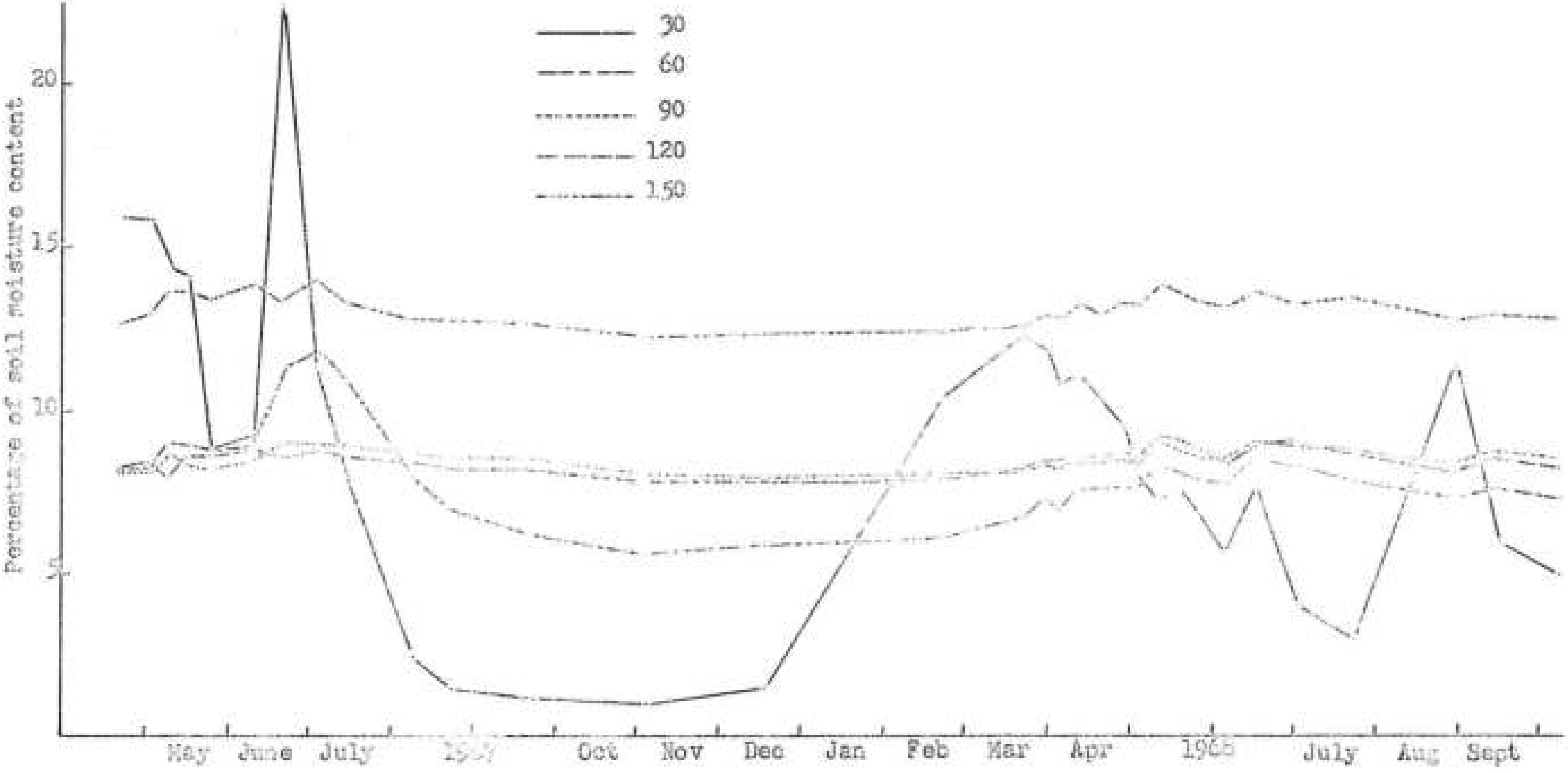


Figure 67. Mean soil moisture percentage by volume in the E. lanata stand at several depths (cm) and dates during the 1967 and 1968 seasons.

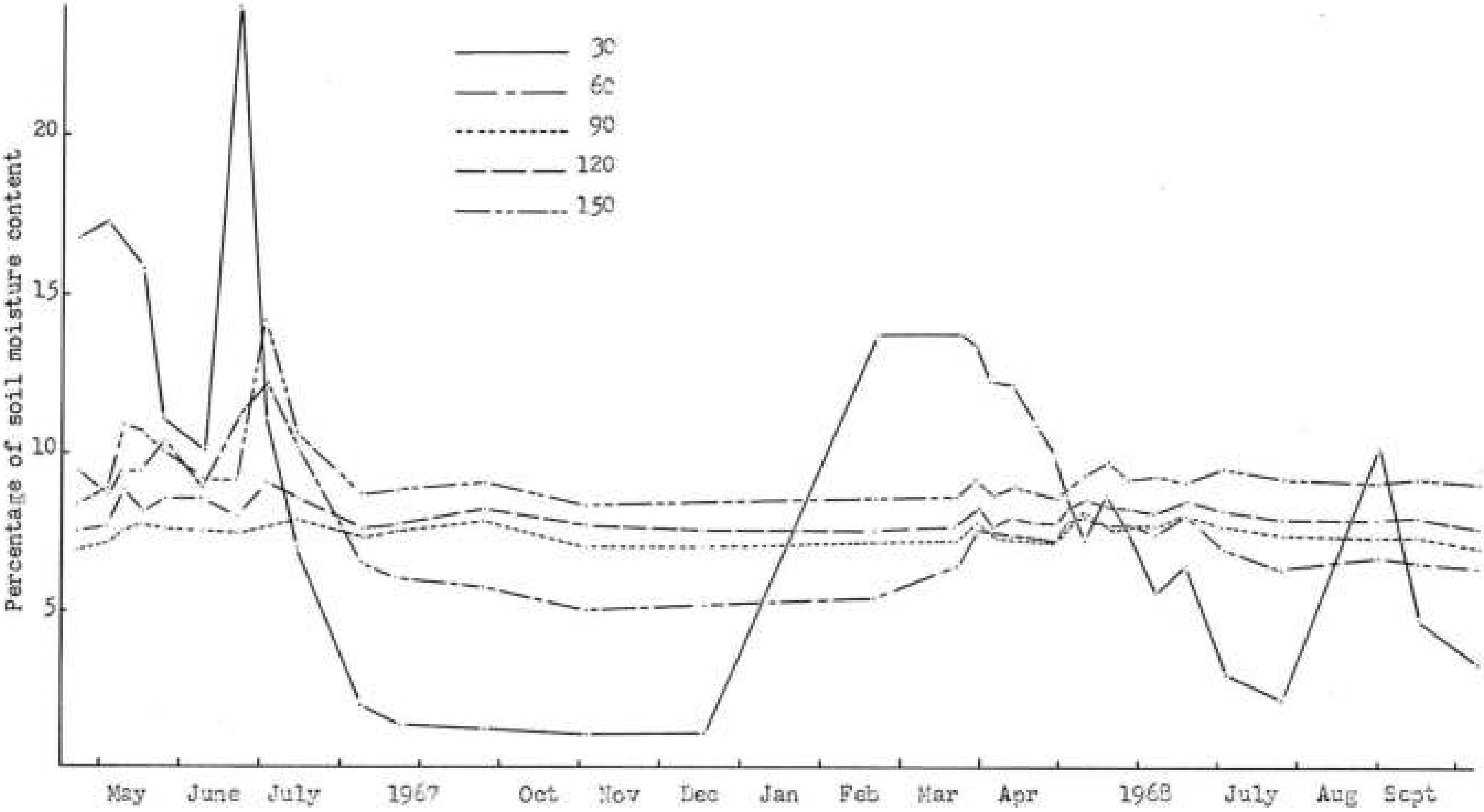


Figure 68. Mean soil moisture percentage by volume in the mixed stand at several depths (cm) and dates during the 1967 and 1968 seasons.

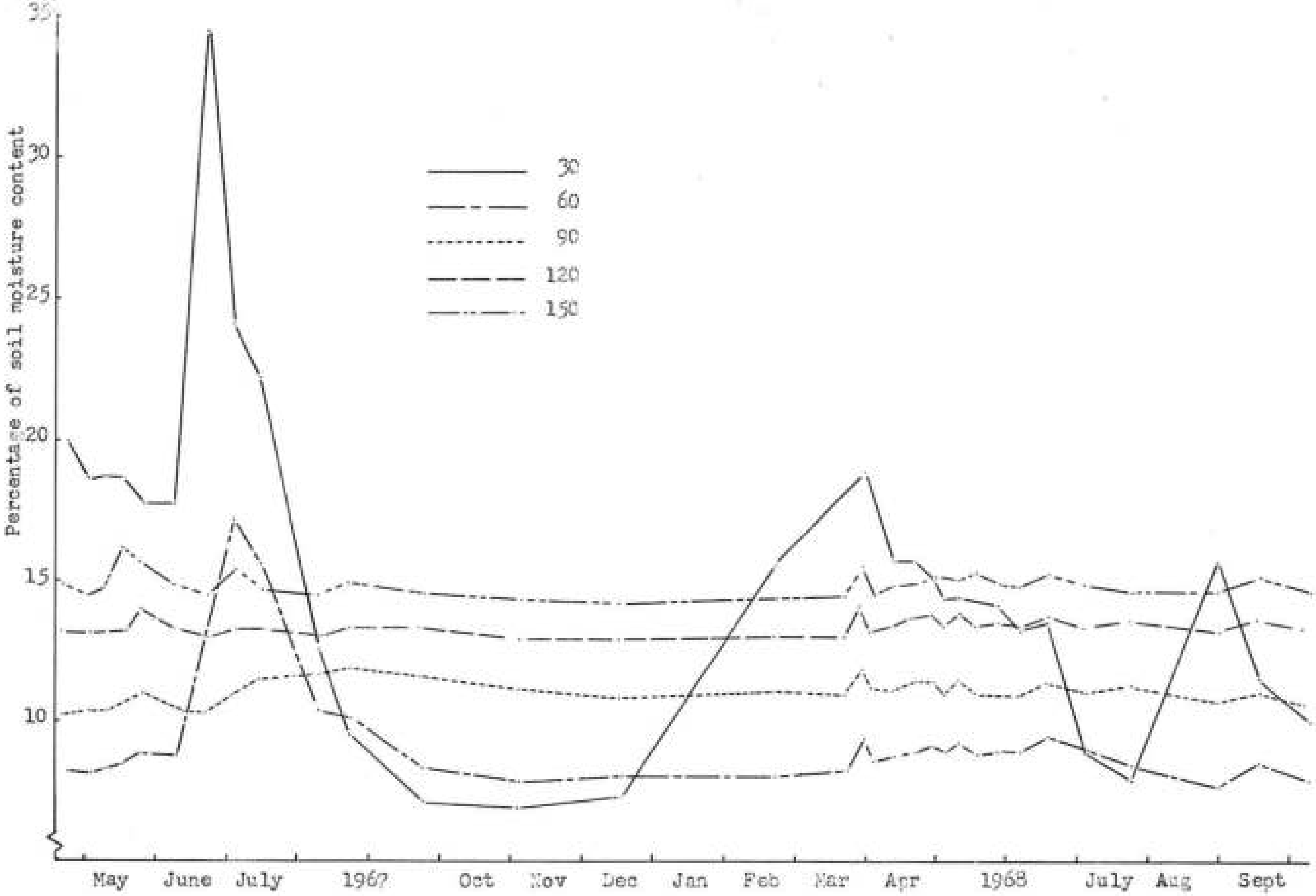


Figure 69. Mean soil moisture percentage by volume in the *A. confertifolia* stand at several depths (cm) and dates during the 1967 and 1968 seasons.

After this, by December 19 a slight increase to 1.5 percent occurred.

The moisture percentage on the 50 cm layer was lower when the first measurements were made on April 24. After that, the moisture percentage increased slightly until the first half of May when it reached a maximum of 9.0 percent. During the remainder of May and the early part of June, only slight reductions on the moisture content occurred lowering it to 8.8 percent.

On June 23 the highest rate of increase in moisture content occurred and the value was raised by 2.5 percent in only 14 days. Ten days later the moisture percentage was even higher, 11.7 and after this it started to decrease, slowly but consistently. On July 13, it was 11.0 while on August 7, it was 8.0 percent. After that date it continued decreasing until on November 4, it reached a minimum of 5.7.

The 90 cm layer showed very little annual variability. The lowest percentages were found in the April to December period, while the largest moisture content occurred between June 23 and July 13. The lowest percentage recorded for the season was 8.0 while the largest was 9.0 percent. This makes a total annual variability of 1.0 percent. As a comparison it may be indicated that the 30 cm layer has a range of moisture variability of 21.4, while the 60 cm layer range was 6.0 percent.

The next deeper layer, 120 cm, showed only slight variability in soil moisture content throughout the year. The minimum recorded was 7.9 percent at the end of the growing season on November 4 and December 19, while the highest was 8.8 in June and July. The range of variability throughout the season was 0.9 percent of moisture content by volume.

The amounts of water stored in the soil at the deepest layer studied differs in many respects from the layer located above. The main difference is that throughout the growing season, the absolute values were always large. Thus the season minimum was 12.3 percent at the end of the season on November 4, while the maximum was 14.0 on July 3. The seasonal range of variability was 1.6 percent moisture.

The magnitude of the moisture content variability throughout the season on the three deeper layers was proportionally very similar. At the upper two sampling points at 60 and 90 cm, it was 1.0 and 0.9 percent while on the last, it was 1.6. However, since the moisture content of the soil in the deeper layer was much greater, proportionally, it represents a similar magnitude of variation.

The soil where the mixed stand of _A_. _confertifolia_ and _E_. _lanata_ occurs basically showed similar patterns of variability to that of the pure stand of winterfat throughout the year.

The upper soil layer studied, above 30 cm, shows greater variation in moisture content. When the measurements were started on April 24, the mean moisture content by volume was 16.7 percent, increasing to 17.2 one week later. After this date, it progressively and slowly decreased until May 16, when it reached 15.7 percent. The rate of evapotranspiration from that soil layer was higher after that date and moisture was reduced to 11.0 percent only one week later and to 10.0 percent on June 9. The large concentration of rainfall which occurred after that date caused a sharp increase to 23.9 on June 23. However, by this time of the year the environmental conditions as well as the developmental stage of the vegetation, are such that a large portion of the moisture in the 30 cm layer is lost from the soil.

The range of variability throughout the season was from a maximum of 23.9 percent on June 23, to a minimum of 1.0 on November 4, that is 22.9 percent. This range is greater, by far, than the ones determined at any other depth. Besides this the absolute maximum moisture percentage determined during the 1967 season, as well as the absolute minimum, were higher and lower respectively than any value determined in the deeper layer.

At the 60 cm depth the maximum moisture percentage recorded was 12.1 percent on July 3, while the minimum was 5.0 percent. The variability in moisture content during the first part of the growing season was small. From April until June 9, the maximum and minimum values varied between 10.3 and 8.6 percent. After that date and because of the greater concentration of precipitation, the percentages of moisture increased to 11.0 on June 23 and 12.1 on July 3. The decrease in water content occurred after July 13. From 10.1 percent on that date it lowered to 6.5 percent on August 7, while it gradually lost water by evapotranspiration until November 4 when it reached the yearly minimum of 5.0 percent. The season's range of variability was 7.0 percent.

The range of variability at the 90 cm layer was only 0.9 percent on the moisture content in the soil. The minimum measurements recorded were those made during the last two months of the year, while the maximum occurred on July 13. The constancy of the moisture content is the most outstanding result provided by this study at this depth in the soil profile.

Deeper than this at 120 cm depth, the range of variability was slightly greater. The minimum was 7.5 in December and April while a maximum of 9.0 percent occurred on July 3.

At the 150 cm depth, the variability was high and in many respects comparable to what occurred on the surface layers of soil. The minimum of the season occurred during the last two months of the year, as well as during April when the moisture content was 8.3 and 8.4 percent. However during the rest of the year, the values calculated are extremely variable for that depth of soil, and also erratic and in many respects difficult to explain.

The moisture percentage measured on May 9 was 10.8 percent, which indicates an increase of 1.9 percent with respect to the measurement recorded the week before. However, where this moisture came from is not clear. After this first seasonal maximum moisture at this point gradually decreased until June 23, when a low of 8.6 percent was reached. After this, on July 3, the percentage raised abruptly to 14.4. This increase occurred only ten days after the maximum at the 30 cm depth, but even earlier than that at the 90 cm depth. Besides this, the moisture potential in the upper layers was low, indicating that gravitional movement of large amounts of liquid water could not have been expected, at least without considerable increase of the moisture content in the upper layers.

The pure stand of A. confertifolia was growing in soil of a different textural class. Thus the water potential curve in relation to the soil moisture content was largely different than for the soils associated with the other two stands. The percentages of moisture determined here are usually greater than those for the other stands. However, this is not necessarily an indication of greater amounts of available water.

The upper 30 cm layer had on April 24 a moisture content of 20.0 percent. This value gradually and slowly decreased to 17.7 percent on June 9. On June 23 the moisture percentage recorded was increased to 34.5 percent. This was the year's maximum. In only 7 days, the moisture loss was 9.5 percent, and on July 13, 22.2 percent soil moisture was observed, while by the first week of August, it had been further reduced to 12.6 percent. This reduction gradually continued until November 4 when the season minimum of 6.9 percent was recorded.

The year's range of variability was 27.6 percent. This was the largest range recorded for all depths and stands. At 60 cm, the range was only 9.3, that is from a maximum of 17.1 percent on July 3 to 7.8 percent on November 4.

On April 4 the moisture content was 8.2 percent. As the season advanced a slight tendency to increase the content was observed until June 9 when it reached 8.7 percent. After that date, on June 23, there was 13.0 percent of moisture content in the soil at the 60 cm depth, 17.1 percent ten days later, and 15.6 percent on July 13. The moisture reduction from that date until August 7 was large but afterwards the water losses were small, until November 4 when the percentage was at its lowest value.

At 90, 120, and 150 cm depths, the ranges of variability throughout the year were relatively small, at least much smaller than in the surface layers. In the upper level, the absolute seasonal minimum was 10.2 percent in April while the maximum was 11.9 percent, that is a range of 1.7 percent.

Measurements at 120 cm depth varied even less, from 12.9 percent during the last two months of the year to 14.0 percent on May 23. That is a range of 1.1 percent.

The variability of the deepest layer of soil studied was of similar magnitude. The minimum value of moisture content measured throughout the year was 14.2 percent, while the maximum was 16.2, a range of 2.0 percent. The moisture percentages throughout the year were greater at the 150 cm depth than at any other point in the profile, except in the surface layer. The upper profile at certain times of the year had much higher soil moisture percentages but at other times it was much smaller.

The absolute moisture percentages in the <u>A. confertifolia</u> stand were high at the 30 cm depth, decreased to a minimum at 60 cm depth and gradually increased at 90, 120, and 150 cm depths. The higher values were found in the surface layer.

The results presented up to this point indicate that there is a main season of replenishment of the soil moisture lost by evapotranspiration during the previous growing season. This recharge starts after the minimum moisture content is reached in November. During the first three months of the year, from January through March, the moisture content increases because of the reduced and almost negligible losses by evapotranspiration. The maximum usually occurs by the end of March.

The increase in soil moisture, due to accumulation during the cold season months, is striking to the 30 cm depth and slight to the 60 cm layer. Below that, despite the fact that the moisture percentage also increased, the season's maximum was not reached until later. The upper 30 cm layer is the only soil layer where moisture percentage decreased from April on.

During the growing season, especially from June to August, there was often great variability in the monthly precipitation. Large concentrations of precipitation were received (as much as 114.7 millimeters in one month) which meant large increases in the availability of moisture in the 30 cm soil layer, while only small variation in the content as the depth increased. At the 60 cm depth, the variation was only a fraction of the fluctuations recorded in the upper 30 cm soil layer. During the 1967 season, the considerable precipitation received in June caused an increase in the soil moisture content as just described, while during 1968, this increase occurred in the second half of August.

Typically, the soil moisture content curve has one maximum and one minimum. The maximum occurred early in the growing season in March to April. The minimum occurred late in the growing season after most of the available moisture in the soil has been removed sometime between September to December. In the surface layers the maximum occurred earlier while in the deeper layers, this maximum occurred two weeks to one month later.

During the active growing season from March to September or October, that is from when the stem buds start to swell until the seeds are ripe and falling, the amount of precipitation is highly variable from year to year. Thus a secondary maximum and minimum may occur, such as happened during the 1967 and 1968 season. These second peaks are largely variable depending on the magnitude of precipitation received. However, in general, the relative duration of the highest percentages of available moisture for vegetation is short, since the potential evapotranspiration during the midsummer months is great. The amount of energy received in the salt desert shrub vegetation type is extremely high. The moisture extracting power of the vegetation during midsummer is considerable because of the large transpiring surface of leaves as well as the growth rates of the plants. The extra moisture received is rapidly lost.

From the results presented here it is obvious that the 30 cm layer possesses great variability in percentages of moisture content throughout the year in all three stands. The 60 cm depth has some variability throughout the year but much less than that recorded in the surface of the profile. Deeper in the soil the amount of variability is minimal. The only exception is in the mixed stand where the deepest layer showed the greatest differences in the moisture content throughout the year.

The small reduction in the moisture percentages, even after long periods of drought, is an indication that only very small amounts of water in the ecosystem is transpired from the deeper layers. Even after long periods of intensive rains, the moisture percentage at the 90 cm depth, as well as the deepest one, showed only small changes in the moisture content, usually amounting to a fraction of one percent. If the soil moisture percentages does not vary much, it means the deeper layers have only a minimum role in the hydric relations of these three communities.

Despite the fact that only negligible amounts of moisture are lost from the deeper layers, their importance is not known. The exact amount of water transferred between layers is not known since the rate of water movement is not known, as well as the rate of the moisture loss. The only figure presented here is the actual moisture content which is the result of two functions, the total amount of moisture added minus the moisture lost by evapotranspiration. Moisture movement through the soil in the deep layers should be small because the water potential is always below the field capacity. Thus, it is expected that little or no liquid movement of water occurs.

The standing root biomass, determined for these same stands and depths, may indicate somewhat different results (Appendix table 44). The weight of roots was considerably greater in the upper soil layers. This is indicative that most of the plant activity occurs in the surface 30 and 60 cm layers. Below these depths, despite the fact that the biomass is smaller, there are, however, considerable amounts of active roots. This is indicative that some of the moisture is lost from the deepest layer by a small but significant amount of roots.

It is sometimes stated that during the late part of summer from July to September when the surface soil is dry, the stand loses its moisture by evapotranspiration from deeper soil layers. However this is not the case here where most of the water loss occurs from the surface layers, while the deepest ones only show slight variations. Even when the soil is almost completely dry in the 30 cm layer, the 90, 120, and 150 cm depths still contain large amounts of stored moisture. This moisture is not utilized at all, even during the driest part of the year and thus their moisture content remains unchanged from year to year.

The moisture content of the whole profile and its variability throughout the year is an indication that the whole ecosystem is expending more or less of the water that it has received during a particular period.

The lowest moisture content occurs in the three soils during the last part of 1967, in November and December. At this time, the vegetation had drawn down the moisture recharge of the previous winter.

During 1968, different results were recorded. The first part of the summer was fairly dry and thus little production of flowers and seeds occurred. By the middle of August, seedlings and plants were almost dormant because of shortage of moisture. However, during the second half of August the precipitation increased and the soil was again wetted. Annual plants started to grow, shrubs produced new leaves, and seedlings turned green and started to grow. The soil moisture added was enough to keep the vegetation active and growing until lowering in the temperature induced a dormancy of the vegetation. That is, during the first year dormancy was induced by drought, while during the second, it was probably caused by low temperatures.

The largest amount of moisture stored in the soil occurred at the beginning of spring, after a season of maximum accumulation and minimum losses. Secondary maximum storage occurred during the summer at various dates. During the 1967 season this maximum was in late

June and early July while in the following year, it happened in the second half of August and early September. Weather records indicate that essentially no summer recharge is more typical.

The amount of moisture stored in the soil varied from stand to stand. This was mostly due to differences in textural characteristics of the soils which vary on all three stands thus presenting differences in percentages but which actually may correspond to similar moisture potentials.

Tables 11 and appendix table 45 present the matric potential values calculated for each soil, depth, and date. In the E. lanata stand, from April until July 3, the matric potential was high on the 30 cm layer. Until May 16 the largest value was -70 Joules per kilogram. On May 16 and June 9, the readings indicated -680 and -560 Joules per kilogram, respectively. On June 23, the soil was saturated. The rest of the season from July 13 until the end of the year, it was -1500 or less. During the following season something similar occurred. The matric potential was -250 Joules per kilogram on February 24, and increased until March 23. After that date it gradually decreased until May 3 when it reached -570. Most of the remaining part of the year it was -1500 Joules per kilogram or less. The only exception is the last part of August and September when the large addition of moisture, because of the increased precipitation, resulted in a high matric potential of -130 Joules per kilogram (Figures 70 and 71).

At the 60 cm depth the matric potential was below -340 Joules per kilogram until June 9. From June 23 to July 13 was the only time in the two-year period of study when values between -320 and -240 Joules per kilogram were recorded. The rest of the year, as

Table 11. Mean soil matric potential in Joules per kilogram on three stands and five depths at several dates during the 1968 season. The value of -1500 Joules per kilogram means equal or smaller than that value.

Depth (cm)	Dec 1967	Feb	March		April				May			
	19	24	23	29	5	12	19	26	3	10	17	25
30	-1500	- 250	- 90	- 95	- 180	- 150	- 260	- 440	- 570	-1500	-1500	-1500
60	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500
90	-1340	-1320	-1300	-1260	-1280	-1240	-1240	-1220	-1260	-1120	-1160	-1220
120	-1500	-1500	-1500	1340	-1320	-1260	-1320	-1260	-1320	- 900	- 940	-1200
150	- 310	- 300	- 290	- 260	- 260	- 225	- 260	- 225	- 225	- 200	- 220	- 225
					Mixed							
30	-1500	- 80	- 80	- 90	- 130	- 140	- 230	- 540	-1500	-1500	-1500	-1500
60	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500
90	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500
120	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500
150	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500
					A. confertifolia							
30	-1500	- 370	- 320	- 260	- 390	- 640	- 640	- 750	- 940	- 940	-1500	-1500
60	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500
90	-1500	-1500	-1500	- 720	-1500	-1500	- 920	- 920	-1500	- 820	-1500	-1500
120	-1160	-1050	-1100	- 720	-1000	- 920	- 850	- 820	- 920	- 800	- 920	- 880
150	-1500	-1500	-1500	- 820	-1429	-1020	- 960	- 880	- 920	- 840	- 990	-1020

Table 11. Continued

Depth (cm)	June		July		Sept.		Oct.
	5	20	4	26	1	19	9
	E. lanata						
30	-1500	-1500	-1500	-1500	- 130	-1500	-1500
60	-1500	-1500	-1500	-1500	-1500	-1500	-1500
90	-1220	01120	-1160	-1180	-1260	-1180	-1220
120	-1320	- 940	- 940	- 940	-1500	-1260	-1480
150	- 240	- 210	- 210	- 220	- 290	- 260	- 290
	Mixed						
30	-1500	-1500	-1500	-1500	- 380	-1500	-1500
60	-1500	-1500	-1500	-1500	-1500	-1500	-1500
90	-1500	-1500	-1500	-1500	-1500	-1500	-1500
120	-1500	-1500	-1500	-1500	-1500	-1500	-1500
150	-1500	-1500	-1500	-1500	-1500	-1500	-1500
	A. confertifolia						
30	-1500	-1500	-1500	-1500	- 630	-1500	-1500
60	-1500	-1500	-1500	-1500	-1500	-1500	-1500
90	-1500	-1500	-1500	-1500	-1500	-1500	-1500
120	- 630	- 820	- 920	- 830	-1000	- 830	- 960
150	-1060	- 880	-1020	-1100	-1100	- 920	-1100

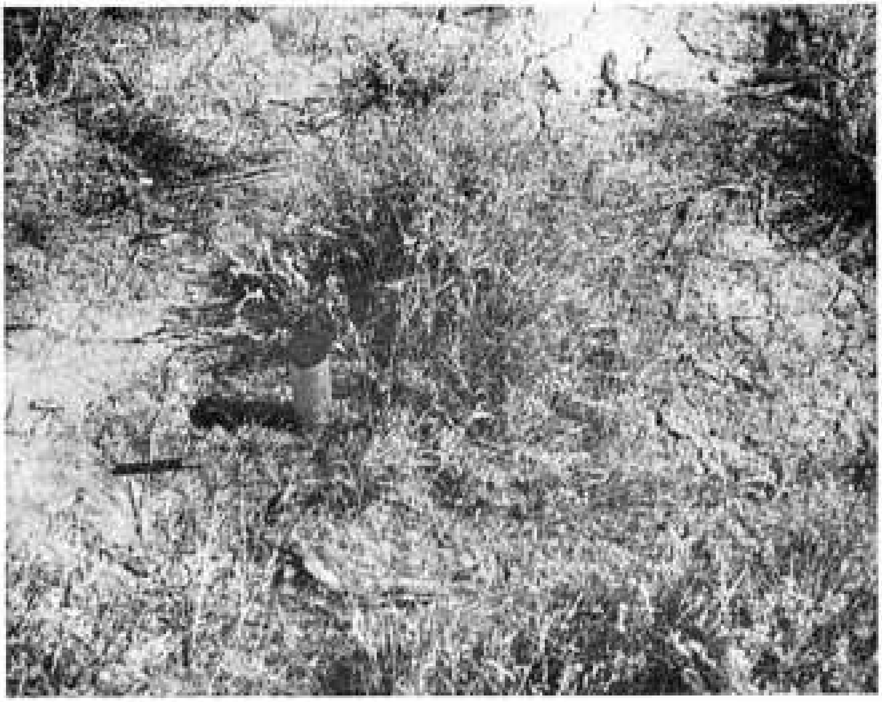


Figure 70. General view of the location of a neutron tube in the mixed stand of A. confertifolia - E. lanata.

Figure 71. General view of the upper 2.5 cm soil moisture sampling, in the grazed E. lanata stand.

well as on the next season, the matric potential was always -1500 Joules per kilogram or below.

Soil matric potential at the 90 cm depth in soil associated with the E. lanata stand was at all times between -900 and -1400 Joules per kilogram during the two-year period. During the first season the largest matric potential occurred on May 9 when -1050 Joules per kilogram was recorded and from June 23 to July 13 when it was -900. After that date, it gradually decreased until December when it was -1400. During the 1968 season, there was even less variability, and the minimum matric potential occurred in February 24 with -1320 Joules per kilogram while the maximum occurred on May 10 and June 20 with -1120.

The next deepest layer, that centered at the 120 cm depth, had larger variability. During the 1967 season and until May 9, the matric potential was -1500 Joules per kilogram or less. Between May 16 and August 7, it varied but the maximum never exceeded -1150. The rest of the year was -1500 or less. During the 1968 season, the matric potential varied between a maximum of -900 and a minimum of -1500 or less. Minima occurred in the first half of May as well as during late June or July. The maximal potential was recorded at the beginning of the season in February and early March and at the end of the year, after September.

The deepest soil layer in the winterfat stand showed root densities different from those recorded at the other depths and stands. The matric potential varied between -340 and -190. It never was below that value even at times of the year when the matric potential on the 30 cm layer was much lower. Thus the large amount of available moisture present at this depth, as well as lack of utilization, are indicators of the reduced significance of this deep layer on the overall water cycle in the ecosystem where E. lanata grows naturally.

Soils of the mixed stand of A. confertifolia - E. lanata showed different results from the other two sites. The 90 and 120 cm soil depths consistently had values less than -1500 Joules per kilogram. The same occurred in the deeper soil layers. The only difference is that here, there was in one reading made on July 3, 1967, a few weeks after intensive rains occurred, a high value of -340 Joules per kilogram. However, this result is inexplicable considering the previous results of soil water movement where the upper layer remained below the permanent wilting percentages.

The matric potential in the upper 30 cm layer varied considerably throughout the season. Until May 16, the matric potential was above -60 Joules per kilogram, as well as on June 13. A few determinations in May, June, and July indicate that the matric potential was at that time -220 and -420 Joules per kilogram. The rest of the year it was always below -1500. During the last growing season, the matric potential decreased from a minimum of -80 Joules per kilogram or below with the exception of September 1, when it was -380.

The matric potential on the 60 cm layer was always below the permanent wilting percentages during the 1968 season and most of the previous year. On July 3, the matric potential was -220 Joules per kilogram and late in June, -480 Joules per kilogram.

The Atriplex confertifolia stand showed similar patterns of soil matric potential variability throughout the year. The highest values in the 30 cm layer were recorded during the early part of the year, from April until July 13. From June 23 to July 13, the matric potential was between 0 and -110 Joules per kilogram. Before that, the values ranged between -200 to -360 Joules per kilogram, which are in general, slightly lower than those determined for the equivalent layer under the other two stands. The rest of the year the matric potential was below the permanent wilting percentages. During February, 1968 season, the matric potential was -670 Joules per kilogram and gradually increased until May 29 when it was at its maximum value of -260. After that date, it gradually decreased until May 17 when it was below the wilting percentage. Late in the season on September 1, the matric potential temporarily increased to -640 because of the additional moisture received from precipitation which fell in August. The matric potential determined at 30 cm was always less under <u>A</u>. <u>confertifolia</u> than on either of the other two stands.

At 60 cm, the matric potential of the <u>A</u>. <u>confertifolia</u> stand was always below -1500 Joules per kilogram during the 1968 season as well as most of the previous year. The highest matric potential occurred between June 23 and July 13.

The soil in the 90 cm layer remained at or below -1500 Joules per kilogram during the two-year period with the exception of three opportunities when it surpassed that value and reached as high as -820.

The deeper two layers studied on the <u>Atriplex</u> <u>confertifolia</u> stand showed some variability throughout the year. The minimum of -1200 Joules per kilogram occurred on the upper level at the end of the 1967 season and was only -1200, while the maximum was -720 and was measured on March 29. During the previous year, the maximum of -770 was determined on May 23.

In the 90 cm layer, the maximum occurred on May 16 and was -690 Joules per kilogram while the minimum, which often reached as low as -1500, was between September 26 and March 23.

Results dealing with the matric potential presented up to this point clearly indicate that with a few exceptions, most of the growth and development of the vegetation which naturally occur in the stands studied happened when the matric potential was very low, usually below the normal permanent wilting percentage or near it. When the atmospheric energy conditions are not sufficient to cause evapotranspiration of the moisture present in the soil, the temperature is so low that the vegetation is inactive and the addition of moisture exceeds the losses. This is what happened during the coldest part of the year, from December to March. During part of March and all of April moisture conditions in the soil are the best. The water potential in the upper layer, where most of the roots are concentrated, is high, and evapotranspiration potential is small. However, temperatures are still too low to have optimum growth.

Later in the season, temperature rises and so do growth of the vegetation and evapotranspiration. The higher evapotranspiration potential which occurs in the middle of summer is responsible for the greater moisture losses as well as the lower moisture potential in the soil.

The actual losses of moisture from the ecosystem have to be less than the potential losses since the energy received during the growing season is capable of producing large water losses, much larger than the actual amount of moisture stored in the soil. However this does not occur because it has been repeatedly demonstrated that the actual evapotranspiration losses decrease as the water potential decreases (Makking and Van Heemst, 1956; Bierhuizen, 1956).

Besides this, there is also a decrease in moisture losses as the depth increases because the amount of energy received also decreases. Thus, the water losses by evaporation from the soil are minimal at 90 or 150 cm, and if it is not lost by the transpiration channel from root conduction to the leaves, the moisture content is not modified. This is what happened in the 150 cm layer in the winterfat stand, where the water potential was high during the whole year, even in late summer. The plants become dormant because of drought but the moisture percentage or the matric potential did not decrease considerably.

The largest component of the total soil moisture potential, matric potential was determined. It is expected that the salinity only modifies the total soil moisture potential slightly. However under any circumstance, even if there is only a small concentration of soluble salts in the soil, this would mean an additional decrease in the total water potential. Shadscale grew satisfactory on matric potentials considerably lower than winterfat. If this is what actually happens, the results reported here can well explain why _E. lanata_ does not grow on the areas where _A. confertifolia_ naturally grows. However, it does not explain the opposite, why shadscale does not grow on the winterfat stands. If shadscale is capable of surviving under lower moisture potential and removes from the soil larger amounts of water, then the mixed stands of both species could not persist for long periods of time and eventually E. lanata should disappear. However, this is not the case. E. lanata does not disappear or die when growing associated with the Atriplex, and neither the pure stands of E. lanata are completely invaded and displaced by it. Quite the opposite was found by Harper (1959). He concluded that E. lanata thrives during drought whereas A. confertifolia fails.

Water relations based on the Law of Limiting Factors alone, and its effect on the adult plants of both species is not the sole simple explanation for the distribution of these two species. The mechanism has to be more complex.

Soil Salinity and Reaction

The percentage of total soluble salts in the upper 2.5 cm of soil associated with the three grazed stands varied according to the time of the year and the stand itself (Table 12). The results indicate that the lowest value for the Eurotia lanata stand occurred on August 13 when the percentage of total soluble salts was 0.05, while the highest value was 0.08 percent on June 20. During the remaining part of the growing season it varied slightly, but most of the time it was around 0.06 percent.

In the mixed stand of Eurotia lanata and Atriplex confertifolia, the lower percentage of total soluble salts was also 0.05 percent on April 20, while the highest was 0.07 percent on June 20 and July 26. During the remaining part of the growing season the percentages were consistently 0.06.

The Atriplex confertifolia stand showed at all times higher

Table 12. Percentage of total soluble salts and soil reaction in the upper 2.5 cm of soil at three grazed stands and at several dates throughout the 1968 season.

Stand	March 18	April 20	May 19	June 20	July 26	August 13	Sept. 17
Salinity:							
E. lanata	0.06	0.06	0.06	0.08	0.07	0.05	0.06
A. confertifolia	0.08	0.10	0.08	0.10	0.10	0.11	0.08
Mixed	0.06	0.05	0.06	0.07	0.07	0.06	0.06
Soil reaction, pH							
E. lanata	7.9	7.9	8.0	8.0	---	8.2	8.0
A. confertifolia	8.0	8.1	8.1	8.0	---	8.2	8.1
Mixed	8.0	7.8	7.7	8.0	---	8.1	7.9

values than the other two. On August 13, the percentage of total soluble salts was 0.11, while the lowest value was 0.08 percent on March 18, May 19, and September 17.

The soil reaction for the upper 2.5 cm of soil is indicated in table 12. These soil analyses indicate that there is only small variability in the pH readings throughout the year from one stand to the other. In the E. lanata stand, the pH varied from 7.9 to 8.2. The mixed stand had a range of variability of the pH from 7.7 to 8.1, while the pure stand of A. confertifolia varied from 8.0 to 8.2.

The percentage of total soluble salts in the upper 2.5 to 7.5 cm of soil is very similar to those already described for the surface (Appendix table 48).

The results indicate that in the E. lanata as well as in the mixed stand, the lowest value during the growing season was 0.05 percent total soluble salts while the maximum was 0.08 percent. However, the grazed stand of pure A. confertifolia had a maximum value of 0.10 percent while the minimum was only 0.07 percent. The results indicate that the mean percentage of total soluble salts was consistently higher for the shadscale stand than the other two.

The soil pH varied slightly throughout the year. Thus on the E. lanata stand the range was from a pH of 7.9 to 8.2, on the A. confertifolia stand the range of pH variability was from 7.9 to 8.3, while on the mixed stand, the range was the same as that for winterfat (Appendix Table 48).

In the upper 15 cm of soil, the percentage of total soluble salts was only slightly different from the results already presented (Table 49). For the pure stand of E. lanata as well as under the A. confertifolia stand, the range of variability was from 0.04 to 0.11 percent.

The range of variability of the soil pH during the growing season for the E. lanata stand as well as on the mixed stand, was from 7.9 to 8.4. Under the pure stand of A. confertifolia, the lowest pH during the growing season was 7.7 while the highest was 8.3.

The results of the soil analyses for salinity determinations show that the variability in concentration determined at several times of the year is small. The percentage of total soluble salts at any time of the growing season was too small to be of considerable effect on the germination and growth of seedlings. This can be demonstrated by comparing these values with those of the study of Workman and West (1968) and Clarke and West (in press). In both cases high percentages of germination were determined with salinity concentrations similar to the salinities determined for this study, or even larger. Besides this, a direct demonstration that there is not a serious salinity limitation for the germination of Eurotia lanata and Atriplex confertifolia seeds was made in this study. The seeds of both species, when placed on soils taken from various stands and depths, did not show effective differences in their germination percentages.

Seedling growth should not be affected with such low concentrations of soluble salts. This was also corroborated in another part of this study, when seedlings of E. lanata and A. confertifolia were grown under greenhouse conditions.

It can be concluded from this study that salinity concentration differences on the three stands at several depths in the upper 15 cm of soil should not be considered important in the regulation of the distribution of the two species in the study area. The limits of tolerance for the two species, both for germination and seedling growth, are greater than the salinity values actually determined in the study area.

Growth as determined by the change in dry weight of the plants is highly relevant to the interpretation of ion effects on the plants. The growth of A. confertifolia under growth chamber conditions is an indication of the biological response of this species to various concentrations of sodium chloride added.

The lowest dry weight of the A. confertifolia plant tissue was determined on those plants growing in the soil from the E. lanata stand without the addition of sodium chloride (Figure 72). The total soluble salts in this treatment was 0.05 percent. The largest dry weight per pot was produced on those soils with 0.35 percent of total salts but as the concentration of salts increased, the dry weight decreased. Concentrations of 1.25 and 2.45 percent were responsible for the death of some of the plants growing in the pots. The lower concentrations of salinity in the soil caused no mortality of the plants despite the fact that the dry weight was reduced.

The effect of salinity could be modified according to the age of the plant. In this particular study, shadscale plants were germinated and grown for several weeks without receiving additional concentrations of salts. However, in a similar experiment, seeds of E. lanata were germinated on petri dishes. Immediately after germination, they were transplanted to pots containing the same substrate used in the previous experiment with shadscale. However, this time no seedlings of E. lanata survived in those pots where any addition of sodium chloride had been made, while all that were planted survived in the check pots without addition of salts, which only had a concentration of 0.05 percent of total soluble salts. However, when additions of sodium chloride to pots were made to 8 week old plants of E. lanata, no mortality was observed at low concentration . Mortality increased as concentration increased and nearly a one hundred percent death rate occurred starting from 0.65 percent of soluble salts, and the death rate was even more prominent at the 1.25 percent salt level.

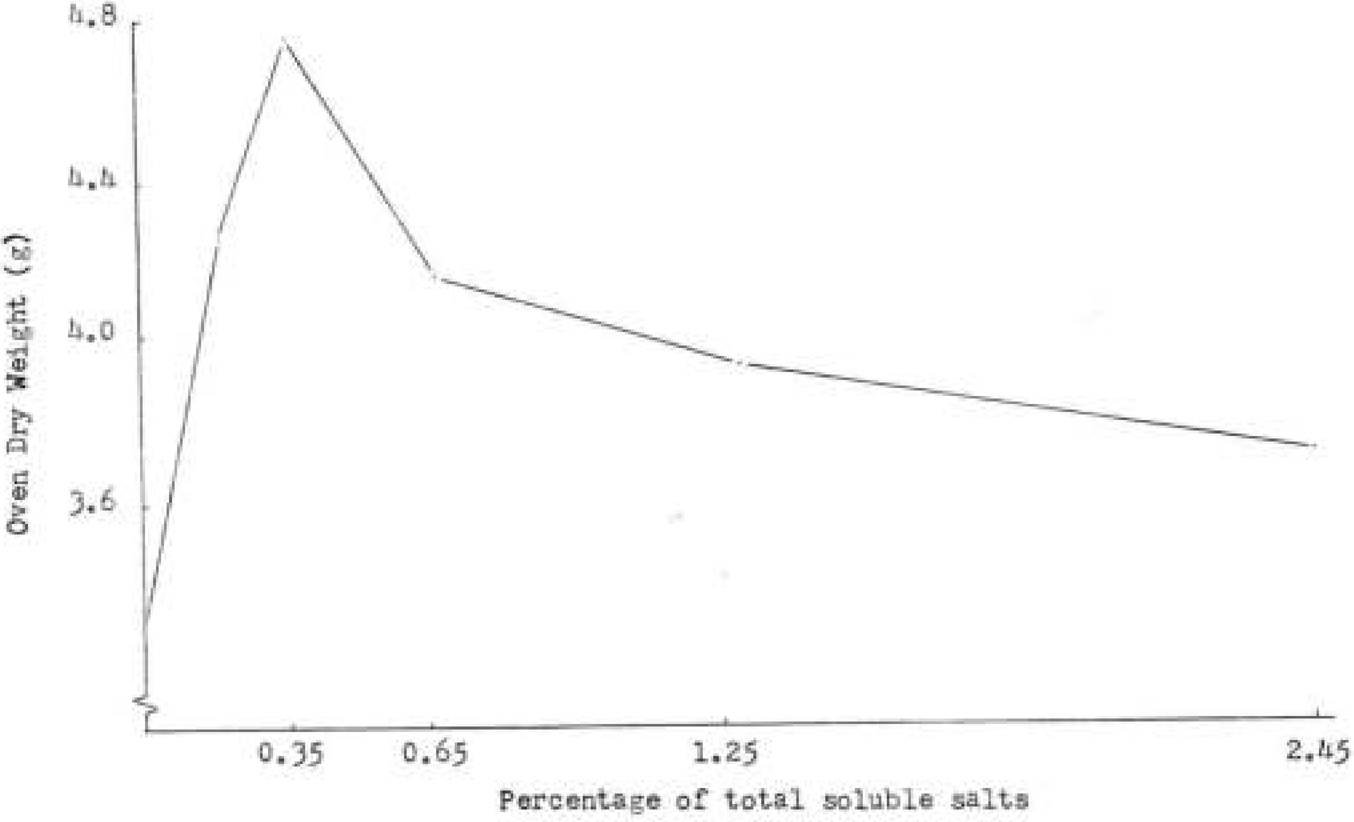


Figure 72. Oven dry weight of A. confertifolia plants grown in pots at various soluble salt concentrations.

General Discussion

A "population" is a group of individuals of the same or similar species limited in space and time. This study deals basically with populations and not with individuals. However to be able to understand the ecological processes which are responsible for the presence of certain species in one area, it is first necessary to know individual behaviour in the environment. The simultaneous reaction of every individual of the same species in the environment where they live is equivalent to the addition of the partial individualistic reactions of every plant in the population.

This research was designed to study the behaviour of several populations of two species, A. confertifolia and E. lanata. For each one of these species three populations were studied; a grazed, an ungrazed, both of which were growing in pure stands with only one dominant, and a population of the same species behaving as a codominant with the other species.

At this point in the discussion it is important to emphasize that there are two main approaches that may be taken to study the distribution of the species in a certain area. One is the "individualistic" approach, while the other is the "population" approach.

A clear delimitation of the approach used in the previous work has not been explicitly made. It seems that the previous work reviewed in connection with this research indicates the main objective in mind was individualistic. There are, however, in certain papers indications that to a small degree, some population thinking was also done.

It seems appropriate to start studying the causes of distribution of the species on a certain area with a individualistic approach. The first question to be asked when studying the absence of a population on a certain area is: are any of the environmental factors, acting alone or holocoenotically, beyond the tolerance limits for the individual of a certain species? If the answer is yes, it means that the individuals are not capable of surviving in the existing environment because they are physiologically unable. The physiology of the organism does not permit the individual organism to live and survive, and so the area has to be utilized by other individuals of other species which are capable of living under the existing environmental conditions.

This is, then, one possible explanation for differential distribution of these two species in the salt desert shrub vegetation type. It could be said that winterfat grows in different areas than shadscale because the physiological limits of tolerance for each of these species are different. Winterfat lives on all those areas where the environmental factors are physiologically fitted for the individuals of this species, and shadscale lives also on the area where the physiological tolerance of the individuals of this species is between its tolerance limits. This is simply the application of Shelford's Law (1937) to individuals in a community.

Most of the previous work has been oriented in this direction. It is supposed that the distribution of the species is regulated by certain unknown limits of tolerance of a certain unknown factor. If this is the case, by simple measurement of the environmental factors where the individuals of the species live, it would be possible to determine factors that control the distribution of the individuals of the species. The exact location of the individuals could then be predicted with only simple environmental measurement.

At the present time there are, however, several arguments which indicate that this line of reasoning is not adequate for explaining the distribution of these plants.

For many years it was thought that the tolerance limits of the species was centered around salinity concentrations. It was also thought that the exact percentage of salinity limiting the tolerance and hence the distribution of these two species could be exactly determined. Time and effort has proven that there is not an exact limit of salinity tolerance. Later other studies indicated good correlation between certain other soil factors and the distribution of the species. However, the limits of those factors were extremely variable.

Later it was also thought that the limit of tolerance should be best expressed at the ecotone or alterne between the winterfat and shadscale stands. However, despite the numerous studies conducted in this respect none of them has proved any limit of tolerance which could completely and exactly delimit the distribution of the species. Besides this it would be very improbable that shadscale and winterfat have evolved fitness toward such a perfect tolerance limit. This line of reasoning would lead to assertions that shadscale cannot grow because the tolerance limits are beyond the actual tolerance for the species at the point at which the range of tolerance for winterfat starts.

To check this point in this research, an experiment was designed to study if there was any inherent characteristic of the soil which would delimit the growth or germination of these two species. The results demonstrated that plants germinated and grew perfectly well, and often better on soils where other shrubby species of the same area naturally grow than on their own soil. This was under absence of interference and uniform climatic conditions.

From an edaphic and climatological point of view all evidence indicates that these two species are physiologically capable of living under the physical environment where other species or ecotypes live. Their range of physiological tolerance is broader than the magnitude of the actual environmental factors found in the areas where they are present. This is the answer to the first question enunciated above.

If a simple physiological explanation is not satisfactory, then an ecological explanation could be the answer. The second question to this problem is: if the individual organisms can successfully live, grow, and develop in an area of much broader characteristics than the one they actually occupy, why is a population of those very same organisms absent?

The answer to this question is "interference." It is obvious that if two or more populations can occupy exactly the same area, because their range of tolerance is beyond the actual magnitude of the environmental factors present on that area, and only one of them is present, this means that the species absent is not there because the other is present.

The explanation of this is based on the principle of competitive exclusion or Gause's Rule, which states that no two species can occupy exactly the same niche. Thus if the physiological tolerance of the individuals of two or more different species or ecotypes permit their growth and reproduction on that particular area, only one population would remain because they are competing for only one niche.

Interference is, however, a term too broad, and in this discussion it would be useful to present it in a more specific way. First, it must be remembered that no matter what is the cause of the presence of a population of individual organisms, the value of r, or rate of population growth is responsible for it.

The population has certain properties that individuals don't have. Among these it is important to remember the birth rate (b), mortality rate (d), and migration rate (m). The magnitude of r is a consequence of these three characteristics of the population.

$$r = b - d \pm m$$

Thus, the rate of population growth is equal to the birth rate minus the mortality rate, plus or minus migration depending upon whether there is immigration of organisms or disseminules or emigration.

At this point, Liebig's Law of Limiting Factors could be useful in understanding the mechanisms which finally are responsible for the presence or absence of a population in one area. Liebig's Law, as enunciated by Wollny (1891), is as follows: "each vegetation factor beginning with a lower limit (minimum) increases the productivity power of plants with each increment of intensity or amount up to a certain optimum value from which point, however, with further increase of the active factor the productive power steadily diminishes until growth finally becomes quiescent or is completely destroyed (maximum)."

The Law as originally enunciated by Liebig's (1855) or as later modified by Wollny (1891) is not fitted to explain the distribution of populations. Liebig, himself, and the other researchers who enunciated and modified it were agricultural chemists or agronomists, and were interested in individual plants or in agricultural crops. They did not try to apply it to more complex ecological situations. The principle was only applied to yield of green tissue or seeds. However, it is now believed that it is also possible to apply it to situations much more complex than it was originally used for.

No matter which is the ultimate cause or factors responsible for the distribution of species in the salt desert shrub vegetation type, the actual mechanisms are centered around r. If any species invades a certain area and remains there, it has to have, when the population is increasing, a value of r larger than zero, while later when the population is in equilibrium r is equal to zero. If a population, at no time and under any circumstance is fitted to have a value of r larger than zero, then it has to become absent from the area. If the mortality plus emigration of winterfat or shadscale on a certain area is always greater than the birth rate plus immigration, the population cannot be found permanently present in that environment.

Under environmental conditions such as those found in Curlew Valley, E. lanata and A. confertifolia are capable of growing and developing on areas where other species dominate. However, despite the fact that their physiological tolerance would permit them to live and reproduce under the edaphic and climatic conditions where other dominants live, they are absent. Their absence under a favorable physiological environment can only be explained on the basis of the rate of population growth.

The Law of Limiting Factors could now be enunciated to explain the absence or presence of populations on certain areas. It would be as follows: each physical, chemical, or biological environmental factor, beginning with a lower limit of less than zero (minimum) increases the rate of population growth with each increment of intensity or amount up to a certain optimum value from which point however, with further increase of the active factor (maximum), the rate of population growth steadily diminishes until it finally becomes less than zero. Thus if any environmental factor, acting independently or holocoenotically, is responsible for having a rate of population growth (r) of zero or less at its maximum possible value which could naturally occur under the natural environment, the species would be absent from the area.

This study has demonstrated that winterfat and shadscale can successfully germinate, grow, and reproduce under soils where other plant communities naturally grow, and this species is completely absent. The only possible reason found at this moment is that the lack of success can be fully explained by the Law of Limiting Factors at the population level as enunciated here.

In this research mortality rate of adult plants and migration were not studied. However, birth rate and mortality of seedlings were studied and constitute an important component of the value of r.

Despite the fact that the information obtained from this study is not complete, it is adding additional data which would help toward a better understanding and interpretation of the distribution of plants and plant communities in the salt desert shrub vegetation type.

The migration value for these two species seems to be very low. The seeds of winterfat and shadscale don't desseminate very far. There are several facts observed and determined in the field which make one think this way. In the first place, no seedling of any other shrubby species was found on the pure stands of winterfat and shadscale. However, only a few meters apart there were enough adult plants which could have produced many seedlings in the nearby stands of the other species.

_A_. _confertifolia_ fruits are heavy and thus most of them fall just under the female adult plant which produces it. However, some of them are found at a few decimeters. _E_. _lanata_ fruits are also mostly concentrated around the adult plant which produced it. These statements can be backed by two facts. First no fruit, seed, or seedling was found further than a few meters from the adult plants from the same species. This indicates that the chances of dissemination for these two species are very small.

A second argument in favor of low dissemination is related with the actual distribution of seedlings in the field. It was found and demonstrated that the chances of germination and emergence under natural conditions increases as the litter concentration over the surface also increases. The litter concentration increases as the distance from the plant decreases. It was concluded in this study that the main reason for the heterogeneous distribution of germinated and emerged seedlings arises from the heterogeneous distribution of seeds. Seeds have the tendency to fall by gravity and remain very near to the place where they are produced.

Among the shrubby species studied there is one exception, that is Artemisia tridentata. Seedlings of this species were found growing in dense, localized clusters in the pure winterfat stand. However, it was always related with the closeness of some isolated group of seed producing plants of big sagebrush. Besides this, seedlings of this species were abundant at only one side of the putative parent and it is precisely on the same direction of the predominant wind; while on the other side, A. tridentata seedlings were absent.

The seeds of big sagebrush are light and the plants produce abundant amounts, and so by the influence of wind it is to be expected that they have a greater chance of seed migration to other areas and also the possibility of germination and establishment. The results also demonstrated that there is not any interspecific interference between this species and winterfat. Seeds germinated, emerged, and established in the pure stand of winterfat.

Similar results were found on the ecotone. Seedlings of winterfat and shadscale emerged and established themselves independent of interspecific interference. Intraspecific interference could be of the same magnitude as the competition produced by other shrubby species.

The chances of germination of seeds on soils from the five different stands were compared and the results indicate that seeds of the two species would have similar chances of germination in all the locations. Besides this, the growth of seedlings in soils from all five stands also indicates that they could develop as well or even better than in the soils associated with their own stands.

All the data presented here lead to one conclusion. Seedlings of these two species were not found because the chances of actually having seeds present in other stands is too low. Despite this, there is some chance of establishment. The few isolated shrubs of shadscale on the pure stand of winterfat are a result of this. For the other species such as big sagebrush, the chances of dissemination are somewhat greater and thus a larger number of plants or groups of plants are found.

An average of 6142 and 2588 fruits of winterfat and shadscale per ten square meters were produced during the 1967 season. Of these only 981 and 566 produced sound seed. During the following growing season 29.7 and 18.1 seedlings per ten square meters emerged but 6.2 and 5.8 respectively remained alive at the end of the season. If the average cohort shrinkage calculated from previous data were used, at the end of the third year only 1.5 seedlings of winterfat and 1.1 of shadscale would be alive.

It is now easy to understand why the immigration rate (m) is so important in all these areas where adult plants of the species are not present. For each 4093 fruits of winterfat migrated only 4 will remain alive at the end of the first year and one at the end of the third year. For each shadscale seedling alive at the end of the third year, 2353 fruits have to migrate to the area and only around 5.3 seedlings would be alive at the end of the first growing season.

Dissemination and migration are the limiting factors and are the reasons why there are not more seedlings of winterfat or shadscale in the pure stands of other species. The chances of dissemination and migration of disseminules decreases as the distance increases. Thus the influence of a pure stand on a nearby stand is mostly in the ecotone or alterne. Beyond these areas chances of dissemination of seeds is very low and thus the probability of producing new seedlings of the other species is negligible.

The few individuals of these two species which descend from immigratory disseminules were established despite the low chances of success. However, under the natural conditions of the environment, the physical, chemical, and biological factors influence the intruding individual or cluster in such a way that the rate of population growth of the invader is less than zero. Thus, after a few months or years the invader population disappears and the stand becomes pure again.

This process is continually occurring on all the pure stands because of the environmental variability and the short distance between stands. Thus chances of dissemination of one species to other stands are low. A few disseminules migrate and establish in the new location, but since the birth rate plus the immigration rate in the new habitat is less than the mortality rate plus emigration, the invader has to finally disappear.

In conclusion, the pure stands of winterfat and shadscale, as well as those of the other species remain there because:

$$(\text{birth rate} + \text{immigration}) - (\text{death rate} + \text{emigration rate}) = 0$$

Thus when a population already present has a value of $r = 0$, there is equilibrium and it does not change. The invader population can survive for short periods of time because of migration of seeds from other nearby stands and because the individual organisms are physiologically capable of surviving in the environment where the other population is in equilibrium. However, since they are unable to indefinitely maintain a value of r equal or greater than zero, they eventually have to disappear.

The results presented in other papers and reviewed for this research seem to indicate that migration and dissemination have not been considered. The relations between environmental factors and their magnitudes actually determine where a population lives. This relation is valid only if $m = 0$. Under these circumstances r is a consequence of only b and d, and the environmental characteristics are solely responsible for the rate of population growth.

In Curlew Valley where the vegetation is composed by such a mosaic of small areas of pure and mixed stands of different species, it is expected that m has to be large. When this occurs the location of the stand is not a consequence of the environment where it lives, but also of proximity from the nearby stands. The location of the ecotones or alternes between stands is not necessarily an indication that the environment at that very same point changes from a value of zero in one side where the population successfully lives to a negative value on the other side of this transition. The actual environmental alterne does not have to be congruent with the vegetational alterne nor of the same shape. They could acutally be located several meters or hectometers apart.

SUMMARY AND CONCLUSIONS

Winterfat produced the most fruits and seeds per plant and per unit area when growing in the mixed, grazed stand of *A. confertifolia-E. lanata* and the least on the ungrazed, pure stand. Seed production differences between the grazed and ungrazed stands of pure winterfat were less than that for the mixed stand. The differences in seed production of shadscale due to grazing were small in comparison with those observed for winterfat.

Seed production results were highly variable. The main factors found to influence seed production were utilization, density, and weather variations from year to year. *A. confertifolia* showed a lower variability than *E. lanata* in relation to these factors. *E. lanata* produced less fruits and seeds during 1968 than during the previous year, but kept the same basic relationships between stands.

The differences in seed viability due to salinity, soil moisture matric potential, seed source, and temperature were proportionally less under the range of magnitude where the species grow naturally, than in the germination studies. Thus the production of viable seeds is not a limiting factor in the distribution of these species.

Under the uniform climatic conditions in the growth chamber where the germination studies were conducted, it was demonstrated that seeds germinated in all the soils tested. The limits of germination tolerance for both species are much broader than the actual magnitude of the edaphic factors where they naturally occur.

E. lanata and A. confertifolia seeds did not germinate best in the soils where they naturally occur. Germination site was more important than edaphic specificity. The differences between buried or non-buried seeds as well as surface and deeper soil samples were greater than the differences between stands.

Seedling growth in pots with different soils showed that the nature of the substrate has important influences in seedling development. Both species were directly affected in their growth when different soils were used. If the plant is used as the best indicator of the integrated effect of the environment acting holocoenotically upon it, the soil alone would not be the cause of the restricted distribution of the species in the salt desert shrub vegetation type. The soil itself would permit a much broader distribution of both species.

The results of the study on seedling growth and production under natural conditions showed that the conditions for seed germination and emergence were favorable only during the first part of the growing season. However, seedling mortality is high during the first part of the growing season.

The pure stand of shadscale and the mixed stand of the two species showed the most unfavorable conditions for seedling production and survival. Two striking differences occurred between the grazed and ungrazed areas. The maximum density of seedlings was greater on the grazed area than in the ungrazed area. The other difference was that the proportion of reduction of density throughout the growing season was greater for the excluded area.

The results obtained in this study indicate that interspecific interference in the mixed stand between the annuals and the seedlings of shrubby species was mainly responsible for the density reduction of the perennials.

The 1966 season was characterized by a fair production of winterfat and shadscale seedlings. The following season was a bad one for winterfat and better for shadscale, while 1968 was excellent for Eurotia lanata seedling production, but very poor for Atriplex confertifolia. The latter year was the only season when seedlings of Artemisia tridentata were recorded.

Those microhabitats where there is a greater density of litter cover show the greatest chance for seedling emergence. However, despite the fact that the real cause of this difference was not determined,it seemed that one of the most important factors is the heterogeneous distribution of seeds in the stand. The seedlings surviving the longest were larger than those dying younger. The size expression of differential mortality appeared early in the season.

Variation of seedling density indicates that the cohort shrinkage of seedlings from the third to the fifth year is minimal or absent. The largest shrinkage in density occurs during the first growing season. During the second season, the rate of mortality of the surviving population was slightly reduced. From the third season on, the reduction was even less. The growth of the seedlings at this time was mostly a function of the availability of environmental resources as well as the competitive abilities of the seedlings. Age was not the primary factor.

Most of the growth and development of the vegetation occurred when the soil moisture matric potential was very low, usually below the permanent wilting percentage or near it. Soil moisture recharge occurred mainly during the coldest part of the year from December to March. During the latter part of March and through April, moisture conditions in the soil were the best. However, temperatures were still too low for optimum plant growth.

Moisture losses from the soil were minimum at the 90 to 150 cm depths. At these depths the moisture content did not vary much throughout the year, and often the matric potential was greater than in the surface soil. The pure stand of winterfat had a matric potential value at the 150 cm depth almost as high as the field capacity during most of the year, even late in the season when the plants became dormant. The greatest variability in soil moisture content throughout the year occurred within the upper 30 cm of soil and decreased at the 60 and 90 cm and deeper levels.

Moisture relations apparently have a greater influence on adult plants than seedlings. Seedling production was mostly a function of viable seed availability and germination sites. Early in the growing season, if there were enough viable seeds, germination was good. Seed availability is the most important factor controlling seedling production, and moisture is directly related to seed production.

The hypothesis developed to explain the distribution of these two species on the area studied is as follows: From an edaphic and climatological point of view, all the evidence reported in this research as well as that previously provided by other authors on this subject indicates that Atriplex confertifolia and Eurotia lanata are physiologically capable of living under the physical environments of other species or ecotypes living in nearby stands. Their range of physiological tolerance is broader than the magnitude of the actual environmental factors found on the area where they are present.

This study has demonstrated that winterfat and shadscale can successfully germinate, grow, and reproduce on soils where other plant communities naturally grow, and these species are completely absent. The most likely explanation for the lack of success is the Law of Limiting Factors at the population level, as enunciated here. It is as follows: Each physical, chemical or biological environmental factor beginning with a lower limit (minimum) of less than zero increases the rate of population growth with each increment of intensity or amount up to a certain optimum value, from which point however, with further increase of the active factor (maximum) the rate of population growth steadily diminishes until it finally becomes less than zero. Thus, if any environmental factor acting independently or holocoenotically is responsible for influencing a rate of population growth of zero or less at its maximum possible value which could naturally occur in the environment, the population would be absent from the area. Only occasional individuals can be found due to chance migration of disseminules from nearby areas.

The results and conclusions reached in this study were obtained only from a limited number of years and one study area, Curlew Valley. The conclusions reached here fit these data and study period. However, under different environmental conditions, in different places or years, the results could be different.

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APPENDIX

Table 13. Mean monthly absolute maximum and absolute minimum precipitation for the period 1956-1965, in Curlew Valley (Fears, 1966). The mean monthly precipitation for the last years is from Cook and Stoddart (1966, 1967).

Month	Precipitation in mm					
	1956 - 1965			Monthly		
	Mean	Absolute Maximum	Absolute Minimum	1966	1967	1968
January	17.7	46.0	0.0	1.5	13.7	12.4
February	16.3	34.2	4.7	11.0	9.7	20.6
March	16.5	36.0	4.5	7.0	31.7	15.1
April	20.0	53.7	0.0	2.7	34.5	12.4
May	41.0	100.0	3.2	22.0	27.7	33.0
June	21.2	62.0	2.0	13.7	114.7	41.2
Junly	11.7	30.0	0.0	1.5	45.5	8.2
August	21.0	76.7	0.0	9.7	1.5	88.0
September	15.5	48.7	0.0	9.7	1.2	16.5
October	13.0	26.7	0.5	0.0	2.7	13.7
November	19.7	65.5	0.0	22.0	1.5	8.2
December	16.5	42.0	0.0	13.7	16.5	31.5
Yearly values	230.2	311.0	168.0	114.5	300.9	300.8

Table 14. Mean monthly temperatures for the period 1956-1965 in Curlew Valley (Fears, 1966), and mean monthly temperature of the years 1967 and 1968.

	Temperature in ° C				
Month	1956 - 1965			Mean monthly	
	Mean	Maximum	Minimum	1967	1968
January	- 5.1	1.5	-11.8	-----	- 6.2
February	- 1.7	4.0	- 7.4	-----	0.3
March	1.4	7.9	- 5.1	-----	3.7
April	6.8	14.1	- 0.7	5.2	4.7
May	11.8	20.0	3.6	13.1	10.8
June	16.7	25.7	7.6	15.6	17.0
July	21.5	31.4	11.6	24.7	23.9
August	20.2	30.2	10.3	25.4	19.9
September	14.8	24.2	5.2	18.0	13.9
October	9.3	18.5	0.3	8.7	-----
November	1.3	8.1	- 5.4	3.2	-----
December	- 3.0	2.9	9.1	- 5.6	-----
Yearly values	7.8	15.8	- 0.1	-----	-----

Table 15. Hypothetical calculations of the number of viable seeds of E. lanata produced per ten square meters. The values were calculated by using the germination percentages obtained by Workman and West (1967), and the actual values of seed production in this study during the 1967 season. The actual number of seeds produced are 898 for the grazed stand, 491 for the exclosure, and 1554 for the mixed stand.

Seed Source	Concentration of NaCl %	Temperture	% Germination	Viable Seeds in Stand		
				Grazed	Exclosure	Mixed
La Sal	0.0	Low	98	880	481	1522
	0.5	Low	93	835	456	1445
	1.0	Low	94	844	461	1461
	2.0	Low	47	422	231	730
	3.0	Low	5	45	25	78
	4.0	Low	0	0	0	0
La Sal	0.0	High	99	889	486	1538
	0.5	High	97	871	476	1507
	1.0	High	82	736	402	1274
	2.0	High	34	305	167	528
	3.0	High	5	45	25	78
	4.0	High	1	9	5	16
Cisco	0.0	Low	96	862	471	1492
	0.5	Low	79	709	388	1228
	1.0	Low	40	359	196	622
	2.0	Low	42	377	206	653
	3.0	Low	2	18	10	31
	4.0	Low	0	0	0	0
Cisco	0.0	High	100	898	491	1554
	0.5	High	88	790	432	1368
	1.0	High	57	512	280	886
	2.0	High	20	180	98	311
	3.0	High	6	54	29	93
	4.0	High	2	18	10	31

Table 16. Hypothetical calculations of the number of viable seeds of *E. lanata* produced per ten square meters. The values were calculated by using the germination percentages obtained by Springfield (1968) and the actual values of seed production from this study during the 1967 season. The actual number of seeds produced are 898 for the grazed stand, 491 for the exclosure, and 1554 for the mixed stand.

Seed Source	Germination Temperature °F	Moisture Stress At.	Germination %	Viable Seeds in Stand		
				Grazed	Exclosure	Mixed
Horse Springs	86-68	0.0	89	799	437	1383
		0.3	90	808	442	1398
		3.0	88	790	432	1368
		7.0	51	458	250	793
		15.0	11	99	54	171
	53	0.0	90	808	442	1399
		0.3	94	844	461	1461
		3.0	83	745	408	1290
		7.0	83	745	408	1290
		15.0	43	386	211	668
	37	0.0	80	718	393	1243
		0.3	81	727	398	1259
		3.0	71	637	349	1103
		7.0	67	602	329	1041
		15.0	32	287	157	497
Corona	86-68	0.0	84	754	412	1305
		0.3	67	602	329	1041
		3.0	57	512	280	886
		7.0	37	332	182	575
		15.0	5	45	25	78
	53	0.0	81	727	398	1259
		0.3	79	709	388	1228
		3.0	79	709	388	1228
		7.0	67	602	329	1041
		15.0	29	260	142	451
	37	0.0	80	718	393	1243
		0.3	80	718	392	1243
		3.0	76	682	373	1181
		7.0	61	548	299	948
		15.0	29	260	142	451

Table 17. Hypothetical calculations of the number of viable seeds of A. confertifolia produced per ten square meters. The values were calculated by using the germination percentages obtained by Vest (1952) and the actual values of seed production from this study during the 1967 season. The actual number of seeds produced are 350 for the grazed stand, 317 for the exclosure and 317 for the mixed stand.

Extract of	Part	Date	Percent	Viable Seeds in Stand		
Bracteoles	Used	Gathered	Germination	Grazed	Exclusion	Mixed
	Whole fruit	Dec. 1 to April 15	0	0	0	0
	Excised Seeds	Dec. 1	20	70	63	206
		Dec.16	15	52	47	155
		Jan. 2	10	35	32	103
		Jan.17	10	35	32	103
		Feb. 1	5	17	16	52
		Feb.16	5	17	16	52
		Mar. 1	2.5	9	8	26
		Mar.15	5	17	16	52
		Apr. 1	15	52	47	155
		Apr.15	30	105	95	310
Full strength	Excised Seeds		0	0	0	0
1:3			0	0	0	0
1:5			Died off	0	0	0
1:10			45	157	143	464
1:20			65	227	206	671
Distilled water			75	262	237	774

Table 18. Mean percentage of emergence of *A. confertifolia* seeded in pots under growth chamber conditions. The soil samples were taken from Curlew Valley from areas where natural communities of *A. confertifolia*, *E. lanata*, *A. nuttallii*, *A. tridentata* and the mixed stand naturally grow. Soil samples were taken from the upper 0 to 2.5 cm and from 2.5 to 25 cm depths.

Source of Substrate		Days After Seeded					
Stand	Depth	4	6	8	10	12	15
Peat Moss		2	16	19	20	20	20
Filter Paper (Petri dish)		7	8	12	15	21	23
E. lanata	0-2.5	1	6	10	12	15	15
E. lanata	2.5-25	0	2	2	3	3	3
A. confertifolia	0-2.5	0	4	6	6	9	10
A. confertifolia	2.5-25	0	3	4	5	6	7
A. tridentata	0-2.5	0	4	7	9	10	13
A. tridentata	2.5-25	0	1	5	6	6	7
A. nuttallii	0-2.5	1	5	7	9	9	10
A. nuttallii	2.5-25	0	1	1	1	1	2
Mixed	0-2.5	0	4	7	11	13	14
Mixed	2.5-25	0	3	4	6	6	6

Table 19. Results of the soil analysis conducted on the soils used for the seedling growth and germination studies.

Source of Soil		CEC me/100g	O.D. Organic Carbon %	Texture			Total Nitrogen mg/g	pH	Total Salinity
Stand	Depth(cm)			Clay %	Silt %	Sand %			
E. lanata	0-2.5	13.7	1.35	24	49	27	1.47	7.8	0.07
E. lanata	2.5-25	13.5	0.75	30	46	24	1.03	8.1	0.04
A. confertifolia	0-2.5	16.7	2.02	31	57	12	1.75	8.0	0.08
A. confertifolia	2.5-25	19.3	0.94	42	47	11	1.01	8.0	0.15
A. tridentata	0-2.5	13.8	1.02	19	41	40	1.24	7.8	0.04
A. tridentata	2.5-25	12.9	0.55	24	42	34	0.72	8.0	0.03
A. nuttallii	0-2.5	13.8	0.88	29	49	22	1.17	7.8	0.08
A. nuttallii	2.5-25	13.7	0.71	21	52	27	0.77	8.1	0.04
Mixed	0-2.5	14.3	1.14	19	41	40	1.30	7.8	0.08
Mixed	2.5-25	14.2	0.55	26	36	38	1.20	8.0	0.04

Table 20. Mean percentage germination of A. confertifolia seeded in petri dishes, on the surface of several substrates under growth chamber conditions. There was a 13-hour light period with 15 C and an 11-hour dark period with 4.5 C, with no control of relative humidity.

Source of Substrate		Days After Seeding			
Stand	Depth (cm)	3	5	7	10
Peat Moss		10	24	29	34
Filter Paper		3	9	11	14
E. lanata	0-2.5	4	7	9	13
E. lanata	2.5-25	7	12	14	17
A. confertifolia	0-2.5	6	10	12	19
A. confertifolia	2.5-25	4	9	11	15
A. tridentata	0-2.5	5	10	19	24
A. tridentata	2.5-25	14	18	20	21
A. nuttallii	0-2.5	8	14	18	22
A. nuttallii	2.5-25	4	10	13	14
Mixed	0-2.5	4	14	18	25
Mixed	2.5-25	7	12	13	16

Table 21. Mean percentage germination of *E. lanata* seeded in petri dishes on the surface of several substrates, under growth chamber conditions. There was a 13-hour light period with 15 C and an 11-hour dark period with 4.5 C, with no control of relative humidity.

Source of Substrate		Days After Seeded		
Stand	Depth (cm)	3	6	10
Peat Moss		23	33	36
E. lanata	0-2.5	21	35	39
E. lanata	2.5-25	28	36	40
A. confertifolia	0-2.5	24	40	43
A. confertifolia	2.5-25	21	28	31
A. tridentata	0-2.5	16	31	35
A. tridentata	2.5-25	15	35	39
A. nuttallii	0-2.5	16	35	35
A. nuttallii	2.5-25	24	41	43
Mixed	0-2.5	23	32	32
Mixed	2.5-25	16	27	28

Table 22. Growth of *Atriplex confertifolia* in pots in the growth chamber and greenhouse in soil from Curlew Valley. Soils were taken at two different depths from areas where five different plant communities naturally grow.

Source of Soil		Height (cm)		Leaves/plant		Weight (g)
Stand	Depth (cm)	30 days	50 days	30 days	50 days	75 days
E. lanata	0-2.5	6.1	8.3	37	70	0.334
E. lanata	2.5-25	6.2	8.7	23	45	0.191
A. confertifolia	0-2.5	6.6	8.5	28	65	0.336
A. confertifolia	2.5-25	6.9	8.6	22	45	0.167
A. tridentata	0-2.5	7.1	10.0	30	61	0.336
A. tridentata	2.5-25	6.2	7.9	20	32	0.136
A. nuttallii	0-2.5	5.2	7.1	17	49	0.206
A. nuttallii	2.5-25	5.7	6.9	21	35	0.131
Mixed	0-2.5	6.3	9.0	23	51	0.248
Mixed	2.5-25	4.8	7.6	19	21	0.083

Table 23. Growth of *Eurotia lanata* in pots in the growth chamber and greenhouse in soil from Curlew Valley. Soils were taken at two different depths from areas where five different plant communities naturally grow.

Source of Soil		Height (cm)			Leaves/plant			Weight (g)
Stand	Depth (cm)	40 days	70 days	110 days	40 days	70 days	110 days	110 days
E. lanata	0-2.5	6.0	13.3	18.1	5	14	22	0.125
E. lanata	2.5-25	4.2	9.6	12.0	3	9	14	0.050
A. confertifolia	0-2.5	4.3	11.5	16.2	4	13	21	0.109
A. confertifolia	2.5-25	3.4	7.4	9.7	3	9	13	0.035
A. tridentata	0-2.5	4.3	12.2	16.9	4	12	20	0.098
A. tridentata	2.5-25	3.7	8.0	9.5	3	8	10	0.024
A. nuttallii	0-2.5	4.1	11.7	16.4	4	13	20	0.127
A. nuttallii	2.5-25	3.5	7.6	9.5	3	7	11	0.029
Mixed	0-2.5	3.9	11.3	15.4	4	12	18	0.091
Mixed	2.5-25	3.5	8.2	10.0	3	8	12	0.034

Table 24. Growth of *Eurotia lanata* in pots in the greenhouse in soils from Curlew Valley. Soils were taken at two different depths from areas where different plant communities naturally grow.

Source of Soil		Height (cm)		Stems Length	Leaves/ Plant	Plants in Flower	Weight
Stand	Depth (cm)	80 days (cm)	125 days (cm)	125 days (cm)	80 days	125 days %	125 days (g)
E. lanata	0-2.5	23.4	48.9	81.3	64.5	50	1.701
E. lanata	2.5-25	13.9	34.5	35.0	32.3	0	0.847
A. confertifolia	0-2.5	18.3	48.2	77.5	46.8	33	1.586
A. confertifolia	2.5-25	11.6	33.9	34.0	26.2	0	0.581
A. tridentata	0-2.5	26.3	53.2	85.2	68.5	50	1.910
A. tridentata	2.5-25	5.8	13.2	13.2	14.8	0	0.195
A. nuttallii	0-2.5	25.0	45.2	79.5	72.8	67	1.670
A. nuttallii	2.5-25	7.1	9.2	9.2	18.0	0	0.112
Mixed	0-2.5	25.8	49.7	63.5	65.8	83	1.447
Mixed	2.5-25	8.9	19.3	19.3	22.8	0	0.307

Table 25. Number of newly emerged seedlings of *E. lanata* and *A. confertifolia* per ten square meters in all locations at several dates during the 1966 season.

Stand and treatment	April			May			June					August
	4	23	30	7	14	21	1	9	15	23	28	19
Ungrazed *E. lanata*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Grazed *E. lanata*	0.0	4.0	2.7	0.0	0.0	2.7	0.0	0.0	0.0	0.0	0.0	0.0
Ungrazed ecotone	29.3	10.7	5.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Grazed ecotone	12.0	33.3	54.6	1.3	0.0	6.7	0.0	0.0	0.0	0.0	0.0	0.0
Mixed	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Grazed *A. confertifolia*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Inside exclosure	14.6	5.3	2.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Outside exclosure	6.0	18.6	28.6	0.6	0.7	4.7	0.0	0.0	0.0	0.0	0.0	0.0
Mean all stands	6.9	8.0	10.4	0.2	0.0	1.6	0.0	0.0	0.0	0.0	0.0	0.0

Table 26. Accumulative number of *E. lanata* and *A. confertifolia* seedlings emerged per ten square meters in all stands at several dates during the 1966 season.

Stand and treatment	April			May			June					August
	4	23	30	7	14	21	1	9	15	23	28	19
Ungrazed *E. lanata*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Grazed *E. lanata*	0.0	4.0	6.7	6.7	6.7	9.4	9.4	9.4	9.4	9.4	9.4	9.4
Ungrazed ecotone	29.3	40.0	45.3	45.3	45.3	45.3	45.3	45.3	45.3	45.3	45.3	45.3
Grazed ecotone	12.0	45.3	99.9	101.2	101.2	107.9	107.9	107.9	107.9	107.9	107.9	107.9
Mixed	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Grazed *A. confertifolia*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Inside exclosure	14.6	20.0	22.6	22.6	22.6	22.6	22.6	22.6	22.6	22.6	22.6	22.6
Outside exclosure	6.0	24.6	53.3	53.9	53.9	58.6	58.6	58.6	58.6	58.6	58.6	58.6
Mean all stands	6.9	14.9	25.3	25.5	25.5	27.1	27.1	27.1	27.1	27.1	27.1	27.1

Table 27. Number of *E. lanata* and *A. confertifolia* seedlings dead per ten square meters in all stands at several dates during the 1966 season.

Stand and treatment	April			May			June					August
	4	23	30	7	14	21	1	9	15	23	28	19
Ungrazed *E. lanata*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Grazed *E. lanata*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	1.3	0.0
Ungrazed ecotone	0.0	0.0	0.0	0.0	0.0	13.3	2.7	8.0	0.0	2.7	2.7	2.7
Grazed ecotone	0.0	0.0	1.3	0.0	0.0	14.6	0.0	9.3	4.0	0.0	1.3	9.3
Mixed	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Grazed *A. confertifolia*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Inside exclosure	0.0	0.0	0.0	0.0	0.0	6.6	1.3	4.0	0.0	1.3	1.3	1.3
Outside exclosure	0.0	0.0	0.6	0.0	0.0	7.3	0.0	4.6	2.0	0.6	1.3	4.6
Mean all stands	0.0	0.0	0.2	0.0	0.0	4.6	0.4	2.9	0.7	0.7	0.9	2.0

Table 28. Accumulative number of *E. lanata* and *A. confertifolia* seedlings dead per ten square meters in all stands and dates during the 1966 season.

Stand and treatment	April			May			June					August
	4	23	30	7	14	21	1	9	15	23	28	19
Ungrazed *E. lanata*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Grazed *E. lanata*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	2.6	2.6
Ungrazed ecotone	0.0	0.0	0.0	0.0	0.0	13.3	16.0	24.0	24.0	26.7	29.4	32.1
Grazed ecotone	0.0	0.0	1.3	1.3	1.3	15.9	15.9	25.2	29.2	29.2	30.5	39.8
Mixed	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Grazed *A. confertifolia*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Inside exclosure	0.0	0.0	0.0	0.0	0.0	6.6	8.0	12.0	12.0	13.3	14.7	16.0
Outside exclosure	0.0	0.0	0.6	0.6	0.6	7.9	7.9	12.6	14.6	15.2	16.5	21.2
Mean all stands	0.0	0.0	0.2	0.2	0.2	4.9	5.3	8.2	8.9	9.5	10.4	12.4

Table 29. Mean number of E. lanata and A. confertifolia seedlings per ten square meters in all locations at several dates during the 1966 season.

Seedlings	April			May			June					August
	4	23	30	7	14	21	1	9	15	23	28	19
						E. lanata						
Alive	2.4	4.1	5.9	5.9	5.9	5.6	5.6	5.6	5.6	5.6	5.3	4.7
New emerged	2.4	2.1	2.1	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0
Accumulative emerged	2.4	4.4	6.5	6.5	6.5	7.7	7.7	7.7	7.7	7.7	7.7	7.7
Dead	0.0	0.3	0.3	0.0	0.0	1.5	0.0	0.0	0.0	0.0	0.3	0.6
Accumulative dead	0.0	0.3	0.3	0.6	0.6	2.1	2.1	2.1	2.1	2.1	2.4	3.0
						A. confertifolia						
Alive	6.4	13.9	23.0	23.5	23.5	17.6	17.1	11.7	10.1	9.6	8.5	5.3
New emerged	6.4	7.5	9.6	0.5	0.0	1.6	0.0	0.0	0.0	0.0	0.0	0.0
Accumulative emerged	6.4	13.9	23.5	24.0	24.0	24.0	25.6	25.6	25.6	25.6	25.6	25.6
Dead	0.0	0.0	0.5	0.0	0.0	7.5	0.5	5.4	1.6	0.5	1.1	3.2
Accumulative dead	0.0	0.0	0.5	0.5	0.5	8.0	8.5	13.9	15.5	16.0	17.1	20.3

Table 30. Number of newly emerged seedlings of *E. lanata* and *A. confertifolia* per ten square meters in all stands at several dates during the 1967 season.

Stand and treatment	March	April			May				June		July	August
	25	7	15	22	3	10	17	24	5	21	19	18
Ungrazed *E. lanata*	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Grazed *E. lanata*	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ungrazed ecotone	0.0	8.0	0.0	0.0	8.0	0.0	0.0	5.3	0.0	0.0	0.0	0.0
Grazed ecotone	0.0	2.7	0.0	0.0	5.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mixed	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Grazed *A. confertifolia*	0.0	0.0	0.0	0.0	0.0	26.7	0.0	0.0	0.0	0.0	0.0	0.0
Inside exclosure	0.0	4.0	0.0	0.0	4.4	0.0	0.0	2.7	0.0	0.0	0.0	0.0
Outside exclosure	0.0	1.3	0.0	0.6	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mean all stands	0.0	1.8	0.0	0.2	2.4	4.4	0.0	0.9	0.0	0.0	0.0	0.0

Table 31. Accumulative number of *E. lanata* and *A. confertifolia* seedlings emerged per ten square meters in all stands at several dates during the 1967 season.

Stand and treatment	March	April			May				June		July	August
	25	7	15	22	3	10	17	24	5	21	19	18
Ungrazed *E. lanata*	0.0	0.0	0.0	0.0	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9
Grazed *E. lanata*	0.0	0.0	0.0	1.3	1.3	1.3	1.3	1.3	1.3	1.3	1.3	1.3
Ungrazed ecotone	0.0	8.0	8.0	8.0	16.0	16.0	16.0	21.3	21.3	21.3	21.3	21.3
Grazed ecotone	0.0	2.7	2.7	2.7	8.0	8.0	8.0	8.0	8.0	8.0	8.0	8.0
Mixed	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Grazed *A. confertifolia*	0.0	0.0	0.0	0.0	0.0	26.7	26.7	26.7	26.7	26.7	26.7	26.7
Inside exclosure	0.0	4.0	4.0	4.0	8.4	8.4	8.4	11.1	11.1	11.1	11.1	11.1
Outside exclosure	0.0	1.3	1.3	2.0	4.6	4.6	4.6	4.6	4.6	4.6	4.6	4.6
Mean all stands	0.0	1.8	1.8	2.0	4.4	8.8	8.8	9.7	9.7	9.7	9.7	9.7

Table 32. Number of *E. lanata* and *A. confertifolia* seedlings dead per ten square meters in all stands at several dates during the 1967 season.

Stand and treatment	March	April			May				June		July	August
	25	7	15	22	3	10	17	24	5	21	19	18
Ungrazed *E. lanata*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Grazed *E. lanata*	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ungrazed ecotone	0.0	0.0	0.0	8.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.7
Grazed ecotone	0.0	0.0	0.0	2.7	0.0	0.0	0.0	1.3	0.0	0.0	1.3	0.0
Mixed	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Grazed *A. confertifolia*	0.0	0.0	0.0	0.0	0.0	0.0	16.0	0.0	0.0	2.7	2.7	0.0
Inside exclosure	0.0	0.0	0.0	4.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3
Outside exclosure	0.0	0.0	0.0	1.3	0.6	0.0	0.0	0.6	0.0	0.0	0.6	0.0
Mean all stands	0.0	0.0	0.0	1.8	0.2	0.0	2.7	0.2	0.0	0.4	0.7	0.4

Table 33. Accumulative number of *E. lanata* and *A. confertifolia* seedlings dead per ten square meters in all stands and dates during the 1967 season.

Stand and treatment	March	April			May				June		July	August
	25	7	15	22	3	10	17	24	5	21	19	18
Ungrazed *E. lanata*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Grazed *E. lanata*	0.0	0.0	0.0	0.0	1.3	1.3	1.3	1.3	1.3	1.3	1.3	1.3
Ungrazed ecotone	0.0	0.0	0.0	8.0	8.0	8.0	8.0	8.0	8.0	8.0	8.0	10.7
Grazed ecotone	0.0	0.0	0.0	2.7	2.7	2.7	2.7	4.0	4.0	4.0	5.3	5.3
Mixed	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Grazed *A. confertifolia*	0.0	0.0	0.0	0.0	0.0	0.0	16.0	16.0	16.0	18.7	21.4	21.4
Inside exclosure	0.0	0.0	0.0	4.0	4.0	4.0	4.0	4.0	4.0	4.0	4.0	5.3
Outside exclosure	0.0	0.0	0.0	1.3	2.0	2.0	2.0	2.6	2.6	2.6	3.3	3.3
Mean all stands	0.0	0.0	0.0	1.8	2.0	2.0	4.7	4.9	4.9	5.3	6.0	6.0

Table 34. Mean number of *E. lanata* and *A. confertifolia* seedlings per ten square meters in all stands at several dates during the 1967 season.

Seedlings	March	April			May				June		July	August
	25	7	15	22	3	10	17	24	5	21	19	18
					E. lanata							
Alive	0.0	0.0	0.0	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8
New emerged	0.0	0.0	0.0	0.8	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Accumulative emerged	0.0	0.0	0.0	0.8	1.6	1.6	1.6	1.6	1.6	1.6	1.6	1.6
Dead	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Accumulative dead	0.0	0.0	0.0	0.0	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8
					A. confertifolia							
Alive	0.0	5.9	5.9	0.0	8,3	19.0	15.4	14.2	14.2	13.0	12.5	12.0
New emerged	0.0	5.9	0.0	0.0	8.3	10.7	2.3	0.0	0.0	0.0	0.0	0.0
Accumulative emerged	0.0	5.9	5.9	5.9	14.2	24.9	27.2	27.2	27.2	27.2	27.2	27.2
Dead	0.0	0.0	0.0	5.9	0.0	0.0	5.9	1.2	0.0	1.2	0.5	0.5
Accumulative dead	0.0	0.0	0.0	5.9	5.9	5.9	11.8	13.0	13.0	14.2	14.7	15.2

Table 35. Number of newly emerged seedlings of _Eurotia lanata_, _Atriplex confertifolia_, and _Artemisia tridentata_ per ten square meters in all stands at several dates during the 1968 season.

Stand and treatment	March		April				May		June	July	August	Sept
	19	30	6	13	20	28	11	25	29	26	29	24
Ungrazed _E. lanata_	53.3	14.2	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Grazed _E. lanata_	70.7	20.0	0.0	0.0	13.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ungrazed ecotone	63.9	5.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Grazed ecotone	118.7	17.3	0.0	5.3	4.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mixed	40.0	7.1	5.3	1.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Grazed _A. confertifolia_	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Inside exclosure	58.6	9.7	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Outside exclosure	94.7	18.6	0.-	2.6	8.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mean all stands	57.7	10.6	0.9	1.3	2.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table 36. Accumulative number of *Eurotia lanata*, *Atriplex confertifolia*, and *Artemisia tridentata* seedlings emerged per ten square meters in all stands at several dates during the 1968 season.

Stand and treatment	March		April				May		June	July	August	Sept
	19	30	6	13	20	28	11	25	29	26	29	24
Ungrazed *E. lanata*	53.3	62.2	62.2	63.1	63.1	63.1	63.1	63.1	63.1	63.1	63.1	63.1
Grazed *E. lanata*	70.7	90.6	90.6	90.6	104.0	104.0	104.0	104.0	104.0	104.0	104.0	104.0
Ungrazed ecotone	69.3	74.3	74.3	74.3	74.3	74.3	74.3	74.3	74.3	74.3	74.3	74.3
Grazed ecotone	118.7	136.0	136.0	141.3	145.3	145.3	145.3	145.3	145.3	145.3	145.3	145.3
Mixed	40.0	47.1	52.4	54.2	54.2	54.2	54.2	54.2	54.2	54.2	54.2	54.2
Grazed *A. confertifolia*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Inside exclosure	61.3	68.4	68.4	68.7	68.7	68.7	68.7	68.7	68.7	68.7	68.7	68.7
Outside exclosure	94.7	113.3	113.3	115.9	124.6	124.6	124.6	124.6	124.6	124.6	124.6	124.6
Mean all stands	58.7	68.4	69.2	70.6	73.5	73.5	73.5	73.5	73.5	73.5	73.5	73.5

Table 37. Number of *Eurotia lanata*, *Atriplex confertifolia*, and *Artemisia tridentata* seedlings dead per ten square meters in all stands at several dates during the 1968 season.

Stand and treatment	March		April				May				June	
	19	30	6	13	20	28	4	11	19	25	13	29
Ungrazed *E. lanata*	0.0	20.4	22.2	2.7	2.7	2.7	4.4	0.0	0.9	0.0	0.9	0.0
Grazed *E. lanata*	0.0	22.6	10.6	10.6	2.6	1.3	5.3	2.6	1.3	0.0	0.0	2.6
Ungrazed ecotone	0.0	24.0	18.7	2.7	2.7	2.7	0.0	2.7	0.0	2.7	0.0	0.0
Grazed ecotone	0.0	17.3	2.6	9.3	17.3	9.3	10.7	5.3	1.3	0.0	5.3	4.0
Mixed	0.0	14.2	2.7	2.7	1.8	2.9	4.4	0.0	0.0	0.0	0.0	6.2
Grazed *A. confertifolia*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Inside exclosure	0.0	22.2	20.4	2.7	2.7	2.7	2.2	1.3	0.4	1.3	0.4	0.0
Outside exclosure	0.0	19.9	6.6	9.9	9.9	5.3	8.0	3.9	1.3	0.0	2.6	3.3
Mean all stands	0.0	16.4	9.5	2.8	4.5	3.1	4.1	1.8	0.6	4.5	1.0	2.1

Table 37. Continued

Stand and treatment	July	August		Sept
	26	7	29	24
Ungrazed *E. lanata*	3.5	0.9	4.4	0.0
Grazed *E. lanata*	6.6	2.6	12.0	0.0
Ungrazed ecotone	10.7	0.0	5.3	0.0
Grazed ecotone	10.7	4.0	13.3	1.3
Mixed	9.8	2.7	1.8	0.9
Grazed *A. confertifolia*	0.0	0.0	0.0	0.0
Inside exclosure	7.1	0.4	4.8	0.0
Outside exclosure	8.6	3.3	12.6	0.6
Mean all stands	6.9	1.7	6.1	3.7

Table 38. Accumulative number of *Eurotia lanata*, *Atriplex confertifolia*, and *Artemisia tridentata* seedlings dead per ten square meters in all stands at several dates during the 1968 season.

Stand and treatment	March		April				May		June	July	August	Sept
	19	30	6	13	20	28	11	25	29	26	29	24
Ungrazed *E. lanata*	0.0	20.4	33.8	36.4	39.1	40.9	45.3	46.2	47.1	50.6	56.0	56.0
Grazed *E. lanata*	0.0	22.6	33.3	44.0	46.6	48.0	56.0	57.3	60.0	66.6	81.3	81.3
Ungrazed ecotone	0.0	24.0	42.7	45.3	48.0	50.7	53.3	56.0	56.0	66.7	72.0	72.0
Grazed ecotone	0.0	17.3	20.0	29.3	46.7	56.0	72.0	73.3	82.6	93.3	110.6	112.0
Mixed	0.0	14.2	16.9	19.6	21.4	24.0	28.4	28.4	34.7	44.5	48.9	49.8
Grazed *A. confertifolia*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Inside exclosure	0.0	22.2	38.2	40.8	43.5	45.8	49.3	51.1	51.5	58.6	64.0	64.0
Outside exclosure	0.0	19.9	26.6	36.6	46.6	52.0	64.0	65.3	71.3	79.9	95.9	96.6
Mean all stands	0.0	16.4	24.4	29.1	33.6	36.6	42.5	43.5	46.7	53.6	61.5	61.8

Table 39. Size of seedlings of the shrubby species on September 24, 1968, in Curlew Valley plots.

Species		Season Emerged				
		1964	1965	1966	1967	1968
E. lanata	H	------	3.0	7.4	5.0	1.9
	L	------	95.0	236.0	75.0	17.0
	HL	------	285.0	1746.4	375.0	32.3
A. confertifolia	H	6.0	-----	6.3	2.5	-----
	L	250.0	------	208.0	60.0	-----
	HL	1500.0	------	1310.4	150.0	-----
A. tridentata	H	-------	------	-------	------	1.9
	L	-------	------	-------	------	21.0
	HL	-------	------	-------	------	39.9

H = height (cm)
L = number of leaves
HL= product of height (cm) x number of leaves

Table 40. Moisture percentage by weight and matric potential in Joules per kilogram in the upper 2.5 cm of soil on three stands and at various dates during 1968. The value of -1500 Joules per kilogram means equal or less than that value.

Moisture	March		April			May		June		July	August	Sept
	18	30	6	13	28	4	19	6	20	4	13	17
					E. lanata							
Percentage	15.5	7.0	16.7	5.4	4.0	1.6	6.2	12.7	2.1	2.0	13.3	5.6
Potential	- 60	-1500	- 45	-1500	-1500	-1500	-1500	- 170	-1500	-1500	- 130	-1500
					Mixed							
Percentage	17.4	9.8	15.9	5.5	3.1	1.6	5.8	12.9	1.9	1.8	15.4	6.8
Potential	- 40	- 500	- 66	-1500	-1500	-1500	-1500	-1500	-1500	-1500	- 60	-1500
					A. confertifolia							
Percentage	20.9	12.0	17.6	8.0	4.9	2.8	9.8	16.3	2.9	2.7	20.8	8.4
Potential	- 120	-1500	- 810	-1500	-1500	-1500	-1500	-1500	-1500	-1500	- 430	-1500

Table 41. Moisture percentage by weight and matric potential in Joules per kilogram in the upper 2.5 to 7.5 cm of soil on three stands and at various dates during 1968. The value of -1500 Joules per kilogram means equal or less than that value.

Moisture	March		April			May		June		July	August	Sept
	18	30	6	13	28	4	19	6	20	4	13	17
E. lanata												
Percentage	15.3	12.4	16.3	12.2	9.8	6.7	11.8	12.7	6.4	6.2	13.8	8.8
Potential	- 80	- 190	- 65	- 150	- 680	-1500	- 240	- 190	-1500	-1500	- 110	-1500
Mixed												
Percentage	16.0	11.4	15.3	10.6	8.7	4.2	11.3	12.0	4.1	3.9	13.6	8.6
Potential	- 65	- 110	- 70	- 300	-1500	-1500	- 210	- 160	-1500	-1500	- 100	-1500
A. confertifolia												
Percentage	19.6	14.1	20.4	16.2	12.4	8.0	16.6	17.0	8.7	8.4	18.6	13.1
Potential	- 550	-1500	- 470	-1500	-1500	-1500	-1000	- 900	-1500	-1500	- 560	-1500

Table 42. Mean soil moisture percentage by volume in three stands at several dates during the 1967 season. Measurements were made by the neutron scattering method.

Depth (cm)	April	May			June		July		August		Sept	Nov	Dec
	24	2	16	23	9	23	3	13	7	22	26	4	19
						E. lanata							
30	15.9	15.8	14.1	8.8	9.2	22.4	11.3	8.0	2.5	1.5	1.2	1.0	1.5
60	8.2	8.3	9.0	8.9	8.8	11.3	11.7	11.0	8.0	7.0	6.2	5.7	5.9
90	8.1	8.2	8.4	8.3	8.5	9.0	9.0	9.0	8.8	8.6	8.2	8.2	8.0
120	8.1	8.3	8.6	8.6	8.6	8.8	8.6	8.6	8.4	8.3	8.3	7.9	7.9
150	12.7	13.0	13.7	13.5	13.9	13.4	14.0	13.4	12.9	12.9	12.8	12.3	12.4
						Mixed							
30	16.7	17.2	15.7	11.0	10.0	23.9	11.1	7.0	2.0	1.3	1.2	1.0	1.1
60	9.3	8.6	9.4	10.3	8.9	11.0	12.1	10.1	6.5	6.0	5.7	5.0	5.1
90	6.9	7.1	7.7	7.6	7.5	7.4	7.6	7.8	7.3	7.5	7.8	7.0	7.0
120	7.5	7.6	8.1	8.5	8.0	7.8	9.0	8.5	7.6	7.7	8.2	7.6	7.5
150	8.3	8.7	10.6	10.0	9.0	8.6	14.4	10.6	8.6	8.7	9.0	8.3	8.4
						A. confertifolia							
30	20.0	18.6	18.7	17.7	17.7	34.5	24.0	22.2	12.6	9.5	7.1	6.9	7.2
60	8.2	81.	8.4	8.8	8.7	13.0	17.1	15.6	11.4	10.1	8.3	7.8	8.0
90	10.2	10.4	10.6	11.0	10.4	10.3	10.9	11.5	11.7	11.9	11.7	11.2	10.8
120	13.2	13.1	13.2	14.0	13.3	13.0	13.3	13.3	13.0	13.3	13.3	12.9	12.9
150	14.9	14.5	16.2	15.7	14.9	14.5	15.4	14.7	14.5	14.9	14.6	14.3	14.2

Table 43. Mean soil moisture percentage by volume at three stands at several dates during the 1968 season. Measurements were made by the neutron scattering method.

Depth (cm)	Feb	March	April		May		June		July		Sept		Oct
	24	23	5	19	3	17	5	20	4	26	1	19	9
						E. lanata							
30	10.4	12.3	10.9	10.3	8.1	7.6	5.6	7.6	4.0	3.0	11.4	6.0	5.0
60	6.2	6.8	7.0	7.6	7.6	8.1	7.9	8.6	8.3	7.9	7.4	7.7	7.4
90	8.1	8.2	8.3	8.5	8.4	8.9	8.6	9.1	8.9	8.8	8.4	8.8	8.6
120	8.0	8.2	8.6	8.6	8.6	9.1	8.5	9.1	9.1	8.8	8.3	8.7	8.4
150	12.5	12.6	13.0	13.0	13.4	13.7	13.3	13.7	13.6	13.5	12.7	13.0	12.7
						Mixed							
30	13.7	13.7	12.2	11.0	8.6	8.6	5.5	6.4	3.0	2.1	10.2	4.7	3.3
60	5.4	6.4	7.3	7.2	7.8	7.7	7.4	8.0	6.9	6.2	6.6	6.5	6.3
90	7.1	7.1	7.3	7.2	7.7	7.7	7.6	8.0	7.6	7.3	7.2	7.3	7.0
120	7.5	7.6	7.6	7.7	8.2	8.3	8.0	8.4	8.1	7.8	7.8	7.9	7.6
150	8.5	8.5	8.6	8.7	9.2	9.1	9.0	9.4	8.9	8.6	8.5	8.6	8.5
						A. confertifolia							
30	15.5	18.1	17.4	15.7	14.4	14.3	13.2	13.5	8.9	7.9	15.7	11.5	10.0
60	8.2	8.2	8.6	8.8	8.8	8.8	8.9	9.4	9.0	8.4	7.7	8.5	7.9
90	11.0	10.9	11.2	11.3	11.0	11.0	10.9	11.4	11.0	11.2	10.7	11.0	10.6
120	13.1	13.0	13.2	13.7	13.4	13.4	13.3	13.8	13.4	13.6	13.2	13.6	13.3
150	14.4	14.4	14.5	15.0	15.1	14.9	14.7	15.2	14.8	14.6	14.6	15.1	14.6

Table 44. **Standing crop biomass of roots in grams per cubic decimeter of soil at several depths on the three stands where soil moisture was determined by the neutron scattering method.**

Stand	Utilization	Depth (cm)										
		Weight (g)						Percentage				
		30	60	90	120	150	Total	30	60	90	120	150
E. lanata	grazed	1.670	1.025	0.071	0.026	0.010	2.801	59.6	36.6	2.5	0.9	0.4
A. confertifolia	grazed	2.398	1.471	0.455	0.209	0.063	4.596	52.2	32.0	9.9	4.5	1.5
Mixed	grazed	1.870	1.295	0.211	0.112	0.051	3.541	52.8	36.6	6.0	3.2	1.5

Table 45. Mean soil matric potential in Joules per kilogram at three stands at several dates during the 1967 season. The value -1500 Joules per kilogram means that it is equal or less than that value.

Depth (cm)	April	May			June		July		August		Sept	Nov	Dec
	24	2	9	23	9	23	3	13	7	22	26	4	19
						E. lanata							
30	-45	-50	-60	-680	-560	-0	-140	-1500	-1500	-1500	-1500	-1500	-1500
60	-1500	-1500	-1350	-1440	-1480	-280	-240	-320	-1500	-1500	-1500	-1500	-1500
90	-1350	-1300	-1050	-1250	-1150	-900	-900	-900	-1000	-1100	-1100	-1300	-1400
120	-1500	-1500	-1500	-1340	-1150	-1340	-1150	-1340	-1490	-1500	-1500	-1500	-1500
150	-290	-260	-210	-220	-200	-230	-190	-230	-270	-270	-280	-340	-320
						Mixed							
30	-50	-45	-50	-230	-420	-0	-220	-1500	-1500	-1500	-1500	-1500	-1500
60	-1500	-1500	-1500	-900	-1500	-480	-220	-1000	-1500	-1500	-1500	-1500	-1500
90	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500
120	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500
150	-1500	-1500	-1500	-1500	-1500	-1500	-340	-1500	-1500	-1500	-1500	-1500	-1500
						A. confertifolia							
30	-200	-280	-260	-360	-360	-0	-60	-110	-1500	-1500	-1500	-1500	-1500
60	-1500	-1500	-1500	-1500	-1500	-580	-200	-300	-1500	-1500	-1500	-1500	-1500
90	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500	-1500
120	-980	-1040	-980	-770	-940	-1110	-940	-940	-1110	-940	-940	-1200	-1200
150	-990	-1500	-1180	-770	-990	-1500	-850	-1180	-1500	-990	-1340	-1500	-1500

Table 46. Mean soil moisture percentage by volume at several matric potentials and depths on the grazed *E. lanata*, grazed *A. confertifolia* and mixed stand.

Matric	Depth (cm)					
Potential	8	30	60	90	120	150
			E. lanata			
- 33	19.04	18.50	22.91	21.01	23.89	32.45
- 67	15.17	15.19	16.26	14.80	14.80	22.00
- 100	14.04	12.80	14.62	12.49	12.57	17.86
- 300	11.28	10.51	11.11	9.81	9.99	12.53
- 500	10.32	9.29	10.45	9.01	9.55	11.29
-1000	8.96	8.20	9.62	8.31	9.18	11.41
-1500	8.76	8.06	8.80	7.83	8.34	10.34
			Mixed			
- 33	19.53	19.58	25.90	30.44	31.97	36.08
- 67	15.42	14.55	18.39	18.76	21.18	24.77
- 100	13.63	12.78	15.80	16.08	17.77	18.17
- 300	10.42	10.80	11.37	11.95	12.37	14.87
- 500	10.13	9.63	11.35	11.81	11.95	13.55
-1000	8.77	8.35	9.98	10.46	10.64	12.10
-1500	8.77	8.35	9.78	9.47	10.56	11.74
			A. confertifolia			
- 33	33.38	27.60	33.85	32.43	34.96	37.77
- 67	29.87	23.32	23.15	24.68	29.21	32.74
- 100	28.03	22.65	20.53	21.53	25.72	29.57
- 300	22.66	18.07	15.15	14.12	17.65	20.64
- 500	20.17	16.61	13.42	12.94	15.06	17.64
-1000	16.62	14.11	12.38	11.22	13.18	14.98
-1500	16.83	14.13	11.95	11.26	12.33	14.49

Table 47. Mean moisture percentage by volume at several matric potentials in the upper 2.5 cm of soil at three grazed stands.

Matric potential Joules per kilogram	Stand *E. lanata*	Mixed	*A. confertifolia*
- 33	19.28	20.63	32.79
- 67	15.54	16.37	27.85
- 100	13.78	14.57	24.84
- 300	11.08	11.65	19.99
- 500	10.50	10.65	17.03
-1000	8.94	9.34	14.35
-1500	8.63	9.35	14.33

Table 48. Percentage of total soluble salts and soil reaction in the upper 2.5 to 7.5 cm of soil at three grazed stands and at several dates during the 1968 season.

Stand	March 18	April 20	May 1	June 20	August 13	Sept 17
Salinity						
E. lanata	0.08	0.05	0.05	0.07	0.05	0.06
A. confertifolia	0.09	0.07	0.08	0.10	0.10	0.08
Mixed	0.05	0.05	0.05	0.08	0.05	0.05
Soil reaction, pH						
E. lanata	8.2	8.1	8.1	7.9	8.2	8.2
A. confertifolia	8.1	8.1	8.0	7.9	8.2	8.3
Mixed	8.1	8.1	7.9	7.9	8.2	8.0

Table 49. Percentage of total soluble salts and soil reaction in the upper 15 cm of soil at three grazed stands at several dates during the 1968 season.

Stand	March		April				May		June	July	August	Sept
	23	29	6	12	20	27	10	24	20	26	13	19
Salinity												
E. lanata	0.05	0.05	0.10	0.05	0.09	0.05	0.05	0.06	0.07	0.06	0.04	0.04
A. confertifolia	0.07	0.06	0.05	0.05	0.05	0.09	0.09	0.06	0.06	0.06	0.07	0.04
Mixed	0.06	0.08	0.05	0.09	0.05	0.05	0.05	0.11	0.10	0.10	0.04	0.07
Reaction, pH												
E. lanata	8.0	8.1	8.3	8.2	8.0	7.9	7.9	8.2	8.4	8.0	8.2	8.0
A. confertifolia	8.0	8.2	8.2	8.0	8.0	8.3	7.7	8.1	8.0	8.1	8.2	8.3
Mixed	8.0	8.1	8.1	7.9	8.0	8.0	7.8	8.1	8.0	8.1	8.3	8.1

VITA

Juan Miguel Gastó (Coderch)

Candidate for the Degree of

Doctor of Philosophy

Dissertation: Comparative Autecological Studies of *Eurotia lanata* and *Atriplex confertifolia*.

Major Field: Ecology

Biographical Information:

Personal Data: Born at Santiago, Chile, November 29, 1935, son of Enrique Gastó Soley and Nieves Coderch Llorens; married Thelma Jean Workman, 1962; three children--Juan Miguel, María Cristina and Verónica Montserrat.

Education: Attended elementary and high school in Santiago, Chile from 1942 and graduated from Colegio de los Sagrados Corazones in 1953; received the degree of Agronomist Engineer (Ingeniero Agrónomo) in 1960 from the University of Chile (Universidad de Chile) with a major in Agronomy (Fitotecnia); completed requirements for the Master of Science in Range Management at Colorado State University in 1963.

Professional Experience: 1959 to present, researcher in Range Science and Ecology at the Agricultural Experiment Station (Estación Experimental Agronómica), and Professor of Ecology and of Range Science in the School of Agriculture (Escuela de Agronomía) of the University of Chile.