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Evaluation of the Early Establishment Phase of Agropyron desertorum, Medicago sativa and Atriplex canescens in Monocultures and Mixtures

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EVALUATION OF THE EARLY ESTABLISHMENT PHASE OF

AGROPYRON DESERTORUM, MEDICAGO SATIVA AND

ATRIPLEX CANESCENS IN MONOCULTURE AND MIXTURES

by

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Oscar Luis Prado Escobar

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES (Continued)

LIST OF FIGURES (Continued)

Figure Page

ABSTRACT

Evaluation of the Early Establishment Phase of
Agropyron desertorum, Medicago sativa and Atriplex
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by

Oscar Luis Prado Escobar, Master of Science
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Department: Range Science

This study evaluated the early establishment phase of various monocultures and mixed species plantings of Agropyron desertorum (AGDE), Medicago sativa (MESA), and Atriplex canescens (ATCA). The study was conducted under both greenhouse and field conditions. In the greenhouse, the experimental design was a split-plot, randomized-block design in time, using transplanted seedlings. The treatments were exposed to three water levels to determine species response to varying moisture availability. Plastic pots of 15.4 cm (diameter) by 17.9 cm (depth) were filled with 2,800 g of sandy-loam soil and brought to field capacity. The pots were weighed twice weekly and the water lost to evapotranspiration was replaced. The plants were measured for plant height on six occasions at two week intervals. On the last measurement date, plants were harvested for above-and-below ground biomass.

The field used the species treatments as in the greenhouse study and these were hand sown in 1 m^2 plots. Using a line-source sprinkler system, species responses at four water levels were examined. Soil water content in the various field plots was determined at various depths via access tubes and a neutron soil moisture probe. The experimental design was a split-plot design in time. Seedling emergence was recorded daily for the first 35 days after seeding. Plant height was measured six times during the growing season. All the species were clipped, oven-dried, and weighed at the end of the experimental period in 1982.

In the greenhouse, AGDE was the dominant species, yet produced more in the MESA combination. MESA exhibited a marked decrease in production when grown with AGDE. ATCA showed a remarkable ability to survive under high water stress.

Variable soil water content created in the field resulted in significant differences in germination, emergence, and establishment among planting treatments. MESA germinated and emerged faster than AGDE and ATCA, allowing it to utilize water and nutrient resources earlier than the competing species. The greatest shoot production occurred when MESA grew alone. In the AGDE-MESA combination, shading apparently reduced AGDE growth and shoot production at the two most favorable water levels. ATCA exhibited poor germination and emergence in treatments with low soil water availability.

(90 pages)

INTRODUCTION

Excessive and improper use of rangelands has occurred throughout the world and over long periods with devastating results. It has caused soil erosion, reduced plant cover, increased undesirable plant species, and led to encroachment of deserts and loss of primary productivity on which herbivorous animals depend for their growth and survival. Proper application of range management principles, particularly those relating to time and intensity of grazing by domestic livestock, is necessary to reduce the problem and restore these depleted rangelands.

Many productive and high-quality forage species have been reduced significantly in numbers or eliminated from many semi-arid rangelands. This has resulted in a serious reduction in range grazing capacity and led to a marked decline in range condition. Deterioration has proceeded to a point on many arid or semi-arid rangelands, where succession or natural plant replenishment will not take place within reasonable time, even with proper grazing management. Consequently, artificial revegetation may offer an acceptable alternative. However, in water-limited environments competition for soil moisture is critical. The availability of water is undoubtedly the major factor limiting the distribution of plants in the large arid and semi-arid areas of the world where rainfall is low and evaporative demand is high. This is particularly true of the early establishment period for young plants.

In the past, range scientists have recommended seeding monocultures of grasses (Vallentine et al. 1963, Cook 1966). However, recent studies have recommended seeding of diverse mixtures of plant species for revegetation of disturbed lands (DePuit et al. 1980a). These studies have demonstrated that mixtures are better suited to the extremely varied terrain and climatic conditions and provide variety in food supply that is desirable for both game animals and livestock. Additionally, mixtures of species considerably prolong the season when green forage is available, produce better overall ground cover than single species (Plummer et al. 1968), and are less susceptible to attacks by various insects and diseases (Haws et al. 1973). However, knowledge of the differences in phenology and rooting pattern of the particular species in these mixtures is necessary to insure the success of such revegetation efforts.

Crested wheatgrass (*Agropyron desertorum* [Fisch. ex Link] Schult.), a highly adapted cool-season grass from Eurasia, has been widely reseeded on degraded sagebrush-grass ranges since the early 1930's when seed first became available in the U.S. (Swallen and Rogler 1950). Most of the early seedings were monocultures of Standard crested wheatgrass (*A. desertorum*) with some Fairway crested wheatgrass (*A. cristatum* [L.] Gaertn.). Crested wheatgrass is well known for its longevity, productivity, and palatability (Cook and Harris 1952).

Inclusion of legumes and shrubs along with grasses for the revegetation of semi-arid rangelands would be beneficial. The increase in quality and quantity of forage could improve animal performance throughout the entire year. Also, such mixtures could affect soil characteristics underneath their canopies and, consequently, the grass growing in these mixtures may respond with superior growth.

The availability of nitrogen, more than any other mineral element, is a critical determinant of both the structure and productivity of natural and agricultural plant communities. Because legumes have root nodules with nitrogen-fixing ability, they have long been recognized as being critically important in agriculture (Vlamis et al. 1964). For this same reason, range managers are also increasingly interested in establishing legumes on rangelands. Alfalfa (Medicago sativa L.) is one of the dominant legume species used in forage mixtures in mesic environments because it provides more forage of higher quality than do grasses alone (McCloud and Mott 1953). It also offers low cost maintenance of soil fertility because it can provide nitrogen at a greater soil depth than surface-applied fertilizers (Jones and Winans 1967).

Browse seeding has been used principally for the purpose of increasing quantity and quality of range forage in fall and winter. During severe winters, heavy losses have been avoided in some herds of cattle and big game because animals have access to nutritious shrub forages that are available above snow when grasses are buried or of inferior quality. Fourwing saltbush (Atriplex canescens [Pursh] Nutt.) is an important browse species in the southwestern United States. Livestock and wild game readily eat the leaves and stems of this plant, especially during the winter (Plummer et al. 1968). It is also drought-tolerant and valuable for soil conservation purposes (Wiesner and Johnson 1977).

Although mixtures of grasses, legumes, and shrubs are desirable in revegetation, little information is available that documents which mixtures minimize mutual interference in the use of limited moisture and nutrients. Plants that are grown in close proximity and that have roots concentrated in the same soil layers will generally compete most vigorously.

Diff. Growth rates create problems of early est.

An evaluation of early establishment of mixed seedings could be useful for range improvement and is also interesting from a theoretical point of view. Species with different phenologies and rooting habits could potentially allow more complete use of soil minerals and moisture on semi-arid rangelands and could lead to significantly increased productivity.

LITERATURE REVIEW

Crested wheatgrass (AGDE[1/]) is native over wide areas of Russia, Siberia, Mongolia, and other Eurasian countries and was introduced to the United States in 1898 (Rogler and Lorenz 1983). Crested wheatgrass has been seeded on millions of hectares in the United States, Canada, and many other countries of the world (Rogler and Schaaf 1963). The first known range seeding with crested wheatgrass in western North America was done in the sagebrush-grass type in southern Idaho in 1932 at the U.S. Sheep Experimental Station near Dubois (Hull 1972). AGDE is well adapted in southern Idaho and other similar semi-arid ranges and produces 21% more than AGCR. It is also grazed more uniformly of grazing use (consistent palatability of individual plants) and has the ability to spread 112% further than AGCR (Hull 1972).

Vallentine et al. (1963), Rogler and Lorenz (1969), and Hughes et al. (1976) suggested the use of crested wheatgrass because it is considered sufficiently drought resistant for foothill areas receiving only 12 inches of annual precipitation. In eastern Nevada Eckert et al. (1961) tested the responses of AGCR, AGDE, and other range grasses. They concluded that AGDE dominated the more xeric upper sites because it was more drought tolerant and competitive than AGCR Plummer et al. (1968) reported that AGDE had characteristics that allowed growth on dry sites, where few other grasses could survive. Cook (1966), in a study conducted in a semi-desert area of central Utah (with only 10 inches of

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[1/] Complete scientific names are described in the Appendix.

annual precipitation), found that AGDE and Russian wildrye (ELJU) were better adapted to arid conditions than tall (AGEL), pubescent (AGTR), or intermediate (AGIN) wheatgrasses.

Hull and Klomp (1966) studying the longevity of crested wheatgrass in stands over 30 years of age, concluded that it still occurred in good density, withstood heavy grazing, and was resistant to heat, drought, cold, fire, and disease. Vallentine (1980) found that crested wheatgrass maintained stands for over 40 years in the Northern Great Plains without showing signs of deterioration. Looman and Heinrichs (1976) concluded that crested wheatgrass was a suitable long-term replacement for native range in dry regions of southern Saskatchewan.

Cook and Lewis (1963) and Robertson (1972) studied competition between crested wheatgrass and sagebrush (ARTR). They concluded that grass roots were more efficient water absorbers when in direct competition with sagebrush roots and that crested wheatgrass was therefore better able to survive under stress or drought. Blaisdell (1949) found that in areas where crested wheatgrass was well established it suppressed sagebrush seedlings or entirely prevented sagebrush establishment for an indefinite period. Harris (1977) observed that crested wheatgrass had favorable root phenology, rapid root extension, and speed and vigor of germination which contributed to its superior competitive ability.

Trlica and Cook (1972), in a three-year study of the carbohydrate reserves in crested wheatgrass and Russian wildrye, concluded that both grass species are physiologically adapted for spring or fall grazing. White (1973) stated that carbohydrate reserves are thought to be used by plants as a substrate for growth and respiration. Adequate carbohydrate reserves are traditionally regarded as being important in perennial plants for winter survival, early spring growth initiation, and regrowth initiation after herbage removal, when photosynthetic production is inadequate to meet carbon demands. Caldwell et al. (1981) studied the abilities of two bunchgrasses (AGDE and AGSP) to cope with herbivory. They found that AGDE recovered more rapidly from severe defoliation than AGSP because of a greater capacity for new tiller formation and greater allocation of total plant biomass to photosynthetic tissues. Their results also showed a greater carbon gain for whole AGDE bunches and somewhat greater photosynthesis/transpiration ratios.

Frischknecht (1968) found in central Utah that cattle did not eat western wheatgrass in the spring until crested wheatgrass had been well grazed. Cook et al. (1956) observed that crested wheatgrass produced spring growth about one and one-half weeks earlier than other introduced wheatgrasses and native grasses. Digestibility of protein, cellulose, gross energy, and other carbohydrates decreased with increased maturity. Crested wheatgrass was highly palatable in early spring but became relatively unpalatable late in the season. Cook and Harris (1952, 1968) stated that crested wheatgrass was ideally suited for early spring grazing because it started growth earlier than most other forage species and furnished adequate nutrients (more digestible protein) for lactation. However, in late summer when it matured, the protein content of crested wheatgrass was too low to supply gestation requirements of livestock. Despite this, stem-cured (mature) grass forage can supply adequate energy to non-lactating livestock (Cook 1972).

Range fertilization has been practiced extensively during the past three decades with notable increases in yield of range grasses. In general, nitrogen is the major growth-limiting factor in range pastures (Jones 1962, Gay and Dwyer 1965, and Power 1972). However, this practice must be repeated every two to three years because the residual effect of nitrogen in the soil disappears (Houston et al. 1973). Lazenby (1981) mentioned three pathways of nitrogen loss in grasslands: (1) volatilization of ammonia, (2) denitrification, and (3) leaching. In native grasslands nitrogen-fixing plants are presumed to occupy an important position in nitrogen cycling (Becker and Crockett 1976). Forage legumes such as alfalfa grown in mesic pastures can provide an inexpensive source of nitrogen to succeeding crops (Heichel et al. 1981). Mixtures of grass and alfalfa provide more forage of higher quality than do grasses alone (Johnson et al. 1983). Also, legumes can increase the protein content of grasses as well as the gain per animal and per hectare (Campbell 1961, 1963; Kilcher et al. 1966; Rumbaugh and Thorn 1965; and Gomm 1964).

Alfalfa is frequently sown in mixtures with grasses in range areas. This is done to maintain a desirable balance of nutrients for animal use (Russell et al. 1982). Rhodes (1970) pointed out that a complex mixture might be more efficient in utilizing available environmental resources. Alfalfa, an introduced legume, has been seeded for years on irrigated and dryland farms in Utah and throughout the West (Plummer et al. 1968). Rangeland alfalfa varieties come from germplasm brought to the U.S. by Dr. N. E. Hansen from Siberia in the early 1900's. Hansen observed their use in Siberia in extremely droughty regions and thought that they would be valuable to introduce into native pastures (Rumbaugh 1979).

Kilcher and Heinrichs (1966) tested the persistence of alfalfa in mixture with grasses. They found that alfalfa and crested wheatgrass was the best mixture and significantly outyielded grasses alone. They also found that the creeping-rooted character of MESA is important because it may contribute to persistence in a dry climate. Vallentine (1980) stated that alfalfa was adapted to mesic and semi-arid sites that receive 350 mm of annual precipitation. He also stated that this species is well adapted to seeding with grasses. Townsend et al. (1975) tested 14 legumes and concluded that cicer milkvetch (ASCI), sicklepod milkvetch (ASFA), and alfalfa merited additional evaluation for potential use under dryland range conditions. Johnson and Rumbaugh (1981), working with several rangeland legume species, found that MESA was particularly notable because of its ability to nodulate and to reduce acetylene in dry soils where other legumes were not active. Holland et al. (1969) found that under dryland conditions in California, nodulated range legumes fixed at least 54 kg of nitrogen per hectare in one growing season.

The questions of persistence and longevity are prime concerns in introducing alfalfa into grasslands. Rumbaugh and Pedersen (1979) found that after 23 years alfalfa was surviving in semi-arid range conditions. Heady and Bartolome (1977), in evaluating the Vale Rangeland Rehabilitation Program in southeastern Oregon, observed that after 15 years alfalfa-crested wheatgrass stands were in good condition. Apparently, even on semi-arid sites, legumes can provide long-term increases in forage quality and quantity.

Grasses commonly grown with alfalfa will have a much higher proportion of the root system in the upper 30 cm than alfalfa. Also, alfalfa roots penetrate the soil to a greater depth than those of most grasses. Once established, alfalfa competes favorably with associated species for available soil moisture (Hanson 1972). Atkins (1953) reported that seeds of more than 60 legume species were collected and evaluated alone and in mixtures with grasses. Alfalfa and cicer milk-vetch, both introduced species, performed best with cool-season grasses, such as intermediate wheatgrass. Townsend et al. (1975), testing legumes at the Central Great Plains Field Station, Akron, Colorado, seeded Ladak alfalfa, five varieties of crownvetch, and four varieties of sainfoin in pure stands and in mixture with Nordan crested wheat-grass. Alfalfa was the only legume capable of competing in a mixture with crested wheatgrass.

Campbell (1961), Heinrichs and Lawrence (1958), and Dahl et al. (1967) suggested grass-legume mixtures for several reasons which included: greater forage yields (51% more); increase in voluntary intake of herbivores; high crude protein content; greater gain per animal and gain per hectare; greater carrying capacity; and a good balance of protein, carbohydrates, and minerals throughout the entire grazing period. Rauzi and Lang (1976) mentioned that during the third year of grazing at the Archer Field Station east of Cheyenne, Wyoming, lamb gains per hectare were 65% higher on the interseeded crested wheatgrass-alfalfa areas than on the untreated native sod. Rumbaugh et al. (1982b) working in Norbeck, South Dakota, from 1977 to 1979 with yearling steers on three forage management systems (native, interseeded, and tame) reported better gains per hectare and per animal from the interseeded than from native and tame pastures. Rumbaugh et al. (1982a) and Johnson et al. (1983), working with crested wheatgrass and several legume species, found that alfalfa produced higher protein yields (29 g/m^2) than sicklepod (15 g/m^2) or cicer milkvetches (10 g/m^2). Also, they found that total yield of alfalfa was 1.5 to 8.0 times greater than the other legumes. Reed and Kenny (1981) found, in a study of lambs on grass and grass-legume pastures, that animal performance was superior in the grass-legume pasture. They also found that the mean retention time of dry matter in the rumino-reticulum was 19% shorter in grass-legume pastures.

Recently, there has been an increasing awareness of the potential of shrubs in mixtures with grasses for livestock and big game production, especially in arid and semi-arid regions. The selection of palatable and superior shrub types could materially improve animal and land productivity.

Fourwing saltbush (ATCA) is a native, dioecious shrub that has an extensive geographic range in western North America (McArthur et al. 1978, Plummer et al. 1966). It is one of the most valuable and wide-spread shrubs on western ranges and occurs from North Dakota to Oregon and south to Mexico (Springfield 1970). Fourwing can tolerate extreme site conditions, is an excellent source of food and cover for domestic livestock and wildlife, and can be planted successfully on harsh sites such as badly eroded areas and mine spoils (Wagner and Aldon 1978). This shrub is one of the most abundant producers of forage and seeds on Utah game ranges (Plummer et al. 1968). It grows naturally on a wide variety of soils derived from calcareous rocks and can grow on sites having as much as 1 percent soluble salts.

Fourwing saltbush has a remarkable ability to maintain a favorable competitive balance when growing in association with grasses. It grows unusually well in summer when other vegetation is drying and the ground appears depleted of moisture. This attribute is apparently associated with the shrub's ability to take up and store moisture in its woody parts during the spring when water is available and temperatures are too low for active growth (Plummer et al. 1966). Cable (1972) and Springfield and Bell (1967) stated that seeding fourwing saltbush has become a common practice of southwestern U.S. land management agencies. Ranchers are also seeding this species either alone or in mixture with grasses. Fourwing saltbush is a long-lived shrub especially adapted to xeric conditions (Springfield 1970, Plummer et al. 1966). Because this shrub can exhibit greater and more sustained long-term productivity than many introduced species on western rangelands, it is used for mined land reclamation (McKell and Van Epps 1978).

Shrub establishment is important in revegetating xeric areas because they are frequently deeply rooted, and thus capable of utilizing soil moisture unavailable to shallow-rooted grasses and forbs (DePuit and Dollhopf 1975). They also can provide forage further into the dry season than herbaceous species alone (Johnson et al. 1983).

Monsen (1980) successfully interseeded fourwing saltbush and crested wheatgrass into southern Idaho rangeland dominated by sagebrush (Artemisia spp.) and annual grass. Shrubs were seeded in separate rows to reduce competition between shrub and grass. This allowed the shrubs to become established and did not reduce grass yields. Rumbaugh et al. (1982a), working with grass-legume-shrub mixtures at Nephi, Utah, found that crested wheatgrass responded dramatically to close association with the saltbush and legumes. The impact of fourwing saltbush and legume species upon forage yield of crested wheatgrass was significant and positive. Crested wheatgrass and fourwing saltbush are compatible and can grow well in association. Successful stands have been obtained from aerial seedings when fourwing seeds were included in mixtures with grasses and legumes (Plummer et al. 1966). However, during early establishment, seedlings were particularly susceptible to competition, freezing, and grazing.

Blaisdell (1949), studying the competition of sagebrush seedlings and reseeded grasses, found that good stands of grass often prevent subsequent establishment of sagebrush seedlings. Where sagebrush plants did invade grass stands, they were markedly suppressed. He suggested that to inhibit the establishment of sagebrush, one needs as little as one year of prior grass establishment. Van Epps and McKell (1978) found that fourwing saltbush normally had a greater survival rate following transplanting than did shadscale (ATCO) under arid field conditions. Johnson et al. (1983) in Nephi, Utah tested mixtures of crested wheatgrass, legumes, and shrubs. They found that higher yields were obtained from crested wheatgrass-shrub (143 g/m^2) and grass-alfalfa (163 g/m^2) mixtures in comparison with crested wheatgrass alone (55 g/m^2).

Plummer et al. (1966) found that the protein and fat levels in fourwing saltbush in winter remained well above those required for animal maintenance. Cook et al. (1959), studying the chemical content in various portions of current growth of salt-desert shrubs and grasses during the winter, found that protein content in grasses decreased from fall to early spring (from 6.8 to 2.7%). In contrast, shrubs such as fourwing saltbush contained more than twice as much protein (9.5 to 12.1%) as cured grasses during fall and winter. Otsyina et al. (1982)

suggested that interplanting of crested wheatgrass and fourwing saltbush would be useful for sheep as a means to avoid supplementation during the critical fall and winter months. Fourwing saltbush could provide protein, while crested wheatgrass could supply energy. Johnson et al. (1983) found that pastures of crested wheatgrass grown with fourwing saltbush produced 71 g/m^2 of crude protein in August of 1978, the highest of any sampling date. This high protein yield was mainly due to the 61 g/m^2 contribution from fourwing saltbush. Cook and Harris (1968) and Sneva and Hyder (1962) also observed that shrubs were able to maintain a consistent protein content further into the dormant season than grasses.

Seeding of diverse mixtures of plant species has often been recommended in the revegetation of semi-arid lands to increase chances of colonization of the varied microhabitats of a given area (Monsen 1975; Plummer 1977). However, interspecific competition is important. A number of early revegetation trials in which a diverse array of native and introduced species were seeded produced plant communities of relatively low floristic and structural diversity (DePuit and Dollhopf 1975). There is also a risk that overly diverse seeding mixtures may result in stands of reduced overall productivity due to increased interspecific competition. Additionally, initial site stabilization may be delayed due to the slow establishment of species less adapted to the site conditions (DePuit et al. 1980b).

Mixtures inevitably require greater management skills because they are subject to compositional changes resulting from differential utilization by animals and tolerance to grazing (Stoddart et al. 1975). However, mixtures have advantages over monocultures because:

1) different rooting habits may result in more efficient use of soil moisture and nutrients from various soil depths (Rumbaugh and Pedersen 1979), 2) a mixed diet is likely to be more desirable to range animals and produce greater gains especially when browse plants and legumes are included, and 3) some plants of the mixtures may have beneficial influences on other plants. Moreover, the combination of plants such as crested wheatgrass, legumes, and shrubs could extend the grazing season and provide a broader ecological base for increased ecosystem stability than monocultures of crested wheatgrass (Johnson et al. 1983).

Although mixtures of species have potential advantages in range improvements, they must be carefully managed. A critical period for these mixtures is the seedling establishment phase. This requires knowledge of the phenological differences among the various species within the mixture. Important considerations include: germination rate, rates of root and top growth, and resistance to environmental and biological stresses. The combined expression of these factors is frequently referred to as seedling vigor. Successful seedling establishment in mixtures may be enhanced by either altering cultural practices or by selecting species that have compatible levels of vigor during the seedling stage.

The purpose of this study was to evaluate the early establishment phase of various seeding mixtures. The species selected for the study were crested wheatgrass, alfalfa, and fourwing saltbush. Measurements of early growth (e.g. growth rate, leaf number, and number of tillers) and survival when the species were grown alone and in various combinations were the basis for statistical comparison. The specific objectives and their associated hypotheses were:

Objective 1: To determine the relationship among grasses, legumes and shrubs during early establishment when transplanted at recommended ratios in greenhouse conditions.

Hypothesis: Fourwing saltbush, crested wheatgrass, and alfalfa show no differential seedling mortality or growth rate when in combination than when transplanted alone.

Objective 2: To determine the relationship among grasses, legumes, and shrubs during early establishment when seeded at recommended ratios in field conditions under controlled moisture regimes.

Hypothesis: Fourwing saltbush, crested wheatgrass, and alfalfa show no differential seedling mortality or productivity when in combination than when seeded alone.

METHODS

Greenhouse Study

This phase of the study was initiated in August, 1981. Plastic pots (15.4 cm diameter by 17.9 cm depth) were used. The pots were lined with plastic bags to avoid water drainage. The soil, a sandy loam, was screened to avoid large soil particles and stones and mixed to assure homogeneity. It was sun dried for three days and mixed daily to insure uniform drying. Each pot and plastic bag combination was weighed to obtain their exact weight. Each pot was filled with 2,800 g of soil. All pots were numbered and color-coded according to water level.

Three water levels were used: high (24.5% water by weight), medium (5%) and low (1.3%) which corresponded to soil matric potentials of -0.002, -0.06, and -4.00 MPa, respectively. The soil water retention curve for this particular soil was determined by the Soil Analysis Laboratory, Soil Science Dept., Utah State University, using standard laboratory procedures. All pots initially were brought to field capacity (24.5%, Figure 1).

Maintenance of soil moisture levels

After bringing the pots to field capacity, they were allowed to dry until the desired moisture levels were reached. The pots were weighed twice weekly and the water lost by evapotranspiration was replaced using a 50 cc syringe. The syringe needle allowed the water to be injected into the middle of the pots (the root zone) and minimized evaporative water loss from the surface of the pots. The difference in weight

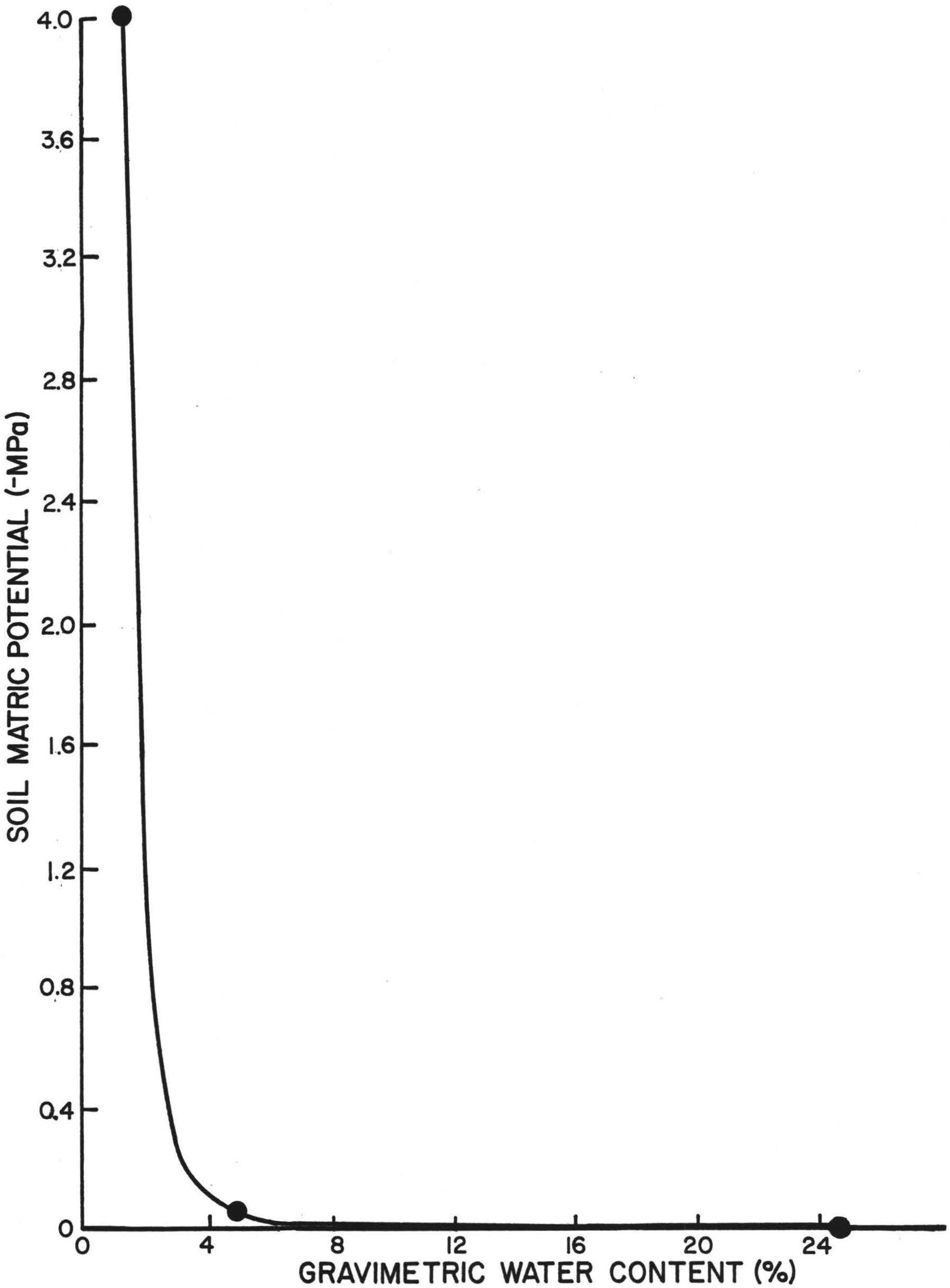


Figure 1. Soil moisture retention curve for the soil mixture used in the greenhouse study.

between water applications provided data on evapotranspiration for each different water level during the 90 days of the experimental period.

Establishment of plants

Greenhouse studies of early establishment involved monoculture plantings and combinations of a grass, forb, and shrub. AGDE seed was obtained as one year old stock from Western Seed Company in Tremonton, Utah. Alfalfa seed (MESA c.v. Spredor 2) was obtained from the Northup King Co. Fourwing saltbush (ATCA) seed was obtained from Dr. E. D. McArthur, research geneticist and range scientist, from the Shrub Science Laboratory, Intermountain Forest and Range Experiment Station in Provo, Utah.

After germinating the seeds according to procedures recommended by the Association of Official Seed Analysts, the seeds were transplanted to the pots. This was done the day after the pots had been brought to field capacity.

The proportion of the species in the various treatments was as shown in Tables 1 and 2.

Table 1. Number of seedlings per pot in the greenhouse.

Treatment	Grass	Alfalfa	Shrub
Grass	5	0	0
Alfalfa	0	3	0
Shrub	0	0	1
Grass + Alfalfa	4	1	0
Grass + Shrub	4	0	1
Alfalfa + Shrub	0	2	1
Grass + Alfalfa + Shrub	4	1	1

Table 2. Number of kg of seeds per hectare at the field study site at Green Canyon.

Species	No. Pure Live Seeds/Pot (.0182 m^2)	No. Seeds/m^2	Seed Wt. (g)	No. Seeds/ha	kg/ha
Grass	5	296	.00226	2,964,602	6.7
Alfalfa	3	165	.00227	1,652,558	3.8
Shrub	1	55	.00625	550,853	3.4

Measurements of plants

Plant height, number of leaves, and number of tillers were measured on six occasions at two week intervals during the 3 months. Root biomass was measured at the end of the study (harvesting time).

Experimental design and data recording

The experimental design was a split-plot, randomized block in time (Steel and Torrie 1980), with the following specifications:

1. Species 3 Crested wheatgrass, alfalfa and fourwing saltbush
2. Water levels 3 High (24.5%), medium (5%), and low (1.3%)
3. Treatments 7 Species alone, mixture of two species and mixture of 3 species
4. Replications 10 Weekly randomization within blocks to reduce variations due to shading and air circulation in the greenhouse.

Analysis of Data

The data were subjected to an analysis of variance via a split-plot computer program. Statistical significance ($P<0.05$) was determined for each treatment by means of a standard F test. Fisher's Least Significance Difference test (LSD) of multiple comparisons (Steel and Torrie 1980) was applied to evaluate differences between treatment means.

Field Study

The field study was conducted at the Green Canyon Experiment area, 4 km northeast of Logan, Utah. Soils at Green Canyon are rocky mollisols (typic Haploxerolls, Southard et al. 1978). They have a dark grayish brown gravelly-loam surface layer, which is moderately alkaline, calcareous and about 40 cm thick. Depth to a very gravelly subsoil layer varies from about 35 to 65 cm. The amount of coarse fragments ranges from about 50% to 80% by volume (Erickson and Mortensen 1974). Features of the climate at Green Canyon are given in Figure 2 (Caldwell et al. 1981).

Establishment of plants

The seeding experiment used the same three species as the greenhouse study. They were sown individually and in mixtures by hand in 1 m^2 plots. Before planting in the field, germination tests were done for crested wheatgrass and alfalfa according to the rules for testing seeds recommended by the Association of Official Seed Analysts. Fifty seeds with four replications each were placed in a closed germinating dish with blotter paper and distilled water. The seed was sprayed with Panogen (mercury) to avoid fungal and bacterial damage. The germination dishes were placed in growth chambers at 25^{o}C for five days.

Germination percentage for crested wheatgrass was 85.5% and for alfalfa was 80.5%. Germinability of the fourwing saltbush seed was 25%

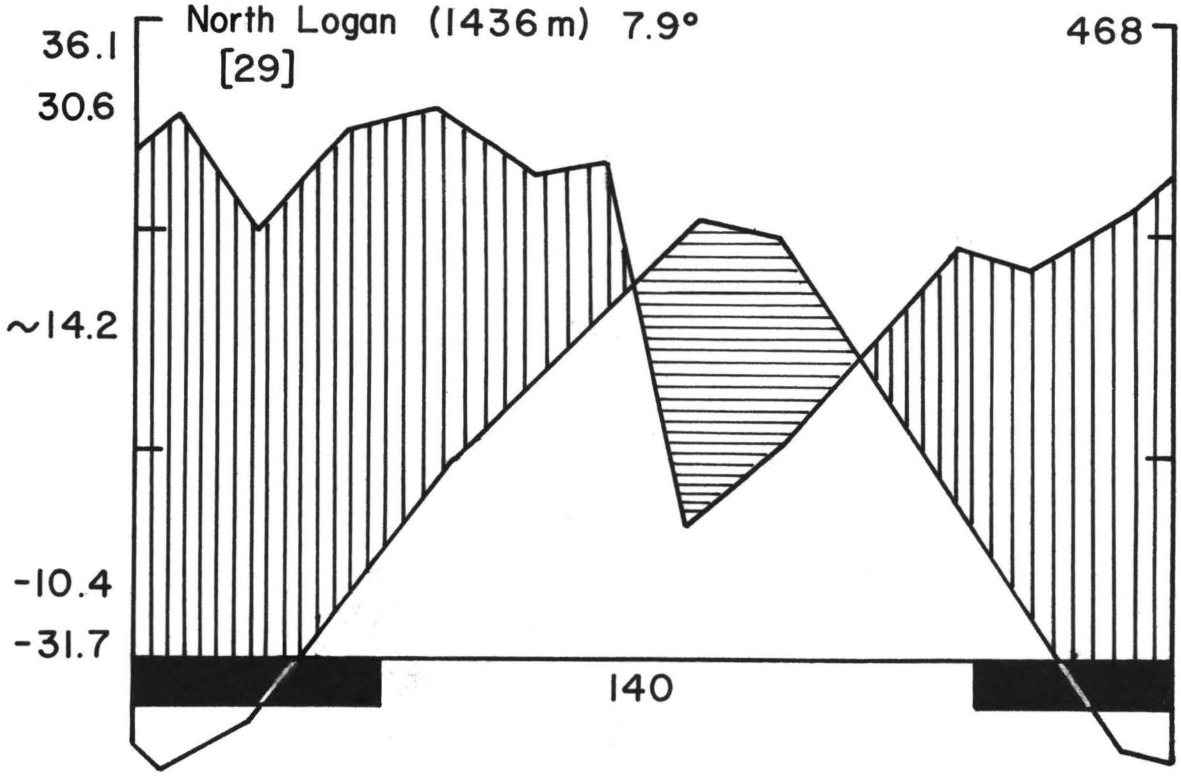


Figure 2. Climatic diagram compiled from weather stations within 2 km of the field study site at Green Canyon (From Caldwell et al. 1981). The abscissa represents the 12 months of the year beginning in January. The blackened box along the abscissa indicates months of the year when the daily minimum is below 0°C. The number below the center of the abscissa indicates the mean duration of the frost-free period in days. One division of the ordinate represents either 10°C or 20 mm precipitation. Numbers to the left of the ordinate beginning at the top represent the highest temperature recorded at this site, the mean daily maximum temperature of the warmest month, mean daily temperature variation, mean daily minimum temperature of the coldest month, and the lowest temperature recorded at this site. At the top of the diagram the site elevation, mean annual temperature, and mean annual precipitation are indicated from left to right and the number of years of observations for this compilation is given in brackets.

according to identical tests run by Dr. D. E. McArthur the same summer at the Shrub Sciences Laboratory, Intermountain Forest and Range Experiment Station, Provo, Utah. Using these germination test results and following the procedures recommended by the Soil Conservation Service (personal communication by D. Erickson 1981), the amount of seed per square meter (Table 2) was sown by hand on August 17, 1981.

Water levels

Four different water levels (1^{st} 36 mm/hour, 2^{nd} 25 mm/hour, 3^{rd} 13 mm/hour, and 4^{th} zero) were applied with a line-source sprinkler system (Hanks et al. 1976). The sprinklers were spaced (6.1 m) along an irrigation line to assure that water distribution was essentially constant along any line parallel to the sprinkler line. A continuous water variable was obtained by applying water so that the amount was decreasing linearly from a high rate next to the sprinkler line to zero at approximately 15.2 m from the sprinkler line.

Soil moisture content

The line-source sprinkler system established a gradient of soil moisture content. The irrigation was applied at intervals to prevent surface runoff. When runoff started, irrigation was stopped. The time intervals between irrigations varied but coincided with nearly complete drying of the soil surface. It averaged about 2 to 3 days, depending on the evapotranspiration rates as affected by daily fluctuations in temperature and wind speed. The water application curve is depicted in Figure 3. The amount of water applied was measured by 12 rain gauges, systematically placed across the first three rows of the plots. Row 4,

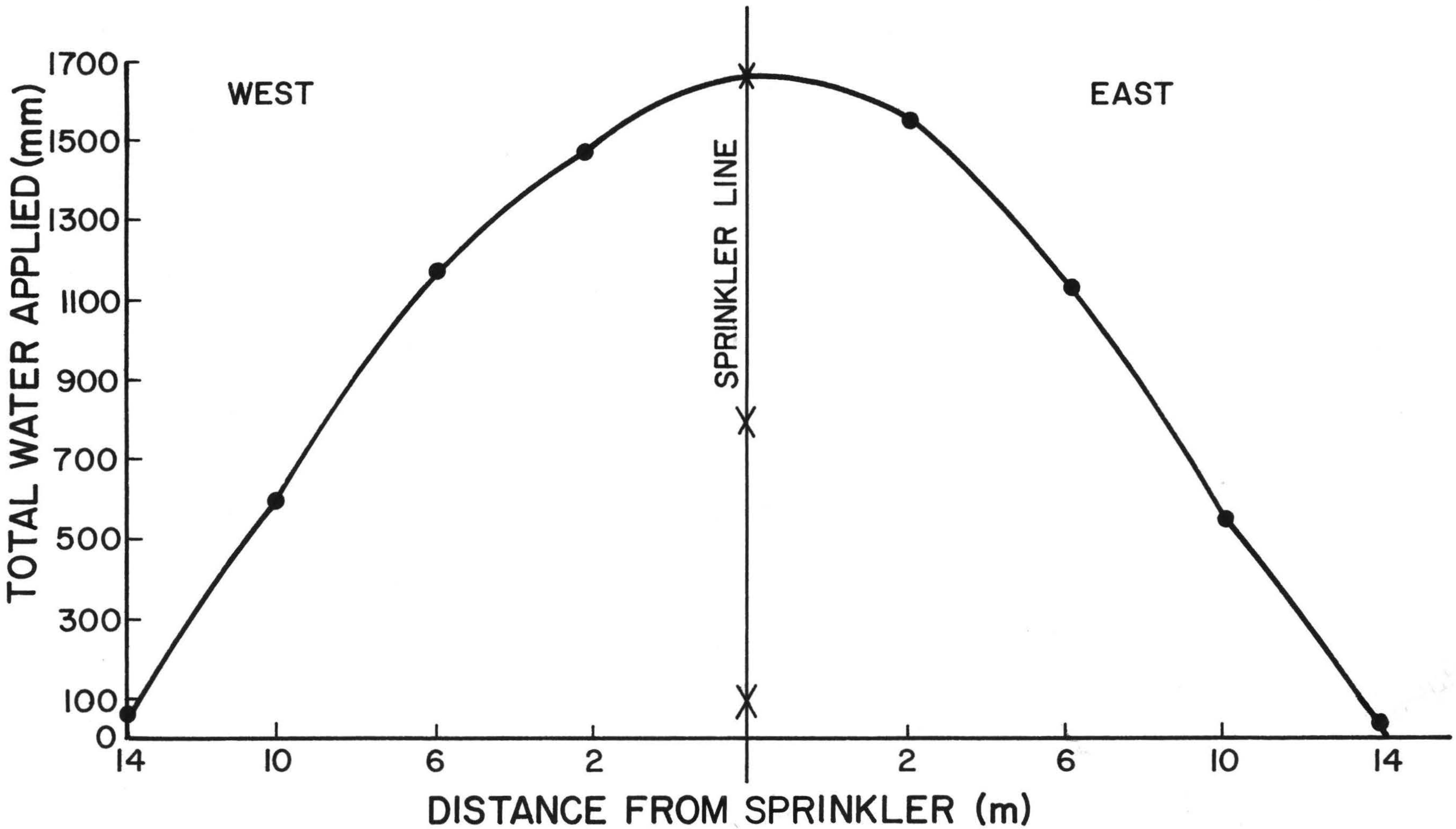


Figure 3. Cumulative irrigation (mm) as related to the distance from the sprinkler line for the field plots at Green Canyon.

which was placed beyond the reach of the sprinkler system, received only natural precipitation.

Soil moisture content was determined with the neutron soil moisture probe (Campbell Pacific Nuclear Inc.) using eight aluminum access tubes (3.2 cm in diameter and 1.20 m long). These were drilled vertically to one meter depth, leaving 20 cm above the ground to support the hydro-probe equipment. The aluminum tubes were placed at the center of each row (Figure 4). This resulted in soil moisture readings at points from a gradient of low to high irrigation levels. The readings at 20, 40, 60, and 80 cm depth were taken before and after each irrigation.

Plant measurements

Seedling emergence in 1981 was recorded every day by counting the number of seedlings present during the first 35 days after seeding. Counts were also taken during June and September in 1982. Plant height, number of leaves, and number of tillers were measured six times (September 20, October 15, 1981, June 15, July 15, July 30, and September 15, 1982).

At the beginning, three plants of the same species in each plot were randomly selected for the purpose of following their responses to different soil moisture levels. The plants were individually marked with colored-wire rings placed around the stem.

Production

Crested wheatgrass and alfalfa were harvested on two separate dates (August and September 1982). The August sampling was just prior to leaf shedding while the September clipping occurred prior to fall greening. Both species were clipped to a 5 cm stubble height. The plant material

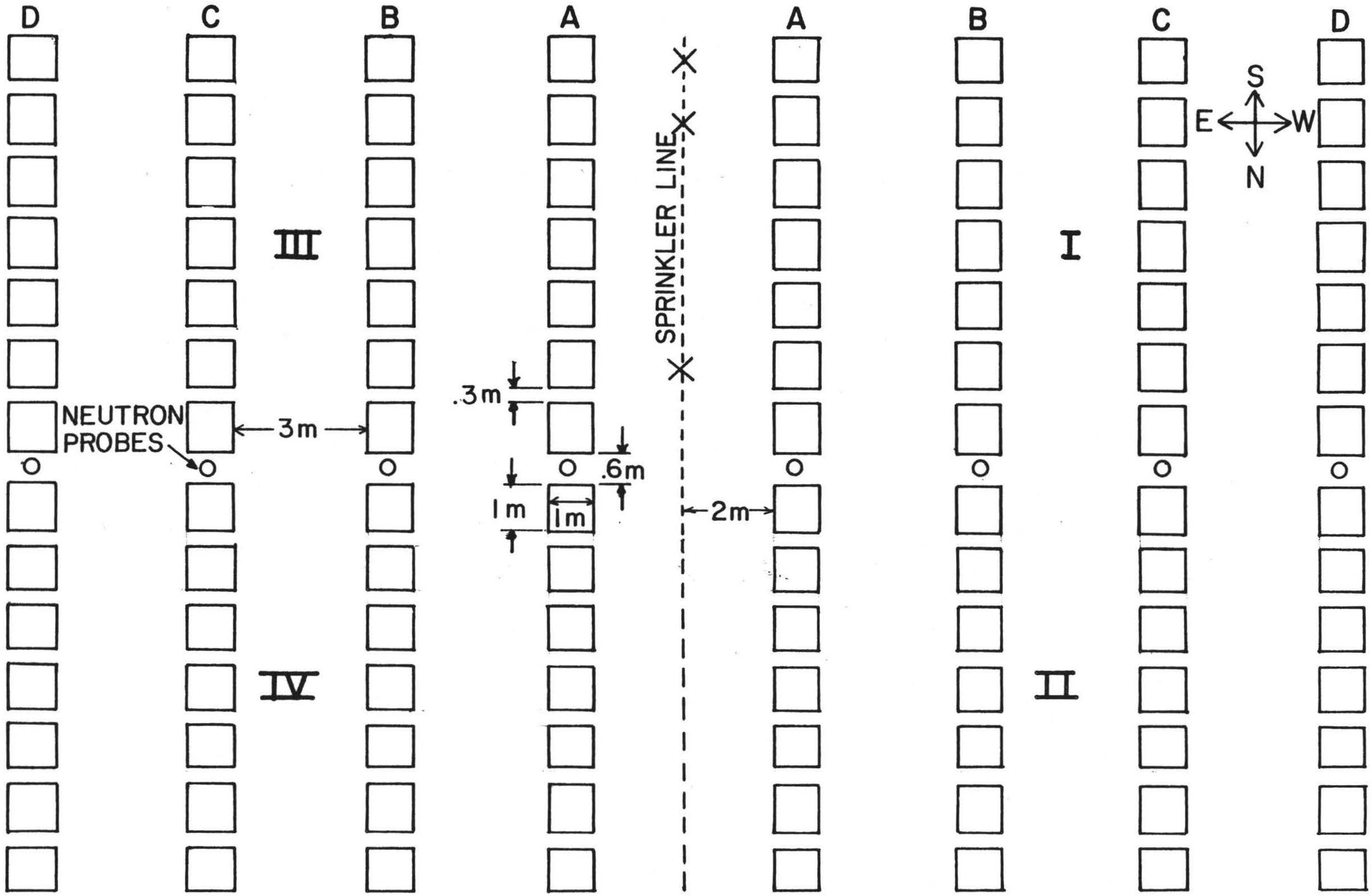


Figure 4. Placement of plots, neutron probe tubes, and the line-source sprinkler system at the field study site at Green Canyon. The roman numerals indicate replications.

obtained from each clipping was oven dried at 68^{o}C for 72 hours and weighed. For fourwing saltbush, which differs phenologically from crested wheatgrass and alfalfa, the peak growth was completed at the end of September. Fourwing was harvested only once (September 1982) and was clipped at ground level. The plant material was dried and weighed as above.

RESULTS

Greenhouse

Plant height

Unless specifically noted, all differences discussed are statistically significant at ($P<0.05$). Initially all the species followed similar growth rate patterns at all water levels as indicated by plant height measurements (Figure 5). Most rapid growth occurred when moisture content was highest (24.5%) and between times 1 and 3. From time 4 to time 6 growth remained almost constant. This pattern is consistent with growth curves from a wide range of other species (Bidwell 1974). According to Bidwell (1974), plants usually exhibit a sigmoidal growth curve that can be divided into three phases: a) exponential; b) linear; and c) senescence, a phase of declining growth rate.

No height differences were found when AGDE was growing alone or in combination with MESA and/or ATCA in the high water level at all time periods (Figure 5). At the second water level, AGDE growing with ATCA exhibited statistically lower heights than all other combinations in time period 6.

At the lowest water level, all the species started growing rapidly (time period 1 to 3) but most plants in all combinations later reduce growth (time periods 4 to 6). From time period 3 to 6, AGDE growing alone or in the MESA combination was significantly shorter than when growing with ATCA or in the three-species combination. By time

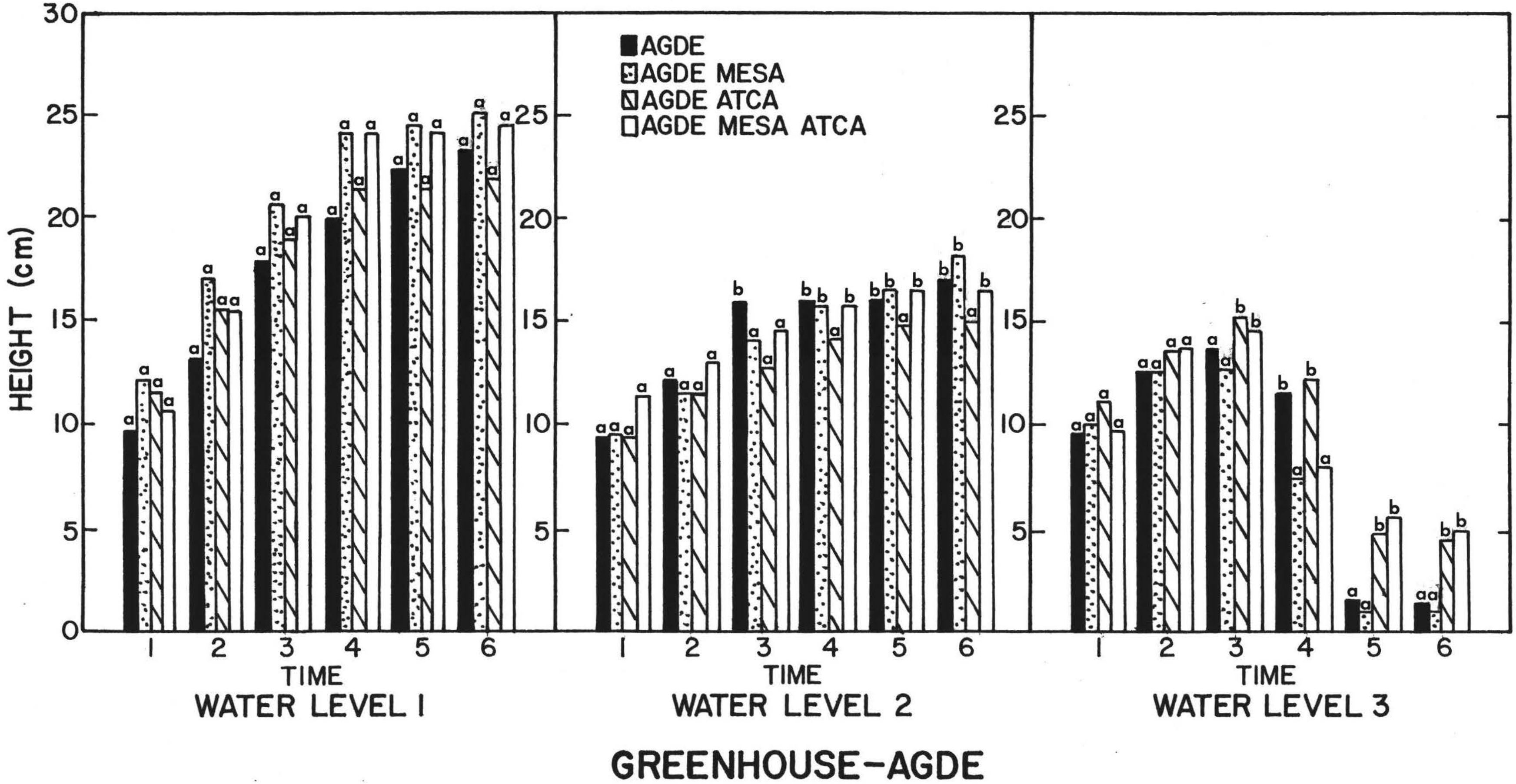


Figure 5. Height (cm) of Agropyron desertorum (AGDE) at three water levels at six time periods growing in four planting treatments in the greenhouse. Bars with same letter within a time period are not statistically significant at P = 0.05.

period 6, few grass plants had survived at the low water level; however, mortality was lowest when AGDE was growing with ATCA or in the three-species combination.

Generally, MESA height at all water levels was significantly less when growing with AGDE or in the three species combination (Figure 6). In time period 5 and 6 when MESA was growing with ATCA in the high water treatment, it exhibited a height equal to that when MESA was growing by itself. MESA was apparently more compatible with ATCA than AGDE. MESA in water level 2 exhibited nearly the same pattern as in water level 1. In the high and medium water levels during harvesting time, several nodules were observed in the roots of the leguem; but the nodules were not cut and weighed. In period 6 both the MESA alone and MESA-ATCA combinations, MESA was statistically taller than in the MESA-AGDE or three species combination. At the low water level, MESA initially exhibited greater plant growth when alone; by time period 4, however, MESA started showing the effects of water stress and began slowing shoot and leaf growth. By time period 5, most MESA plants had died and only those in the three-species combination had any surviving plants.

ATCA plants tended to grow best alone at water level 1 (Figure 7). However, ATCA in the ATCA-MESA combination exhibited a height nearly equal to ATCA plants growing alone through time periods 3 to 6. ATCA plants grew least in combination with AGDE from time period 2 to 5. Atn the second water level, ATCA exhibited the greatest height when growing alone (time period 4 to 6). At water level 3 as soil moisture became limiting, growth leveled off. ATCA plants growing alone exhibited the statistically highest growth from time periods 4 to 6. It is clear from Figure 7 that ATCA was remarkable in its ability to maintain growth at

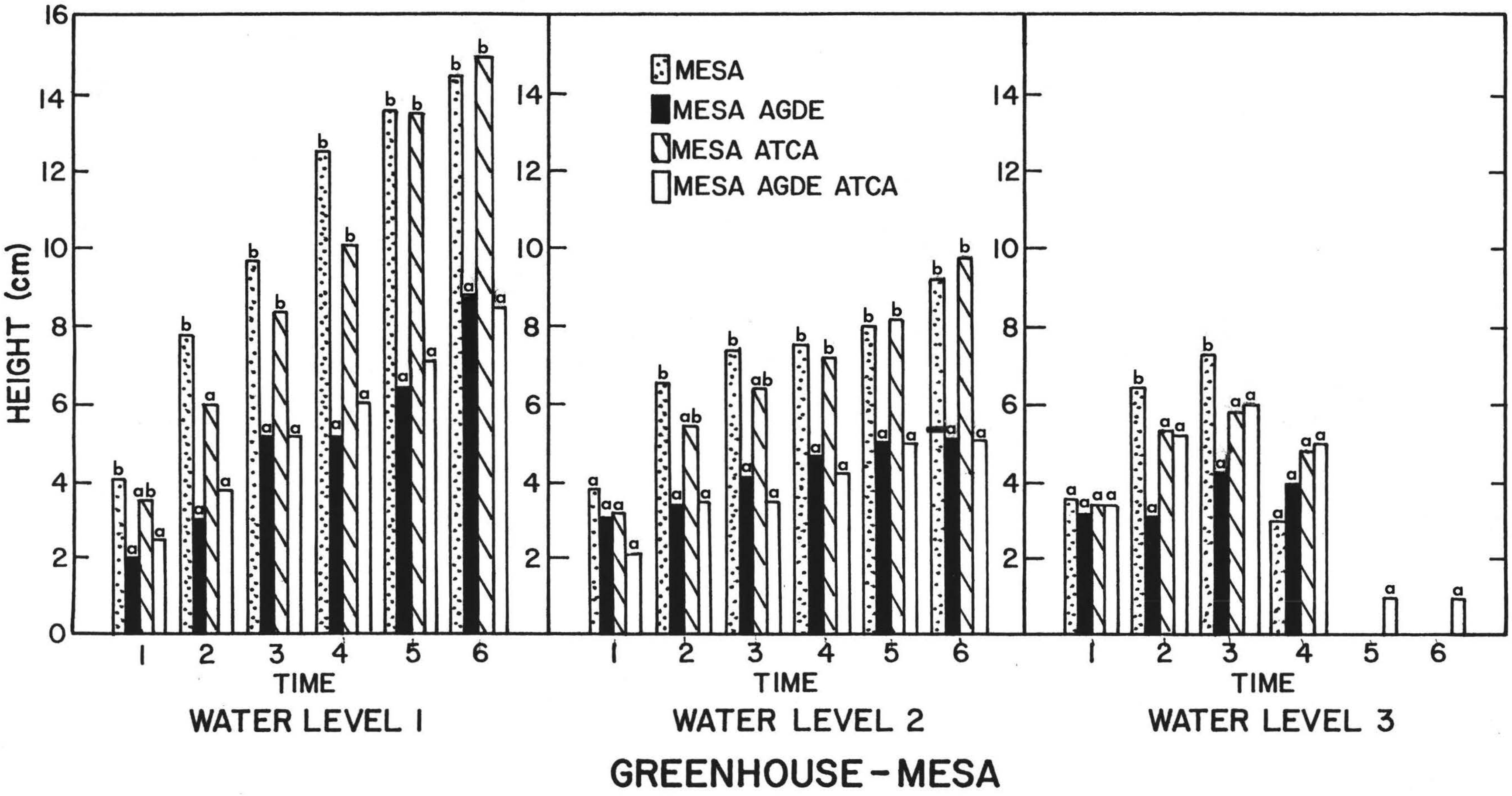


Figure 6. Height (cm) of Medicago sativa (MESA) at three water levels at six time periods growing in four planting treatments in the greenhouse. Bars with the same letters within a time period are not statistically significant at P = 0.05.

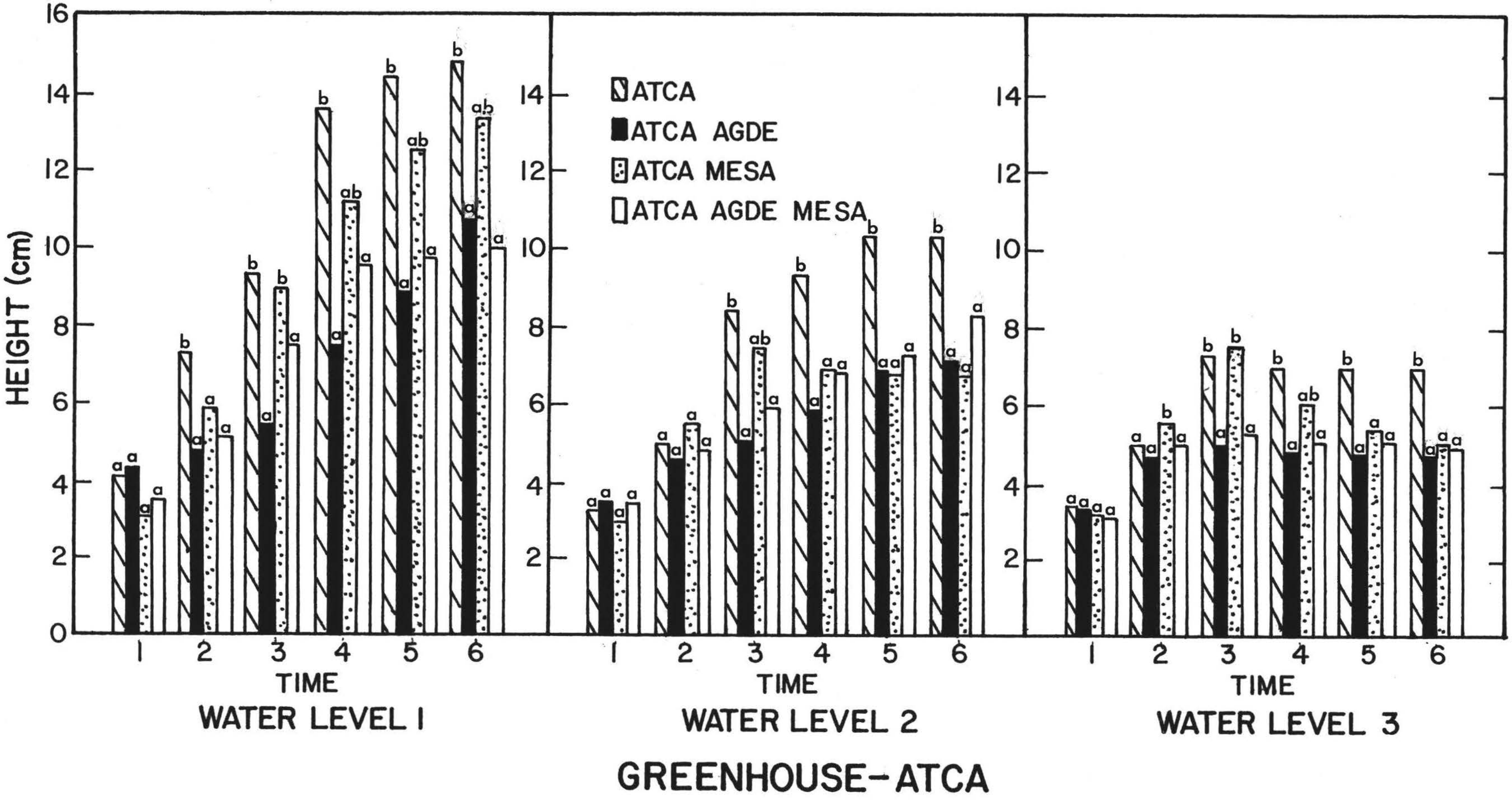


Figure 7. Height (cm) of Atriplex canescens (ATCA) at three water levels at six time periods growing in four planting treatments in the greenhouse. Bars with the same letters within a time period are not statistically significant at P = 0.05.

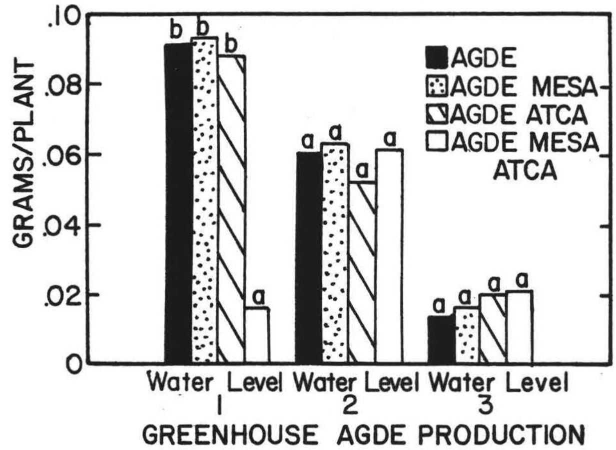
the lowest water levels, even when growing in combination with either AGDE or MESA.

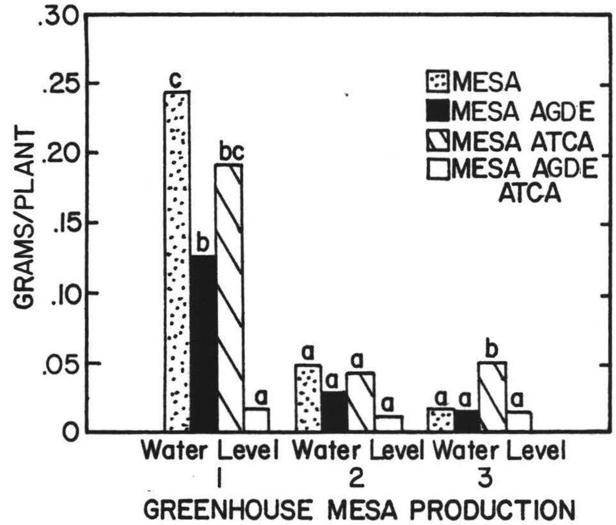
Shoot production per plant

Shoot production per plant was also examined in this study (Figure 8). At the high water level AGDE plants attained almost the same shoot weight, whether they were growing alone or in combination with MESA or ATCA with 0.091, 0.093, and 0.088 g/plant, respectively. AGDE plants in these combinations exhibited statistically greater shoot weights than in the three-species combination. At the second and third water levels, AGDE plants produced the same shoot weight whether they were growing alone or in combination with other species.

MESA shoots at the high water level were significantly heavier when growing alone (0.244 g/plant) than in the MESA-AGDE and three-species combinations. Conversely, the least shoot production occurred in the three-species combination (0.016 g/plant). No statistically significant differences in MESA shoot weight were found at the second water level. At the low water level, MESA plants exhibited the greatest production per plant when growing in combination with ATCA.

ATCA plants produced significantly more forage at the high water level when grown alone (0.183 g/plant) than when they were grown in any of the other species combinations. In the second and third water levels, no differences in ATCA shoot production existed between treatments. Additionally, there were no apparent reductions in growth in any of the treatments between water levels two and three. These data suggest that ATCA, which is well adapted to arid and semi-arid environments, does extremely well when growing under considerable water stress.





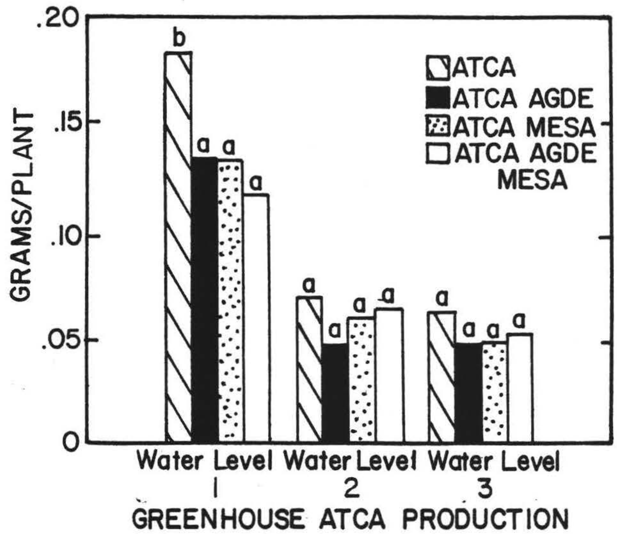


Figure 8. Final greenhouse production (grams per plant) of Agropyron desertorum (AGDE), Medicago sativa (MESA), and Atriplex canescens (ATCA) at three water levels in four planting treatments in the greenhouse. Bars with the same letters within a water level are not statistically significant at P = 0.05.

Total shoot production per pot

Water level #1. MESA growing alone exhibited significantly greater production (0.786 g/pot) than any of the other treatments. This was 2.4 and 2.8 times greater than the monoculture production of AGDE and ATCA, respectively (Figure 9). The ATCA-MESA combination was second in total production with MESA contributing 82% of the total production (0.732 g/pot). In the AGDE-MESA-ATCA combination, AGDE was the greatest contributor with 46% of the total production (0.249 g/pot), then MESA with 30% and ATCA with 24%. ATCA growing alone exhibited statistically the lowest production, while AGDE growing alone was intermediate. When AGDE was grown in combination with MESA or ATCA, it produced 68 and 71%, respectively of the total production.

Water level #2. In the second water level there were no significant differences among treatments. However, it is important to note that AGDE in any combination with MESA and/or ATCA contributed the greatest proportion of total production.

Water level #3. At the lowest water level there were no significant differences in total production among treatments. However, it is important to note that ATCA growing alone or in combination with AGDE and MESA produced the same quantity of shoot mass.

Total root production per pot

For all the species, there was a decrease in root production from the high to low water level.

Water level #1. The three-species combination was significantly greater in total root production than any other treatment with 0.48 g/pot (Figure 9). In that combination, AGDE produced 69%, MESA 23%, and

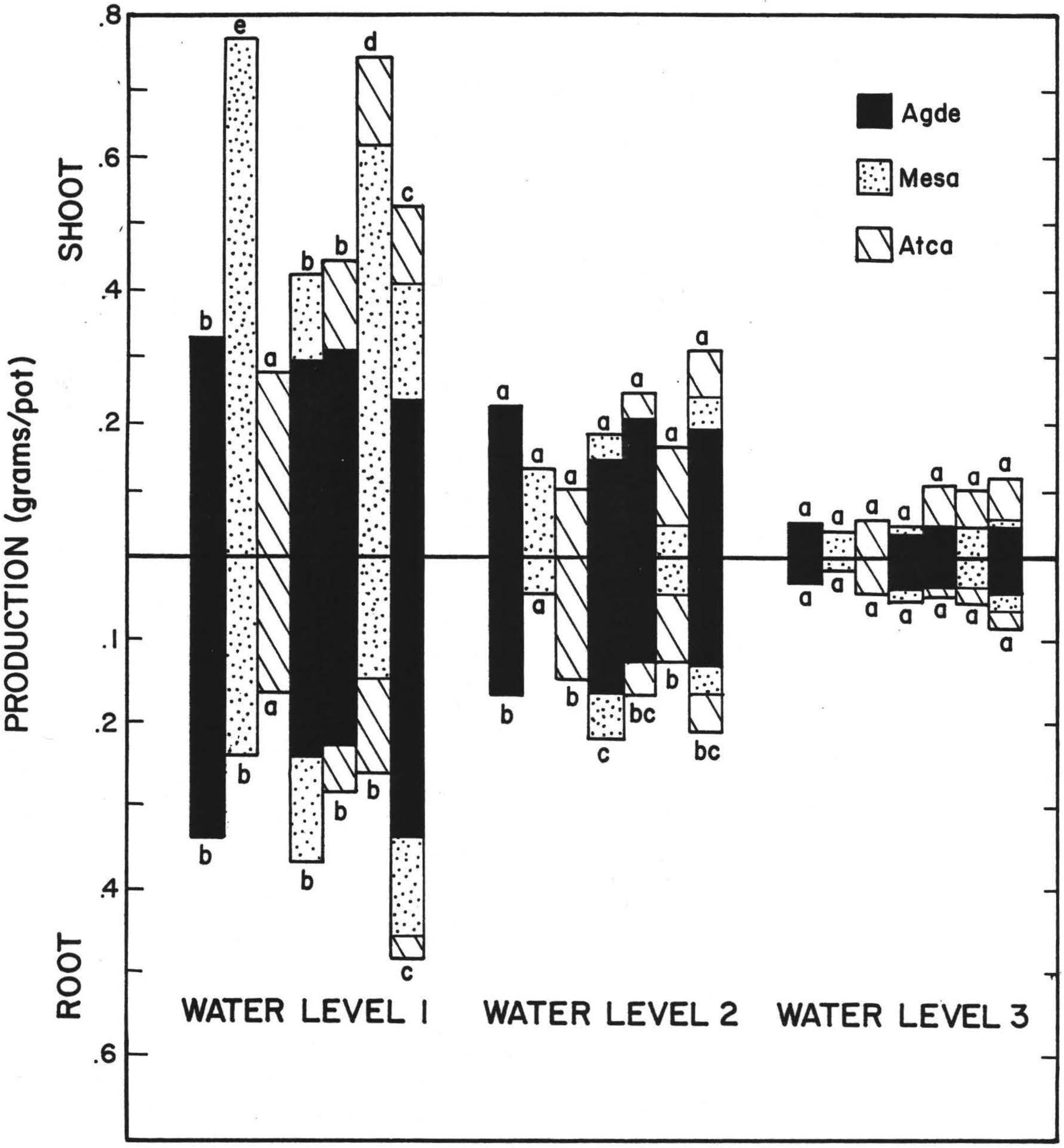


Figure 9. Final shoot and root production (grams per pot) for Agropyron desertorum (AGDE), Medicago sativa (MESA), and Atriplex canescens (ATCA) at three water levels growing in monoculture and each species in mixed planting treatments in the greenhouse. Bars with the same letters within a water level are not statistically significant at P = 0.05.

ATCA 8% of total production. The second highest root production occurred in the AGDE-MESA combination (0.37 g/pot) where AGDE made up 71% of total production. However, this combination was not significantly different than the AGDE-ATCA and MESA-ATCA combinations or AGDE and MESA growing alone. ATCA growing alone exhibited the significantly lowest root production among the treatments with 0.16 g/pot.

Water level #2. The AGDE-MESA combination exhibited more root production than AGDE, MESA, and ATCA grown alone. Again, AGDE in the AGDE-MESA combination accounted for the greatest percentage (73%) of total root production. MESA growing alone exhibited the statistically lowest root production.

Water level #3. At the lowest level, no statistically significant differences existed among treatments. However, ATCA growing alone tended to have a greater root biomass than when growing in combination with other species.

Green Canyon

Precipitation and soil moisture

Annual precipitation at Green Canyon in 1981 and 1982 was 8.9 cm and 20.5 cm greater than the long term average, respectively (Figure 10). The precipitation pattern in 1981 was generally closer to the long-term average than 1982. The summer of 1981 was a period of drought with only 2.4 cm precipitation received during August and September.

As expected, soil moisture varied among plots according to the amount of water applied along the line-source sprinkler system (Figure 11). Soil moisture measurements were taken at four depths (0-20, 20-40, 40-60, and 60-80 cm). The low water treatments were generally dry at

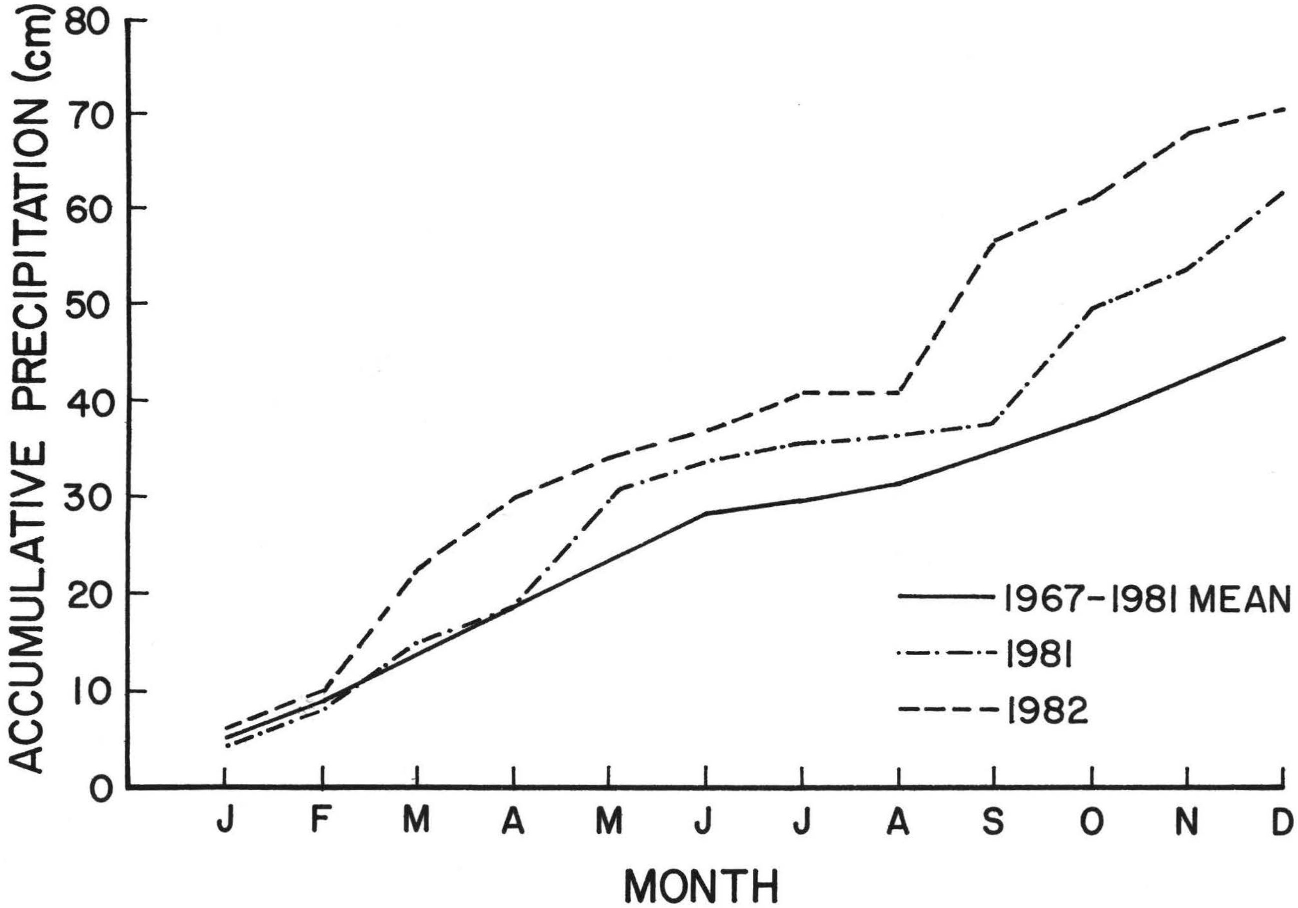


Figure 10. Accumulative annual precipitation (cm) for 1981 and 1982 as compared to the long-term average for the field study site at Green Canyon.

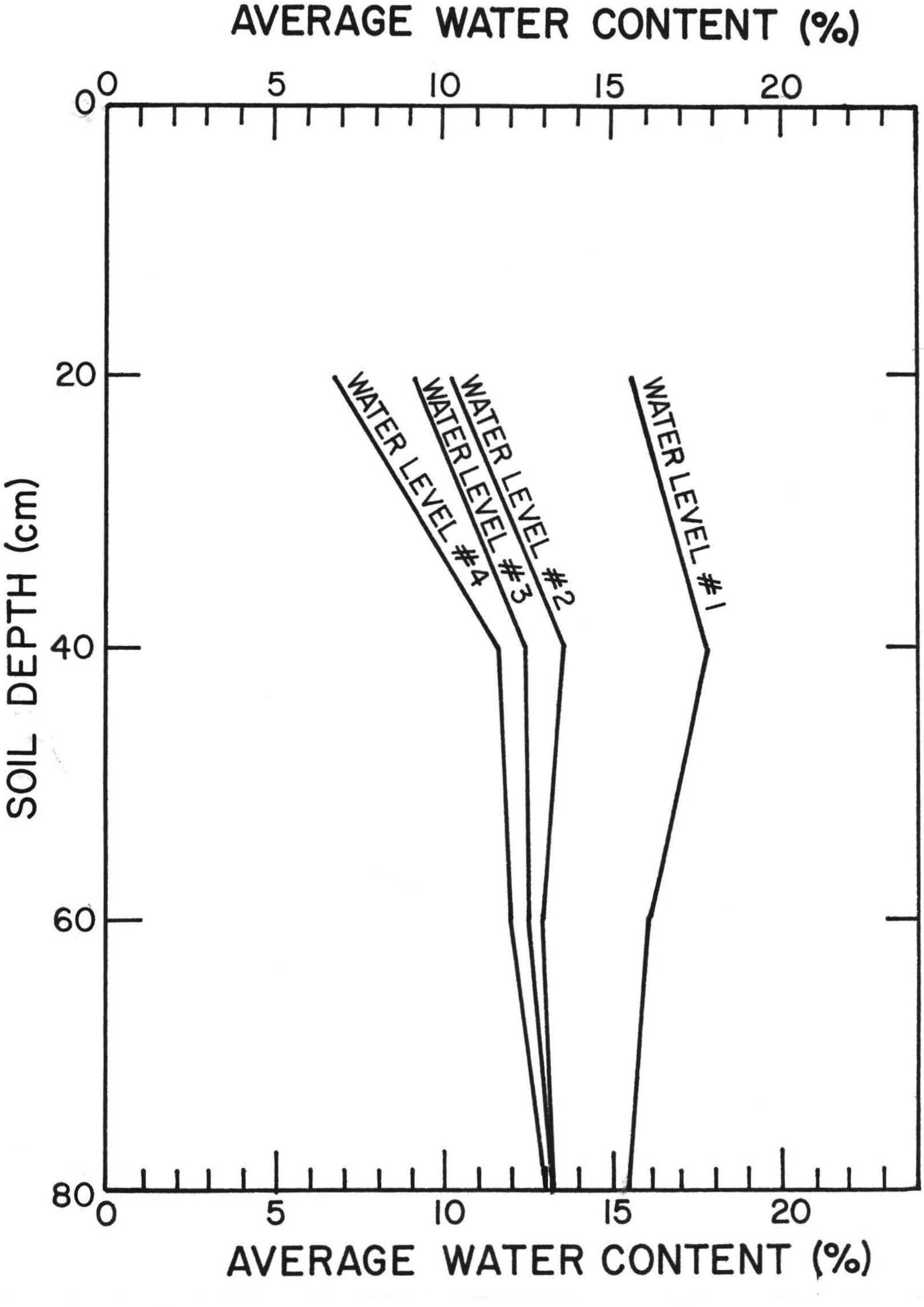


Figure 11. Profiles of gravimetric soil moisture content (%) for the four water levels at the field study site at Green Canyon. Values are averages for 20 measuring dates for July to August in 1982.

the surface with higher water contents at greater depths in the soil profile. Soil moisture content averaged 8.6, 9.3, 10.1, and 16.4% from the lowest to the highest water level in August, 1982.

The temperatures during the establishment phase in 1981 were 2^{o}C higher than the long-term average (Figure 12). The winter of 1981-1982 was characterized by early storms and long periods of cold temperatures, especially during February, when temperatures were lower than -20^{o}C. The spring was late and had great variations in maximum and minimum temperatures. However, the summer of 1982 followed the long-term maximum and minimum temperatures closely.

Emergence

Seed germination and subsequent seedling emergence in the summer of 1981 was significantly faster at the two highest water levels and occurred five days after seeding. Initial emergence was considered successful under arid and semi-arid conditions for AGDE and MESA at water levels 2 and 3, but not for ATCA (Figures 13, 14, and 15). AGDE and MESA had completed germination and subsequent emergence at the end of the 35-day observation period. However, new ATCA plants were still emerging at the end of the summer. Laboratory data indicated that even when seeds of this species were scarified, they did not germinate as readily as seeds of AGDE and MESA.

The emergence percentages were affected by and varied in relation to water levels. The difference in water distribution created by the line-source sprinkler resulted in different levels of soil moisture. As expected, fewer seedlings emerged at the lower water levels. The last row of plots, which received no water, few seedlings of any species

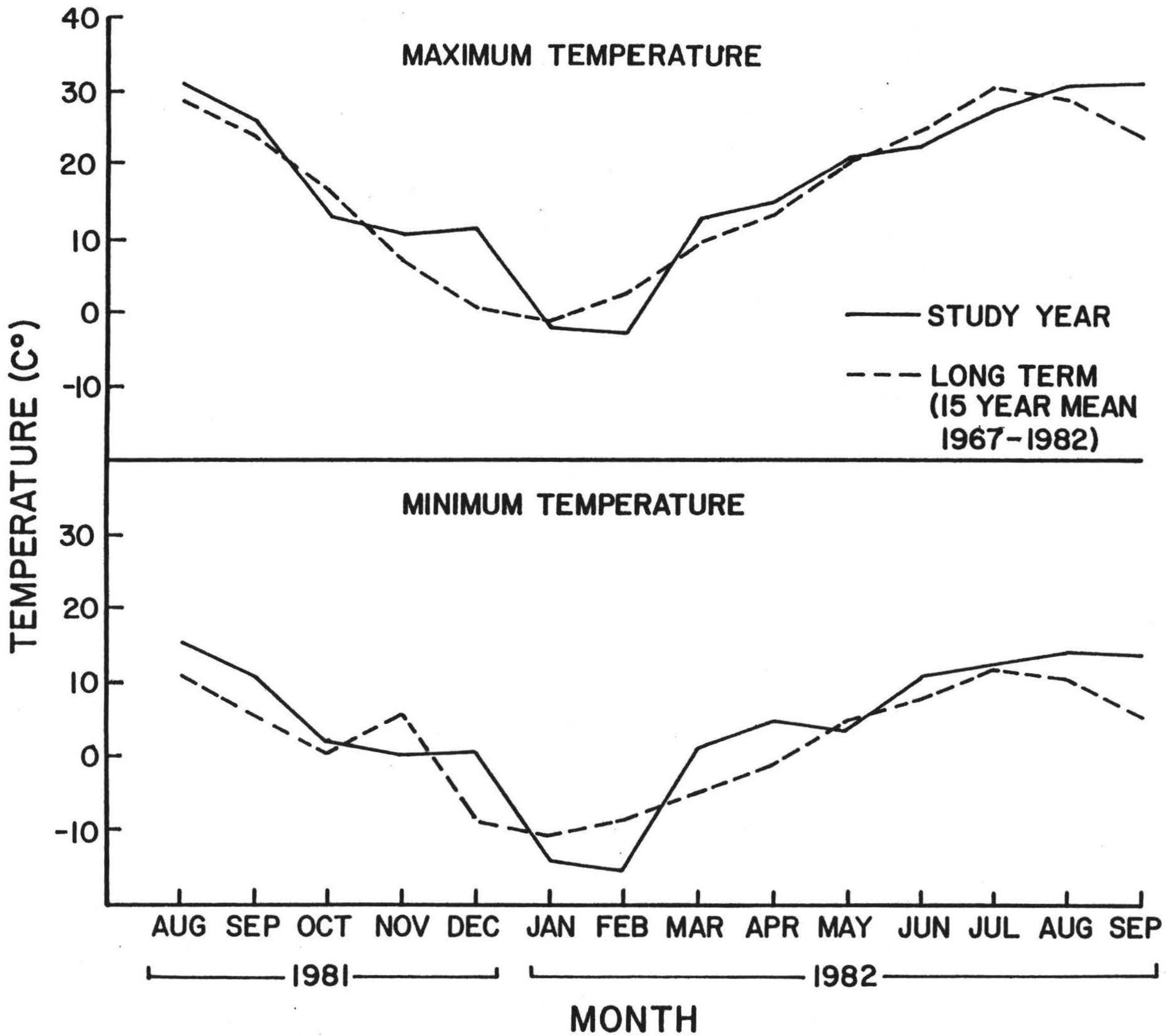


Figure 12. Monthly maximum and minimum temperatures (^{O}C) for 1981 and 1982 as compared to the long-term averages for the field study area located at Green Canyon.

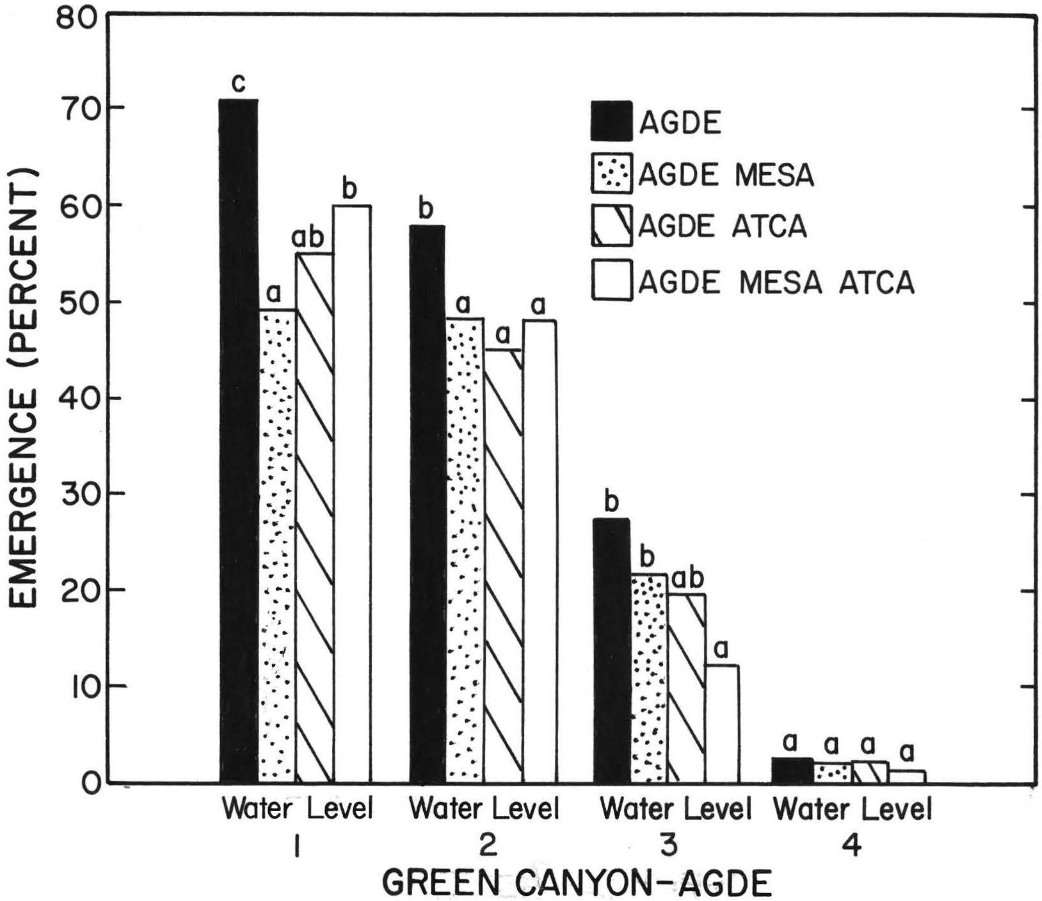


Figure 13. Seedling emergence (percent) of Agropyron desertorum (AGDE) at four water levels growing in four planting treatments at the field study site at Green Canyon. Bars with the same letters within a water level are not statistically significant at P = 0.05.

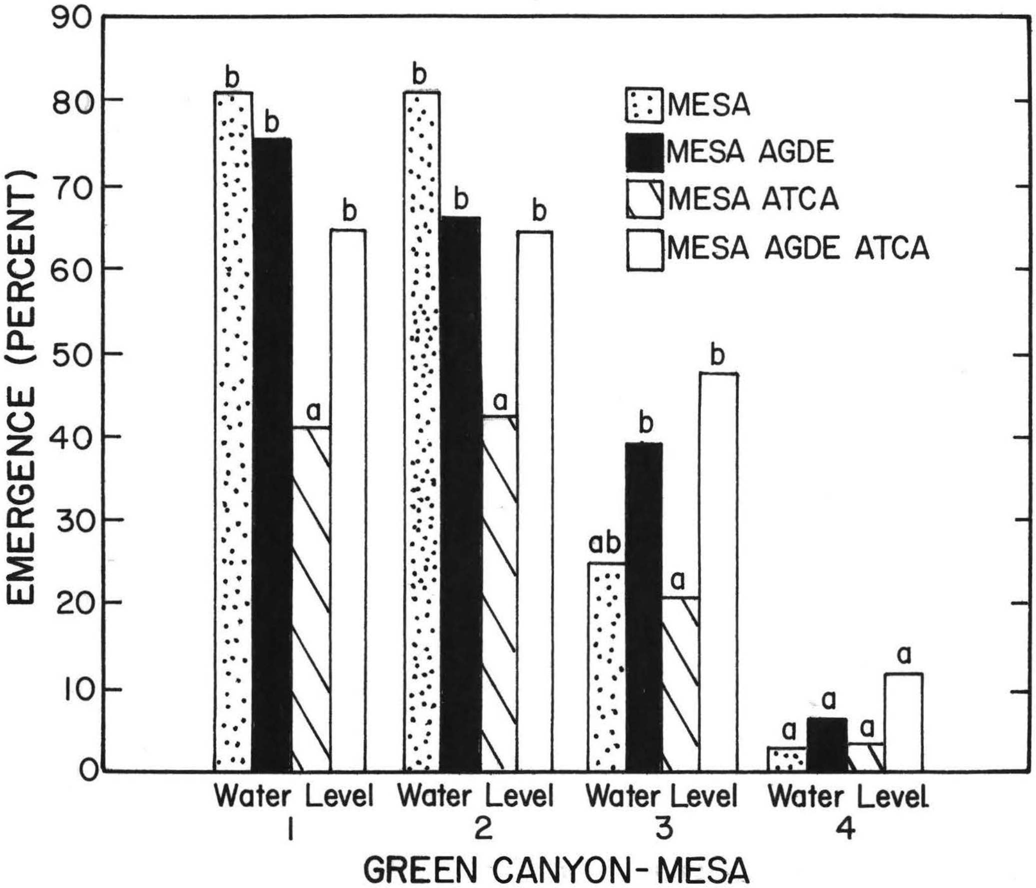


Figure 14. Seedling emergence (percent) of Medicago sativa (MESA) at four water levels growing in four planting treatments at the field study site at Green Canyon. Bars with the same letters within a water level are not statistically significant at P = 0.05.

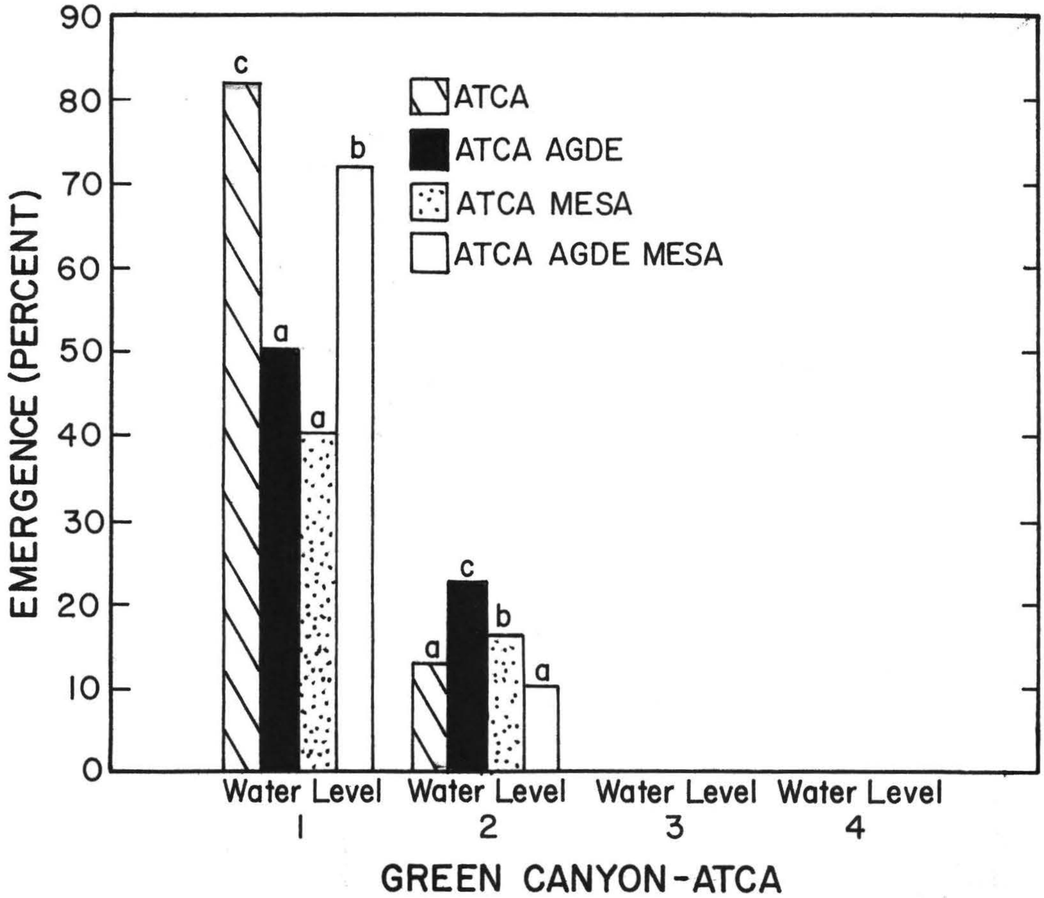


Figure 15. Seedling emergence (percent) of Atriplex canescens (ATCA) at four water levels growing in four planting treatments at the field study site at Green Canyon. Bars with the same letters within a water level are not statistically significant at P = 0.05.

emerged during 1981. However, some seedlings did emerge the following spring (1982), presumably because of enhanced soil moisture resulting from winter precipitation.

At water level one, AGDE growing alone exhibited a significantly greater emergence rate (71.8%) than any of the other species combinations (Figure 13). AGDE in combination with MESA exhibited significantly lower emergence percentages than AGDE growing alone (48%). Also, in the three-species combination, AGDE emergence was 18% lower than when it was grown alone. At the second water level no statistically significant differences existed among the other three planting treatments. At water level 3, the highest emergence percentages were attained when AGDE was growing alone or in combination with MESA or ATCA. AGDE in the three-species combination exhibited the lowest emergence rate (12.3%), which was statistically lower than when AGDE was grown alone or in combination with MESA. At water level 4, there were no statistically significant differences among treatments.

In the first two water levels, MESA growing alone exhibited the same emergence percentages with 81.8% (Figure 14). The MESA-ATCA combination had significantly the lowest emergence rates of any of the other planting treatments in water levels 1 and 2. The emergence percentages for the MESA-AGDE and MESA-AGDE-ATCA combinations were not statistically different in water levels 1 and 2. At water level 3, MESA growing in the AGDE-MESA-ATCA combination attained significantly higher emergence (47%) than only combination of MESA-ATCA. At water level 4, emergence percentages among treatments were not statistically different.

ATCA growing alone at the first water level attained significantly higher emergence rates than any of the other combinations (81.8%)

(Figure 15). ATCA in the three-species combination exhibited the second highest emergence rates (12% less than ATCA alone). ATCA in combination with MESA or AGDE showed the lowest emergence percentages. At the second water level, ATCA exhibited statistically greater emergence percentage (22.5%) when grown with AGDE than any other combination. In combination with MESA exhibited the second highest emergence rate. Alone and in the three-species combination, ATCA had significantly lower seedling emergence. No emergence was detected at the two lowest water levels.

Mortality

The percent of seedlings that dies during the second growing season (from May to September, 1982) was designated as the mortality percent. Competition among seedlings for moisture became more severe as they grew. Thus, phenology is an important factor influencing competition among seedlings. Although variations in survival among plants were also evident during the severe winter of 1981-82, these are not expressed as part of this mortality percent.

The portion of the two null hypotheses (p. 16) relating to percent mortality of the three species under greenhouse and field conditions exhibited no real differences and consequently were not rejected at the $P \leq 0.05$ level (Figures 16, 17, 18).

Plant height

Plant height attained by the end of the summer in 1981 varied among species and among water levels. The height attained ranged from 10 to 50 cm depending upon the species.

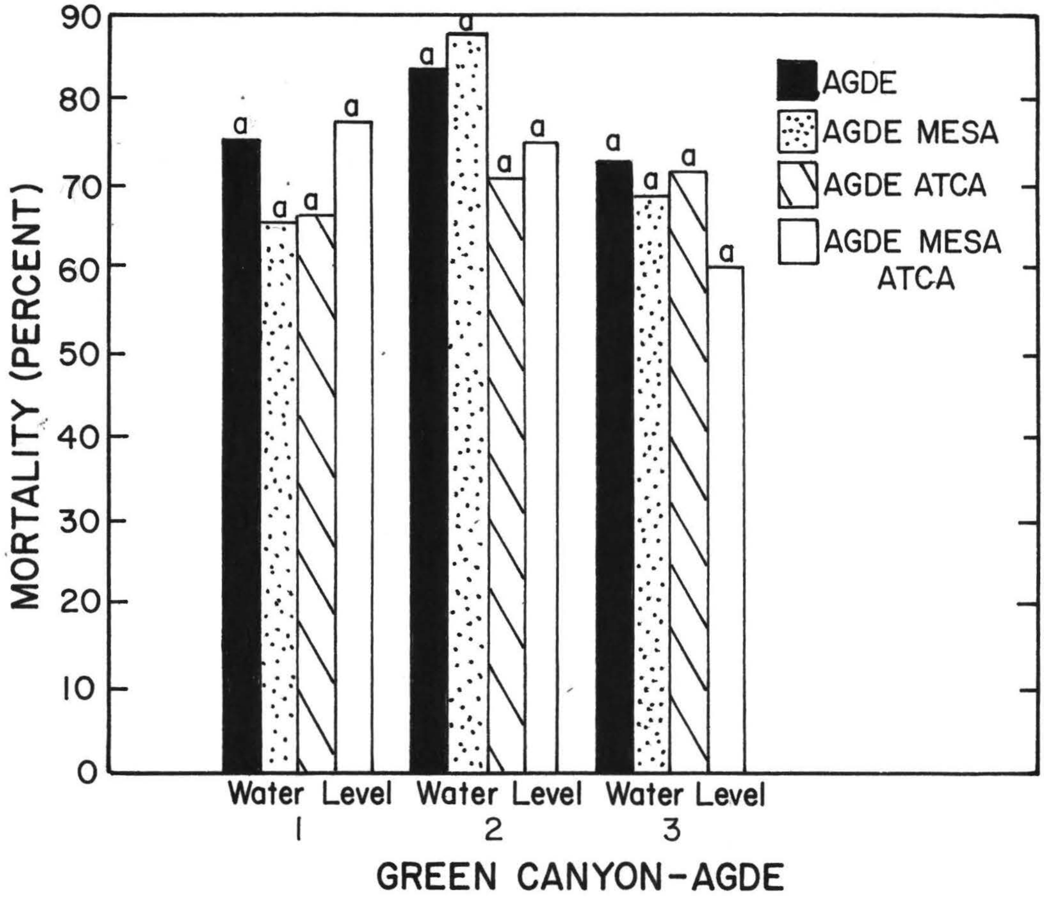


Figure 16. Mortality (percent) of Agropyron desertorum (AGDE) at four water levels growing in four planting treatments at the field study site at Green Canyon. Bars with the same letters within a water level are not statistically significant at P = 0.05.

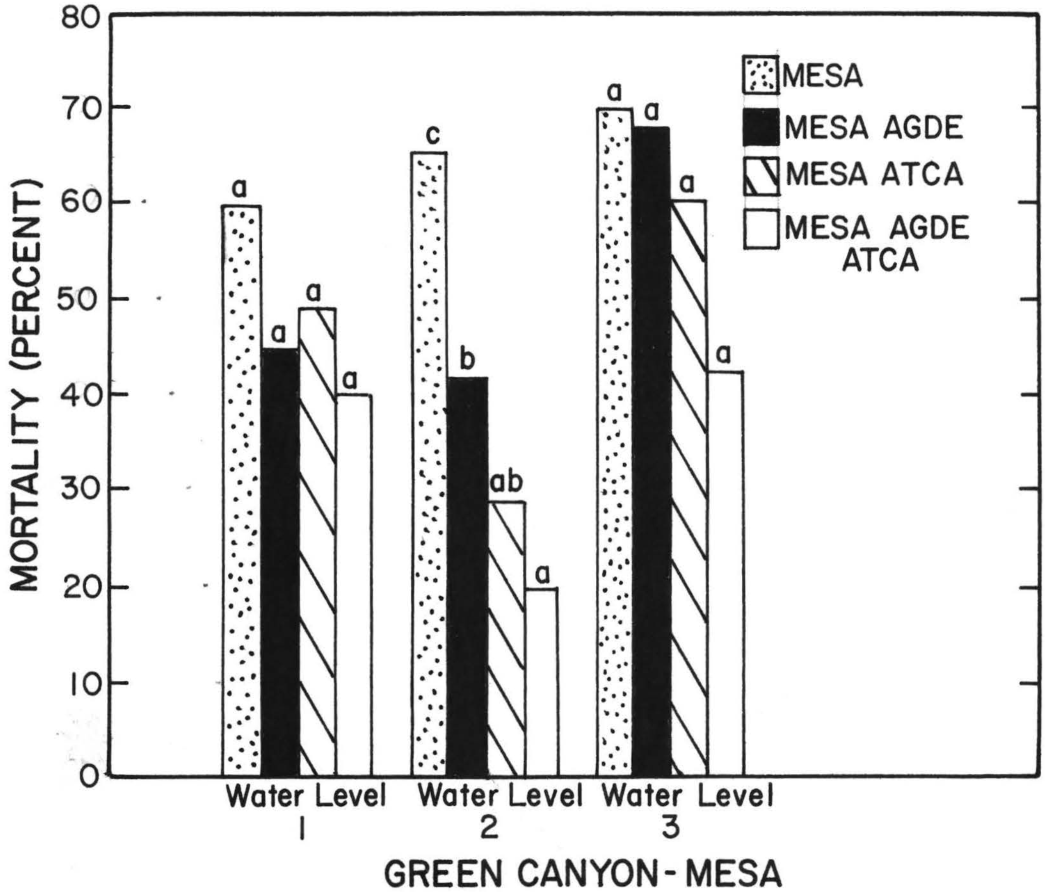


Figure 17. Mortality (percent) of Medicago sativa (MESA) at four water levels growing in four planting treatments at the field study site at Green Canyon. Bars with the same letters within a water level are not statistically significant at P = 0.05.

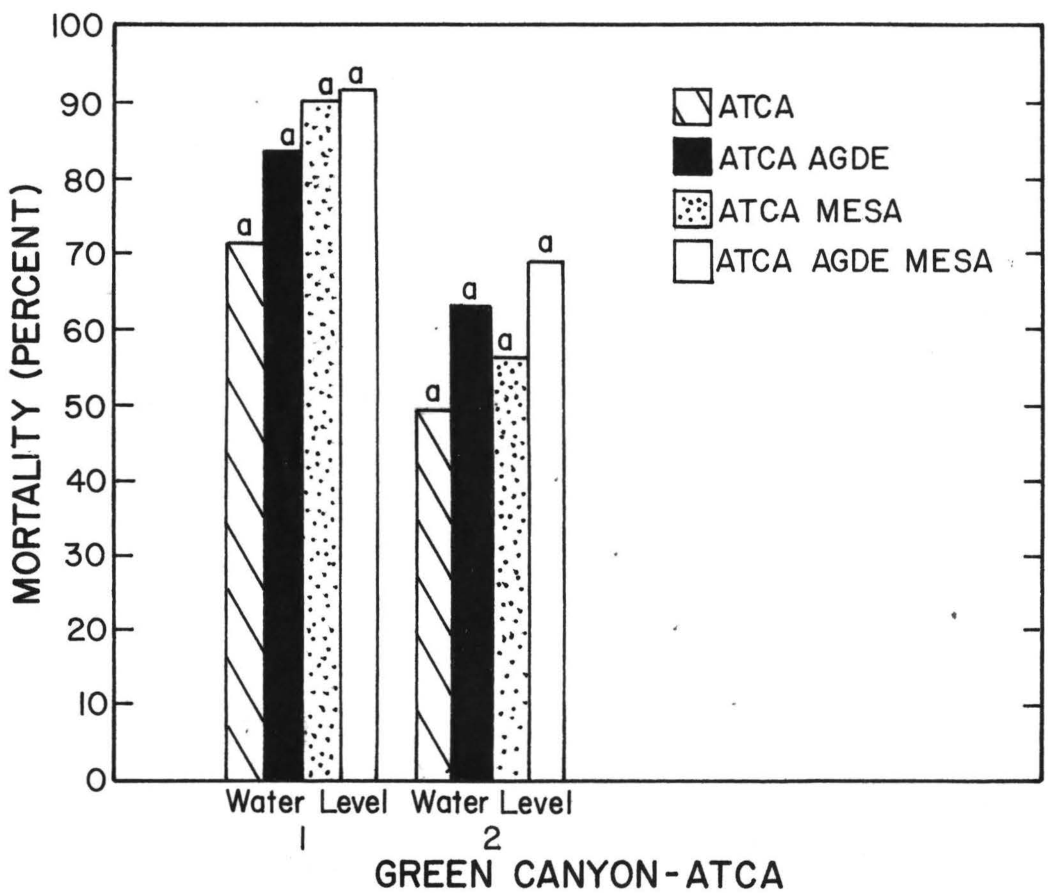


Figure 18. Mortality (percent) of Atriplex canescens (ATCA) at four water levels growing in four planting treatments at the field study site at Green Canyon. Bars with the same letters within a water level are not statistically significant at P = 0.05.

AGDE. At water level 1 when AGDE was growing with ATCA, it had 17% greater height than when growing alone (Figure 19). AGDE grew least in combination with MESA, achieving a height 11% less than AGDE alone and 27% less than the AGDE-ATCA combination.

At the second water level, AGDE in the ATCA combination attained the greatest height (19.5 cm). AGDE alone or in the three species combination exhibited the next greatest heights of 17 and 17.5 cm, respectively. The least heights for AGDE occurred in the AGDE-MESA combination (14.4 cm).

At water levels 3 and 4, no statistically-significant differences were detected among planting treatments. However, at both of these water levels, AGDE tended to be higher in the AGDE-ATCA combination.

MESA. At water level 1, MESA exhibited the greatest height (50 cm) when growing in combination with ATCA (Figure 20). MESA in the three-species combination and with AGDE exhibited the same height (44.6 and 44.1 cm, respectively). The shortest height at this water level was reached when MESA was growing alone (41 cm).

At the second water level, MESA growing in the three-species combination, alone, and with AGDE attained the greatest heights (42, 38.5, and 37.2 cm, respectively). The lowest height for MESA at this water level was reached in the MESA-ATCA combination. No statistically-significant differences were found among the planting treatments in water levels 3 and 4.

ATCA. ATCA growing alone achieved the greatest height in both water levels 1 and 2 with heights of 35 and 17.5 cm, respectively (Figure 21). No significant differences occurred among the other planting treatments

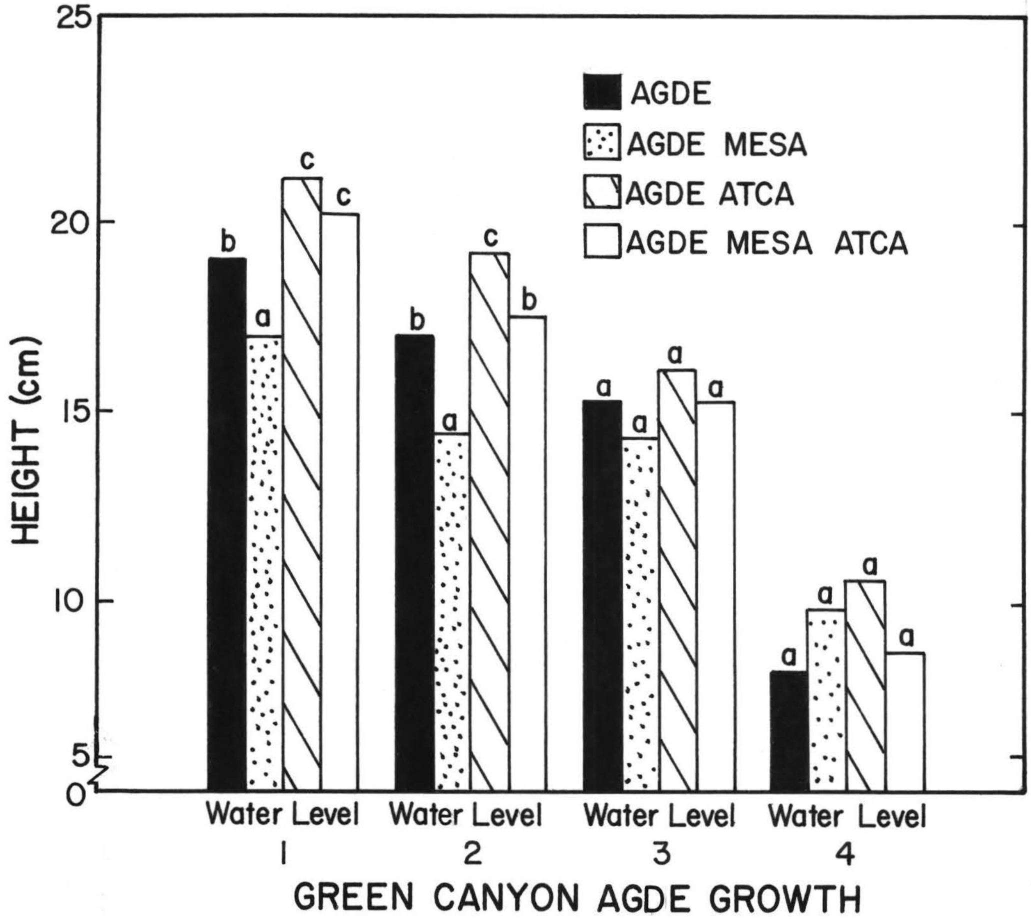


Figure 19. Height (cm) of Agropyron desertorum (AGDE) at four water levels growing in four planting treatments at the field study site at Green Canyon. Bars with the same letters within a water level are not statistically significant at P = 0.05.

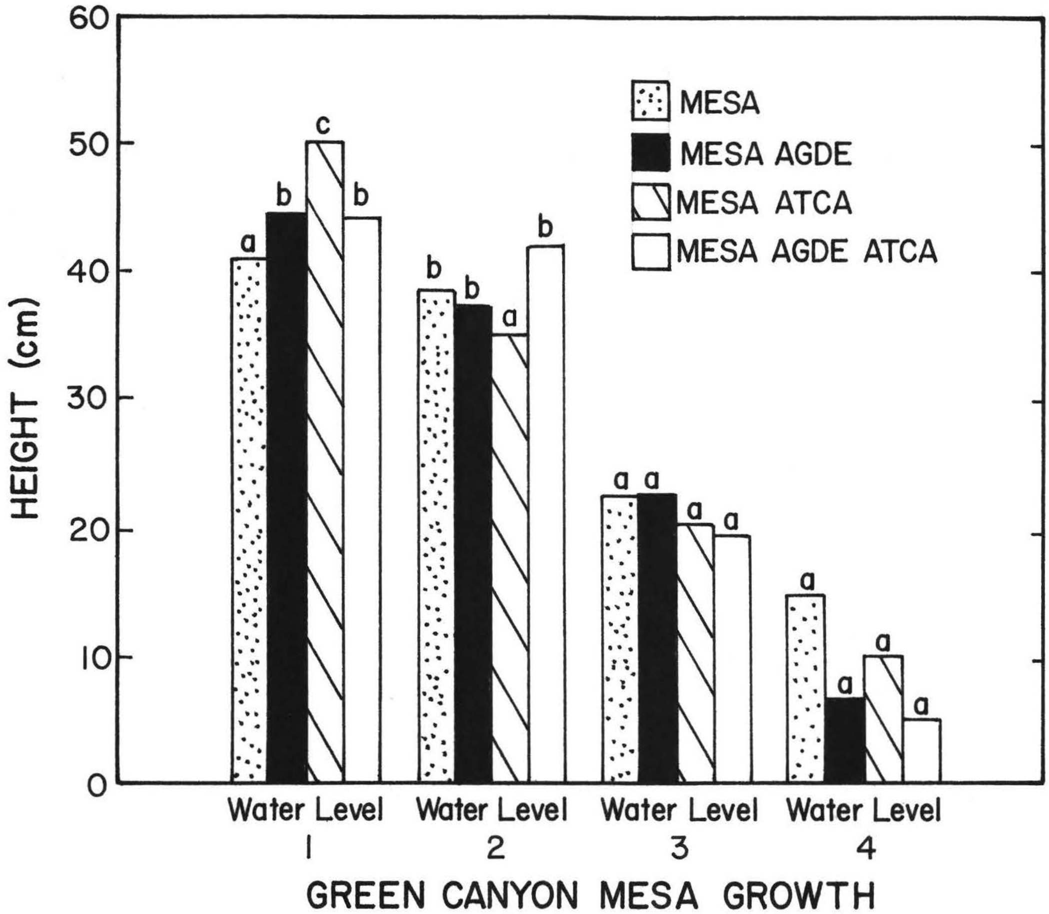


Figure 20. Height (cm) of Medicago sativa (MESA) at four water levels growing in four planting treatments at the field study site at Green Canyon. Bars with the same letters within a water level are not statistically significant at P = 0.05.

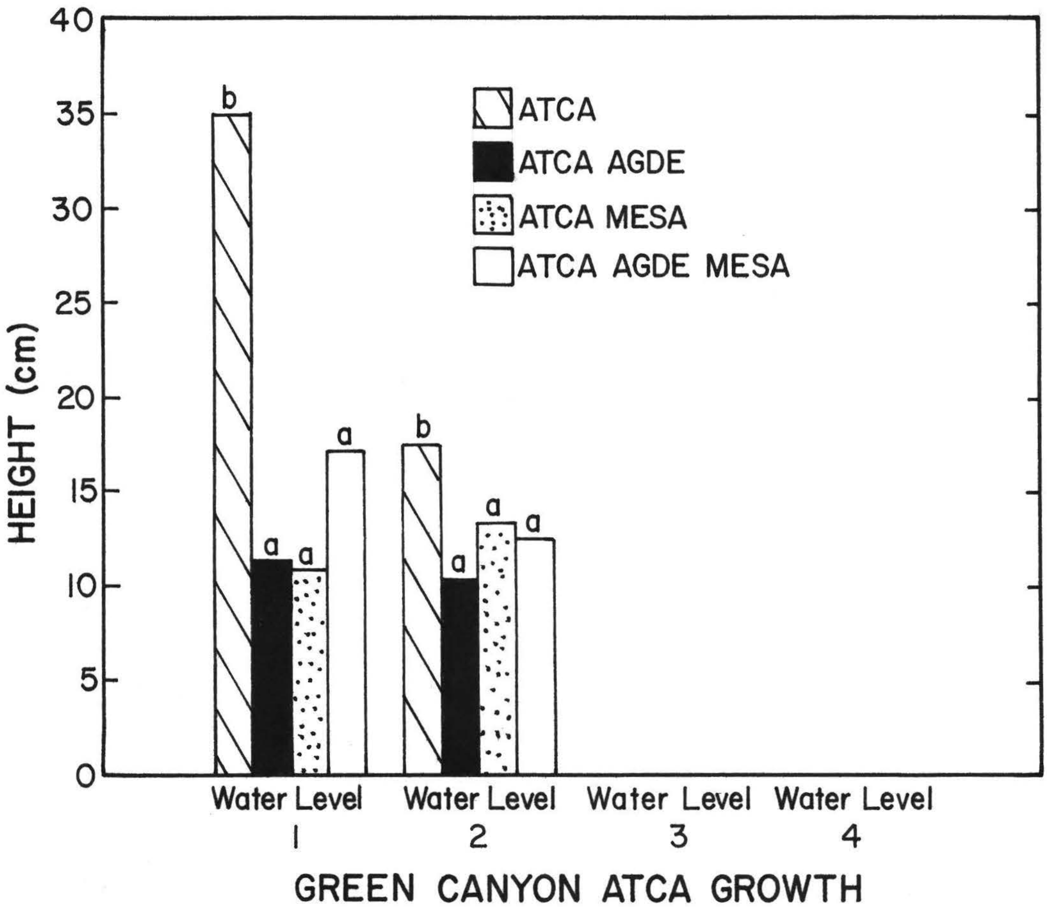


Figure 21. Height (cm) of Atriplex canescens (ATCA) at four water levels growing in four planting treatments at the field study site at Green Canyon. Bars with the same letters within a water level are not statistically significant at P = 0.05.

where ATCA was growing in combination with the other species. No plants of ATCA were present at water levels 3 and 4.

Weight per m^2

AGDE at the first two water levels exhibited the greatest production when it was growing alone and in combination with ATCA (Figure 22). In both the first and second water levels, AGDE growing in the three-species combination and with MESA exhibited the lowest shoot production. No statistically-significant differences existed among planting treatments in either the third or fourth water levels. However, there was a trend for AGDE growing alone to have the highest shoot production at both of these water levels.

MESA exhibited the greatest shoot production at the first water level when it was growing alone while the second highest production occurred when it grew in combinations with ATCA and AGDE (Figure 23). MESA growing in the three-species combination in the first water level had the least shoot production, with 56% less than when growing alone. For MESA at the second water level, the greatest shoot production was produced in the plot with the MESA-ATCA combination (562 g/plot) and MESA alone (469 g/plot) was second, respectively. However, when MESA was in the AGDE or three-species combination, shoot production was 46% and 56% less, respectively, than when MESA was growing alone. Although no statistically significant differences were present among planting treatments in water levels 3 and 4, there was a trend towards higher shoot production in the plots where MESA was growing alone and in combination with ATCA.

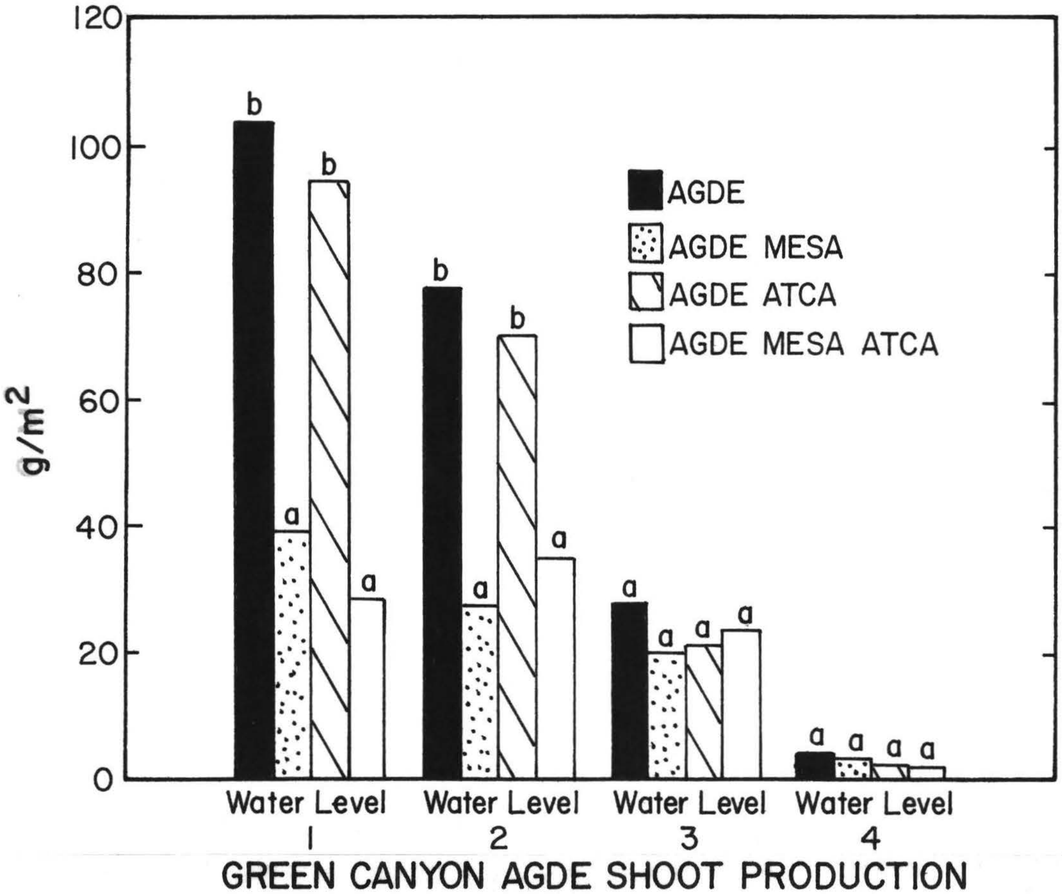


Figure 22. Shoot production (g/m^2) of Agropyron desertorum (AGDE) at four water levels growing in four planting treatments at the field study site at Green Canyon. Bars with the same letters within a water level are not statistically significant at $P = 0.05$.

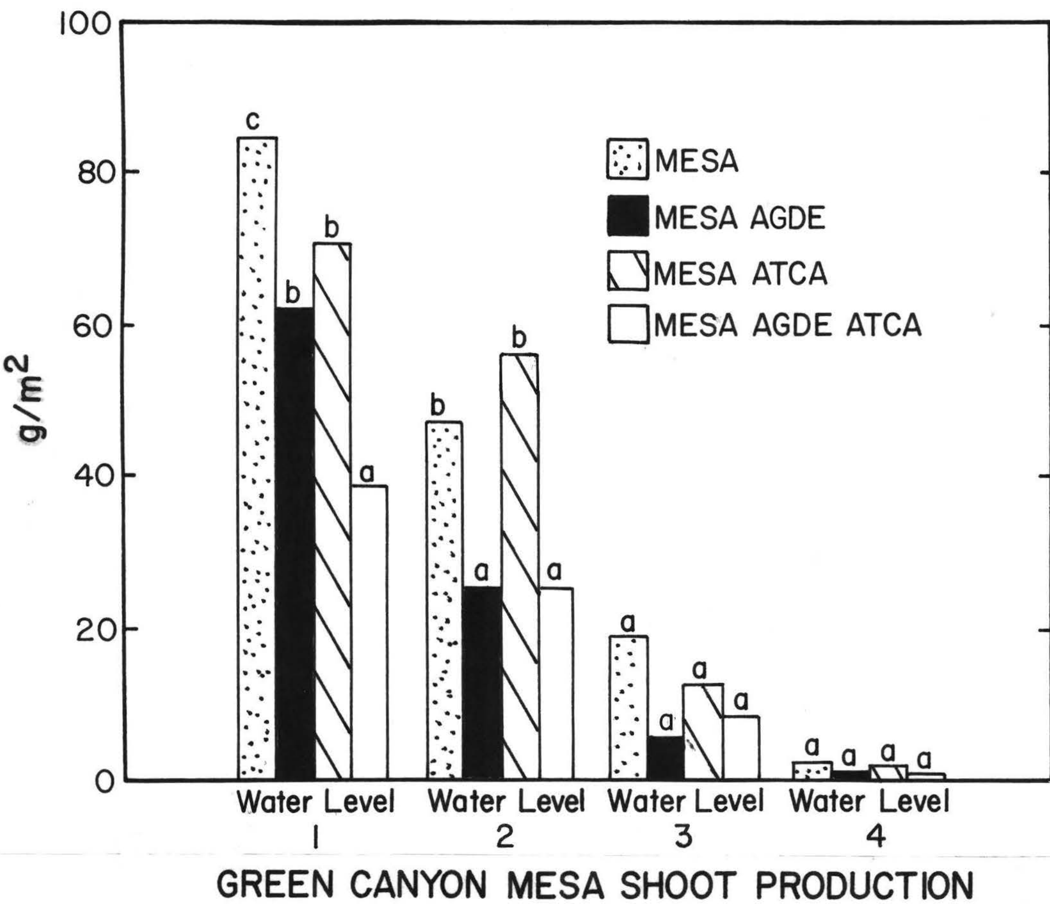


Figure 23. Shoot production (g/m^2) of Medicago sativa (MESA) at four water levels growing in four planting treatments at the field study site at Green Canyon. Bars with the same letters within a water level are not statistically significant at P = 0.05.

At the first two water levels, ATCA exhibited the greatest shoot production when grown alone (140 and 35.5 g/plot, respectively; Figure 24). The other planting treatments at these water levels showed no statistically-significant differences. No shoot production occurred for ATCA at water levels 3 and 4.

Total shoot production per m^2

Water level #1. MESA growing alone exhibited significantly greater shoot production (845 $g.m^2$) than any of the other treatments (8.0 and 6.0 times greater than AGDE and ATCA production, respectively; Figure 25). The MESA-ATCA and AGDE-MESA combinations yielded the second highest total shoot production. In the AGDE-MESA-ATCA combination, MESA contributed 76% of the total shoot production (106 g), followed by AGDE with 23% and ATCA with 1%. The lowest shoot production occurred in plots where AGDE and ATCA were growing alone and in the AGDE-ATCA and AGDE-MESA-ATCA combinations.

Water level #2. This water level exhibited the same pattern of shoot production as the first water level with MESA growing alone attaining statistically the greatest production (469 g/m^2). The MESA-ATCA combination exhibited the second highest production (281 g/m^2) followed by the AGDE-MESA combination (140 g/m^2). However, ATCA growing alone in this water level produced 46% less (77.5 g/m^2) than AGDE growing alone. The monocultures containing AGDE and ATCA, the AGDE-ATCA combination, and the three-species combination were not statistically different.

Water level #3 and #4. At these two water levels, no statistically-significant differences occurred among the planting treatments.

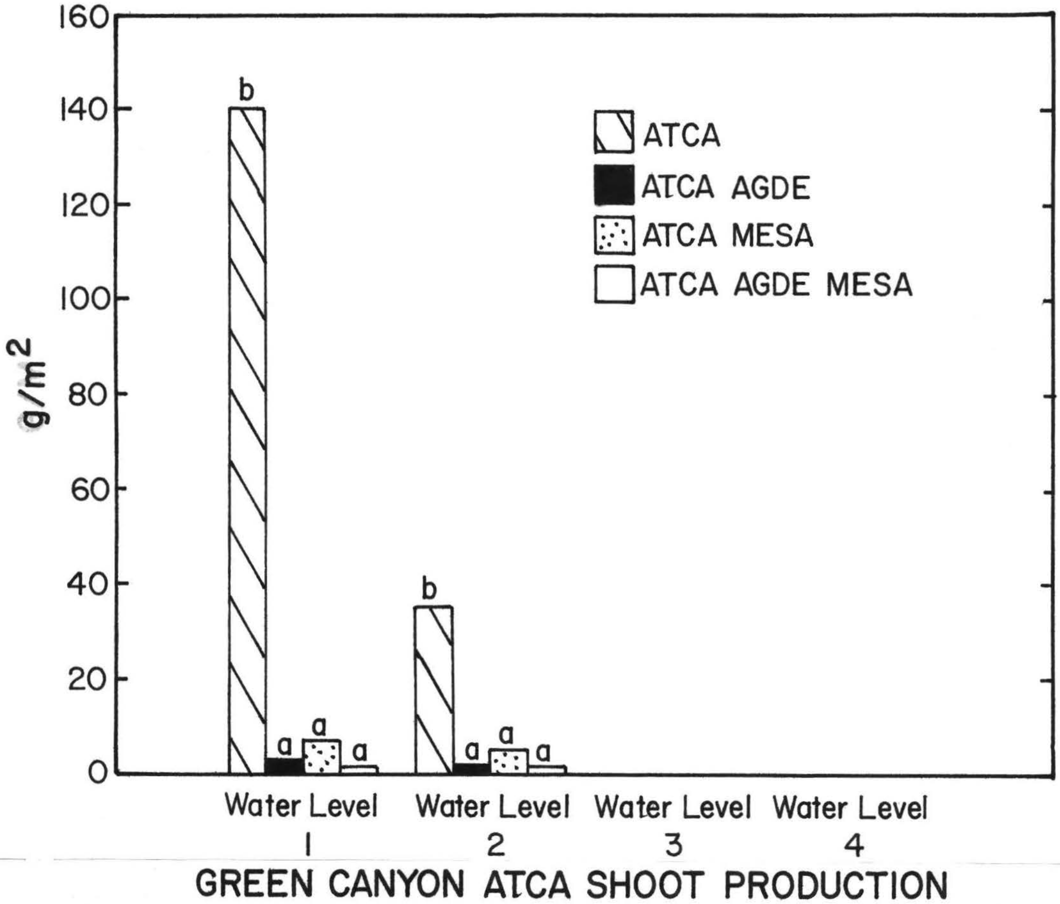


Figure 24. Shoot production (g/m^2) of Atriplex canescens (ATCA) at four water levels growing in four planting treatments at the field study site at Green Canyon. Bars with the same letters within a water level are not statistically significant at $P = 0.05$.

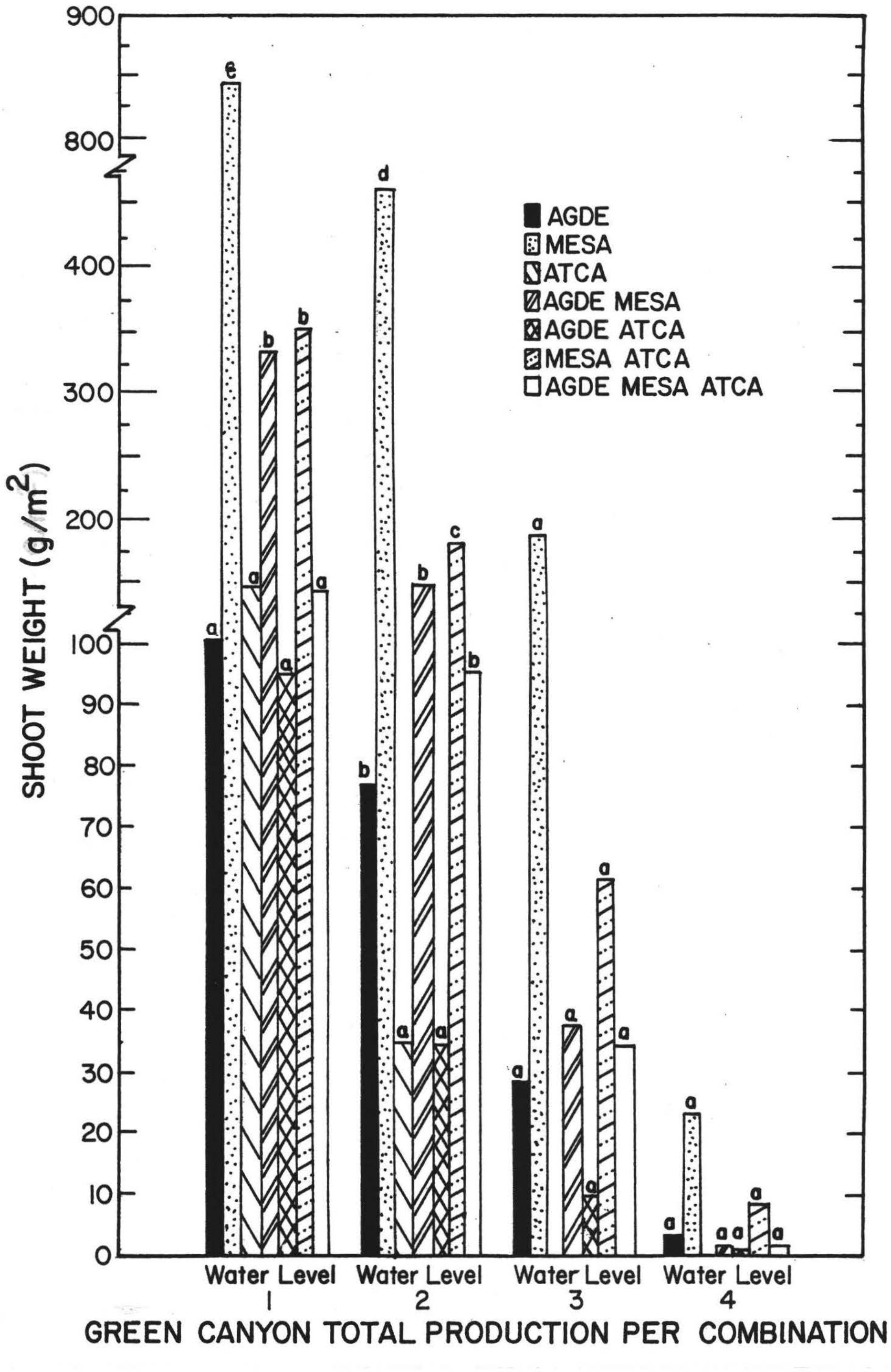


Figure 25. Shoot production (g/m^2) of AGDE, MESA, and ATCA growing alone and in combination at four water levels at the field study site at Green Canyon. Bars with the same letter within a water level are not statistically significant at P = 0.05.

However, at both water levels, there was a trend toward greater production in the plot with MESA growing alone.

DISCUSSION

At the first two water levels at Green Canyon, emergence was significantly higher when all species (AGDE, MESA, and ATCA) were grown alone. The lowest emergence rates were found for AGDE in the MESA or ATCA combination, for MESA in the ATCA combination, and for ATCA in the MESA combination. These results indicated that interactions can occur among species at early stages of plant development. One such interaction could be occurring below ground during germination. For example, Harper (1977) mentioned that some seeds can release toxic compounds that can influence the germination of other species. Leaching of allelopathic substances formed in some seeds can lead to toxic interaction. At high water levels, these substances can be transported to seeds of other species, inhibiting their germination. However, there are few examples where such interactions have been quantitatively documented as ecologically relevant.

AGDE in combination with MESA exhibited greater growth rates and weights per plant than when grown alone or in combination with ATCA. This may have been due to nitrogen fixation by alfalfa at the first two water levels, as evidenced in the greenhouse by observation of nodulation on the alfalfa roots. Johnson et al. (1983), Rumbaugh et al. (1982a), and Campbell (1963) found a similar beneficial effect when MESA was interplanted in stands of AGCR. AGCR produced significantly more forage when growing in combination with MESA than with ATCA. Protein content also was enhanced.

Harper (1977) used the term non-competitive interference when one plant symbiotically fixed nitrogen that could be used by another plant species. Hanson (1972) and Johnson et al. (1983) suggested that under severe moisture conditions MESA also may supply N for growth of associated grasses by root excretion, sloughing of nodules, or decay of the root system. These amounts may be substantial as documented by Dilz and Mulder (1962) who reported that MESA supplied 8% of the N contained in rye grass shoots during the main growing period.

Pot cultures force mixed species to use the same root space and soil resources. Thus, the nitrogen provided by MESA could be rapidly used by AGDE. Such greenhouse results could possibly be related to some field situations where rooting volume is restricted by soil limitations, such as caliche or hardpan layers, that prevent or inhibit root penetration.

At all water levels, MESA in combination with AGDE exhibited the least growth. The competitive advantage of AGDE over MESA in the greenhouse was evident. This dominance suggested that AGDE had a greater growth rate and also had the ability to extract more resources from the limited soil volume than MESA. AGDE may have a particular advantage over MESA because of its finer and more abundant roots. Hanson (1972) found similar results and concluded that grasses commonly grown with MESA have a much greater proportion of their root systems in the upper 30 cm of the soil layer than MESA. For this reason, grasses may more efficiently utilize the upper soil resources than MESA.

However, when MESA was grown in combination with ATCA, biomass production and growth of MESA was not suppressed. MESA in this combination grew faster than ATCA and may have utilized the limited resources, such as water and light, more efficiently. Light can be extremely important in that the species with the faster growth rate could shade and, thereby, restrict the growth of the other species. This may reduce the rate of photosynthesis in the subordinate species. This shading may have been particularly detrimental for ATCA, a C_4 species which would require high light intensities for light saturation. Because maximum photosynthetic activities could not be achieved with shading, growth rates would be reduced (Ehleringer 1978, Ehleringer and Bjorkman 1977). Black (1959) noted that the optimal utilization of solar radiation will not be realized unless there is maximum absorption by the leaves. Consequently, it is important that a high leaf area index be developed early to optimize energy absorption.

Clearly, no two species have exactly the same resource requirements. Nevertheless, AGDE, MESA, or ATCA have unique potentials to compete when they are exploiting the same resources. Their success depends, therefore, either on partitioning the resource to minimize competition or in the establishment of competitive superiority.

Undoubtedly, the behavior of plant populations grown in pots is far removed from the complexities of range ecosystems. In the greenhouse experiment, extremes of environmental conditions that may be critically important in the field, may have been avoided. Also, in the field study (Green Canyon) environmental factors, such as soil moisture levels and removal of competition from weedy vegetation, were altered. However, MESA at Green Canyon behaved differently than in the greenhouse. In the greenhouse AGDE was the dominant species probably because the plants were transplanted at the early seedling stage. MESA growing in the greenhouse in the three-species combination at water levels 2 and 3 exhibited the lowest growth rates and biomass productions; however, in the field MESA was the dominant species. Also, when the AGDE and MESA species were sown at the same time under field conditions, MESA exhibited the ability to germinate and emerge faster than AGDE. MESA seedlings subsequently gained an advantage in exploiting resources. The growth rates of young MESA plants were greater perhaps because they became established before AGDE and ATCA, and consequently were able to preempt resources in the upper soil layers and capture more sunlight. In this way, MESA could have restricted the growth of the other two species. Also, the success in production of MESA could have been due to the favorable precipitation received during the second growing season (Figure 25).

MESA growing in the field at the highest water level and in combination with ATCA exhibited greater height than when in combination with AGDE or growing alone. These results suggested that for MESA, ATCA with its slower growth rate was less competitive than AGDE. At this water level, moisture was not limiting.

ATCA in both the greenhouse and field environments in any of the combinations with MESA and/or AGDE exhibited lower growth and production than when alone. This was particularly the case at the two highest water levels where water and nutrients were available and may have been utilized faster by AGDE and MESA. Species with rapid shoot growth typically exhibit high root absorption capacity and nutrient demand (Chapin 1980). ATCA is a species which predominates in infertile and arid habitats and has evolved a low relative growth rate. Results of this study show that ATCA, when growing at the same time and in the same soil layers with species of higher growth rate, does not do as well as when growing alone. Similar results were reported by De Puit et al. (1980a), who attempted to establish diverse native plants on strip-mined coal fields in Montana. They found that biomass production by ATCA was significantly reduced when grown with dominant perennial grasses and noted that ATCA was particularly susceptible to competition during early establishment.

Seedling growth of MESA-AGDE-ATCA may be seriously suppressed by high densities of weeds, because weeds are effective competitors for limited soil moisture
moisture and favorable temperature in the spring caused large numbers of weed seeds to germinate. Furthermore, the winter environment may break the dormancy of many weed seeds so that they germinate in early spring and are able to germinate and emerge soon after the species mixture is planted. By the time the AGDE-MESA-ATCA seedlings emerge from the soil, weed seedlings frequently have made some growth and have a competitive advantage. Consequently, greater mortality in the AGDE-MESA-ATCA seedlings occur than would be the case where weed control is practiced.

Water is often the critical factor determining what vegetation will grow in a given area. Therefore, the average annual precipitation received by an area should be checked before planning any reseeding program that includes species mixtures. Plummer et al. (1968) suggested that annual precipitation usually should be more than 9 inches where artificial seeding of the most drought tolerant species is part of the restoration program. The results from Green Canyon agree with this suggestion because at the lowest two water levels ATCA did not germinate and only a few plants of AGDE and MESA were established. However, the fact that seeding was done in mid-summer likely influenced my results adversely, particularly in respect to ATCA.

The time of seeding AGDE-MESA-ATCA mixture could markedly influence the emergence and seedling growth of the individual species, because temperature could affect germination, emergence and competition indirectly as it affects seedling growth of each species. Hanson (1972) mentioned that alfalfa established itself quickly under the higher temperature conditions and developed a deep primary root system. For this reason the reseedings should be done in a season that can provide the optimum moisture conditions for establishment. Fall is generally considered the optimum season because the seed lies in the cool environment of the soil, and dormancy can be broken during the winter. Later when the temperature rises to a degree sufficient to permit it, germination can begin during March through April when precipitation from snow provides enough soil moisture.

In pot culture, where plants are forced to utilize the same resources, species which have a greater ability to exploit these resources have a competitive advantage. When MESA and ATCA were grown in any of the combinations with AGDE, they exhibited a decrease in plant weight. Harper (1977) noted that the frequency distribution of plant weight became strikingly skewed by the end of the growing season. At this time a hierarchy of individuals had established with few large dominants and a larger number of suppressed plants. However, it is important to understand the inter-related growth between roots and shoots. Roots and shoots perform functions that are distinct, but which are mutually important. A reduction in nutrient supply to the shoots caused by root competition will lower the plant's ability to compete for light. This in turn will reduce the flow of assimilates to the roots, thereby impairing root function (Fitter and Hay, 1981).

In both the greenhouse and field environments, MESA produced more when growing alone than in combination with AGDE and/or ATCA. However, MESA did not exhibit the same production responses for the various combinations in the greenhouse and Green Canyon studies. For example, when MESA was growing with AGDE, it produced the least proportion of total production in the greenhouse, but the most in Green Canyon. In the greenhouse, AGDE contributed the highest proportion of total production in any of the planting combinations with MESA or ATCA. However, in the same planting combinations under field conditions MESA provided the greatest proportion of total production.

Harper (1977) explored the competitive relationships between planting mixtures of DAGL and MESA. He found that sometimes dominance was incomplete and that a transgressive behavior existed in which the mixture yielded less than the lowest or more than the highest yield of the pure stand. A similar response was found by McCloud and Mott (1953). They reported that the performance of legume-grass mixtures varied and, depending on environmental and competitive situations, could be mutually beneficial, have no interaction, or be beneficial to only one species. All of these responses clearly illustrate the wide diversity of competitive and associational effects that grasses may have in different years when grown with alfalfa.

AGDE, MESA, and ATCA have differences in basic morphological and physiological characteristics of their roots that may have affected the nature of competition among species in various mixtures. In the greenhouse study at the high water level, AGDE proliferated a greater root mass at a faster rate than MESA or ATCA. This greater root mass for AGDE likely affected competition among the species. Water and mineral uptake was likely influenced by both soil factors and plant demand, and the depletion zones around adjacent roots may have frequently overlapped. This may have resulted in interference among roots from the various species. In the greenhouse study, AGDE at the high water levels may have extracted water resources faster for growth and biomass production, and at the same time deprived MESA and ATCA of these resources. However, at low water levels, ATCA produced more above and below ground biomass than AGDE and MESA. ATCA, which typically grows in arid habitats, tended to survive better than either AGDE and MESA under drought stress. This may have resulted from either its ability to minimize water loss or its capacity to osmotically adjust.

CONCLUSIONS

The conclusions reached in this study are:

1. The production of MESA was severely reduced when it was grown in combination with another species.

2. In the field, conditions for germination, emergence and subsequent seedling establishment were more favorable for MESA and allowed it to dominate over the other two species at the two highest water levels.

3. Based upon the low establishment at the low water levels in the field for all three species, species mixtures will be difficult to establish from seed under arid or semi-arid conditions. However, these results must be evaluated in light of the atypical seeding in August.

4. After successful establishment, ATCA is a species which is highly tolerant to water stress and can compete well for water and nutrients.

5. Species with relatively slow growth rates, such as ATCA, will exhibit poor establishment when seeded in the same season in mixtures with species of high growth rate.

6. The germination, emergence, and establishment of AGDE, MESA, and ATCA ~~was~~ were higher when grown alone than when grown in combination with other species suggesting that the establishment of seed mixtures from field plantings could be difficult.

7. The proportion of species that established in the mixed species plantings in the field were markedly different than the proportion of seeds in the original seeding mixture.

8. The mortality of seedlings was high at low water levels, despite control of weeds as a factor in early establishment. Weed competition would provide even greater competitive stress and presumably greater mortality.

Data from the field (Green Canyon) confirmed that the early establishment phase of mixed species plantings is one of the most important factors that should be considered in reseeding rangelands. This is particularly true when dealing with species differing in phenology, such as AGDE, MESA, and ATCA. The lack of successful seedling establishment of ATCA was particularly disappointing. Establishment conditions greatly favored MESA and AGDE.

The results of this study suggested that other planting designs should be examined. These planting arrangements might minimize the stress from interspecific competition. Future studies should be designed to investigate the effect of competition between species when grown in separate rows. Additional research is needed to derive successful methods for establishing species with low germination, emergence, and growth rates in mixtures of species with high growth rates to efficiently exploit resources and increase rangeland production.

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APPENDIX

Agropyron cristatum (L.)	= AGCR
Agropyron desertorum (Fisch. ex Link) Schult.	= AGDE
Agropyron elongatum (Host) Beauv.	= AGEL
Agropyron intermedium (Host) Beauv.	= AGIN
Agropyron spicatum (Pursh.) Scribn. and Sm.	= AGSP
Agropyron trichophorum (Link) Richt.	= AGTR
Artemisia tridentata Nutt.	= ARTR
Astragalus cicer L.	= ASCI
Astragalus falcatus Lam	= ASFA
Atriplex canescens (Pursh) Nutt.	= ATCA
Atriplex confertifolia (Torr. and Frem.) S. Wats	= ATCO
Dactylis glomerata L.	= DAGL
Elymus junceus Fisch.	= ELJU
Medicago sativa L.	= MESA

VITA

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