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Paul B. Baker
Utah State University

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NUTRIENT AND WATER INTERRELATIONSHIPS BETWEEN CRESTED WHEATGRASS AND TWO SHRUB SPECIES

by

Paul Brian Baker

A thesis submitted in partial fulfillment
of the requirements for the degree of
MASTER OF SCIENCE
in
Range Ecology

Approved:

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TABLE OF CONTENTS

Chapter

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

Nutrient and Water Interrelationships between Crested Wheatgrass and Two Shrub Species

by

Paul B. Baker, Master of Science
Utah State University, 1988

Major Professor: Dr. James H. Richards
Department: Range Science

When crested wheatgrass (Agropyron desertorum) grows in mixture with sagebrush (Artemisia tridentata), its production declines. Its production increases when grown in mixture with fourwing saltbush (Atriplex canescens), according to previous reports. This study investigated soil water extraction and potassium (K) nutrition of the two shrubs to identify possible causes of the differential responses of crested wheatgrass.

Crested wheatgrass had reduced, rather than increased, nitrogen (N) and K yield in mixture with fourwing saltbush. No differences in N and phosphorous (P) concentrations were observed between sagebrush and fourwing saltbush, but fourwing saltbush had a much higher K concentration and returned nearly twice as much K to the soil as sagebrush by throughfall and litterfall. Throughfall additions were much greater than those from litterfall.

A K-fertilization/water-stress, two-factor greenhouse experiment was conducted with crested wheatgrass. High- and medium-K-fertilization treatments had highest tissue K concentration, but biomass yield was reduced in water-stressed plants with high K-fertilization. A difference of 1.56 MPa in osmotic adjustment was observed between water-stressed plants with high K-fertilization and irrigated, low-K-fertilization plants. These results suggest that K accumulation in fourwing saltbush may be a factor for enhanced crested wheatgrass productivity.

Crested wheatgrass grown in mixture with fourwing saltbush had lowered predawn and mid-day xylem water potentials compared with monoculture and sagebrush mixture plots, but no other treatment differences were observed for any species. Fourwing saltbush monoculture plots had the most uniform water extraction rates and may compete less for water than sagebrush when crested wheatgrass extraction rates are highest.

(63 pages)

CHAPTER I

INTRODUCTION

Many studies have attempted to quantify nutrient and water use by various species of plants; however, few of these have determined how two or more species interact through the use of these resources. The primary purpose of this study was to examine several possible physiological interrelationships between crested wheatgrass (Agropyron desertorum (Fisch. ex Link) Schult.) and two species of shrubs, mountain big sagebrush (Artemisia tridentata ssp. vaseyana (Rydb.) Beetle) and fourwing saltbush (Atriplex canescens (Pursh) Nutt.).

Interactions between crested wheatgrass and sagebrush or fourwing saltbush, and reasons for differing productivity of crested wheatgrass in mixed versus monoculture plantings are not known. Rumbaugh et al. (1982) found a 103% increase in forage yield, and increases in protein concentration and yield of crested wheatgrass when it was grown in association with fourwing saltbush. They found a positive, significant correlation between the forage weights of the shrub and grass species. The increased yield of crested wheatgrass, they stated, was probably in response to one or more of several factors: nitrogen and other mineral accumulations under the shrubs from leaf fall, capture of wind-transported soil, or nitrogen fixation by microorganisms.

In contrast to the increased growth of crested wheatgrass under fourwing saltbush, crested wheatgrass production decreases when it is grown in association with sagebrush (Blaisdell, 1949; Passey and Hughie, 1962; Frischknecht, 1963; Robertson, 1972; Rittenhouse and Sneva, 1976). Among the possible causes are interspecific competition for water and other resources, allelopathy, or negative relationships with associated soil microflora.

The objective of this study was to examine some of the factors that might be involved in the differential production of crested wheatgrass when grown in monoculture or in mixed plantings with sagebrush or fourwing saltbush. The results of this study could be used to guide future research concerning potential mechanisms for the increased productivity of crested wheatgrass when grown with fourwing saltbush.

Both shrub species and crested wheatgrass have been used extensively for revegetation. Fourwing saltbush is palatable to livestock and maintains high forage quality from late summer through winter (Welch and Monsen, 1984) when other forage, mainly grasses, has low quality (Shoop et al., 1985). Sagebrush is not generally considered desirable for livestock, but it is important forage for wildlife, especially in the winter when it is high in protein (Welch and Monsen, 1984). Crested wheatgrass was introduced from Eurasia and has been seeded widely for range improvement and revegetation (Plummer et al., 1968).

Literature Review

Island of Fertility

Soils under the canopies of nearly all arid land shrubs show higher nutrient availability than soils in interspaces (Charley, 1972). Fourwing saltbush may be exceptional in this as Fairchild and Brotherson (1980) found that soil beneath fourwing saltbush consistently had higher concentrations of mineral nutrients than soil beneath five other shrubs that were studied in Arizona. Romney et al. (1980) presented similar results for a site in Nevada. Mineral accumulation beneath fourwing saltbush was especially great for potassium (K). Surface soil samples taken at the Nephi Experiment Station, where Rumbaugh et al. (1982) conducted their study, showed soil under the canopies of the fourwing saltbush to have K concentrations approximately four times higher than soils at a 2 m distance in a crested wheatgrass monoculture (1600 vs. 430 ppm water extractable K at 0-10 cm depth).

These differences in soil K concentrations may be accounted for by large K accumulations in the leaves and stems of fourwing saltbush. Wallace et al. (1973) reported the elemental compositions of several species of plants from the Nevada Test Site. Except for hopsage (Grayia spinosa (Hook.) Moq. in DC.), fourwing saltbush had higher concentrations of K than any of the other plants tested, including sagebrush (Table 1). Concentrations did not differ significantly for any of the other nutrients. Romney et al. (1973) reported similar results for another Nevada location. Thus, the degree of K accumulation beneath fourwing saltbush and sagebrush may be a major difference between the two shrub species that might affect grass growth.

Richardson (1982) reported the existence of two biotypes of fourwing saltbush, one which tends to accumulate K and one which accumulates sodium (Na). He speculated that Na may partially substitute for K in those plants with high

Table 1. Cation contents (% of dry weight) of leaves and stems (2-7 samples averaged) of species selected from a total of 27 studied by Wallace et al. (1973) in the Mojave and Great Basin deserts.

	Leaves		Stems	
	K	Na	K	Na
Artemisia tridentata	1.26	0.01	1.07	0.04
Atriplex canescens	8.59	0.32	5.58	0.08
Atriplex confertifolia	7.07	6.83	4.93	2.40
Ceratoides lanata	3.94	0.10	3.48	0.01
Grayia spinosa	8.62	0.16	8.06	0.01
Larrea divaricata	2.38	0.06	1.50	0.03
Lycium pallidum	3.93	2.25	1.94	0.22

Na concentrations, but this does not explain the physiological reason for unusually high concentrations of these cations in fourwing saltbush.

Rumbaugh et al. (1982) suggested that accumulation of wind-blown soil or organic debris beneath fourwing saltbush might add nutrients to the soil under its canopy and increase crested wheatgrass production near fourwing saltbush at the Nephi, Utah, site. The shrubs in their study were situated in a single row perpendicular to the prevailing winds. In addition, dryland grain is produced in the surrounding area. Thus, the potential for transport and deposition of nutrient-rich, fine topsoil under the row of fourwing saltbush may be high. Snow depth observations and soil moisture measurements (Rumbaugh et al., 1982) showed that available soil water was similar under the row of fourwing saltbush and in the crested wheatgrass monoculture. Because fourwing saltbush and sagebrush have similar aboveground architectures, these two species probably do not differ in their ability to trap wind-transported soil, litter or snow.

Crested wheatgrass, sagebrush, and fourwing saltbush are mycorrhizal (Miller, 1979; Caldwell et al., 1985). Crested wheatgrass and sagebrush do not have detrimental mycorrhizal influences on each other (Caldwell et al., 1985), and there is no evidence of effects of fourwing saltbush mycorrhizae on crested wheatgrass.

Farnsworth et al. (1976) reviewed the limited literature concerning nitrogen fixation associated with desert plants. Neither fourwing saltbush nor sagebrush has been reported to exhibit this phenomenon. It thus appears that differential K accumulation beneath sagebrush and fourwing saltbush may be the only major difference between these two shrubs in the island of fertility effects that they induce.

Root Growth and Water Extraction

One of the explanations given by Passey and Hughie (1962) and Frischknecht (1963) for the decreased growth of crested wheatgrass when in mixture with sagebrush is competition for water and nutrients caused by an overlap in the root zone. The former authors describe sagebrush roots as having a "highly developed system of laterals for absorption in the shallower soil." The fibrous roots of grasses extract most of their water from approximately the same levels of soil, resulting in decreased growth of both grass and sagebrush. Quantitative data given by Fernandez and Caldwell (1975) and Thorgeirsson (1985) confirmed that depths and timing of water extraction were, indeed, very similar for sagebrush and crested wheatgrass.

In contrast to sagebrush roots, Fairchild and Brotherson (1980) stated that the roots of fourwing saltbush extended deeper than those of other shrubs, and Wallace and Romney (1972) reported that it may be a phreatophyte. Wallace et al. (1980) gave data on the distribution of roots in the Mojave Desert, including fourwing saltbush. Their data indicate no clear difference between fourwing saltbush and the other shrub species. However, sagebrush sampled from a different location were generally more shallowly rooted, (Wallace et al., 1980).

Gulmon et al. (1983) studied an annual grassland in California where water and nutrient resource partitioning occurred. In their study, addition of a species with deep roots to a stand of a shallow-rooted species increased total production over that of the monoculture because of increased resource use.

Potentially, the different reactions of crested wheatgrass to sagebrush and fourwing saltbush could be due to different depths or timing of water (and nutrient) extraction from the soil. Increased production of crested wheatgrass growing with fourwing saltbush, if dependent on this mechanism, would also require greater or more efficient resource utilization. The magnitude of the response reported by Rumbaugh et al. (1982) seems too great to be accounted for in this manner. Nevertheless, the potential for differential soil water partitioning between crested wheatgrass and the two shrubs exists and was addressed in this study.

Potassium in Water Relations

Potassium is important in the regulation of the osmotic component of water potential within the plant. Such regulation can allow osmotic adjustment, an important factor in turgor maintenance during water stress development (Turner and Jones, 1980). Maintenance of turgor results in an increased ability to continue cell elongation, maintain stomatal opening and photosynthesis, survive dehydration, and continue root expansion resulting in greater exploration of the soil for more water (Turner and Jones, 1980).

Ruess and Wali (1980) stated that K^+ and chloride (Cl^-) were the dominant ions in the regulation of water potential of fourwing saltbush. In their study, the water potential in the leaves and stems of fourwing saltbush varied from -1.55 to -4.51 MPa with diel fluctuations averaging 2.19 MPa and rates of change as great as 1.2 MPa per hour. These water potentials were directly related to changing tissue concentrations of K and Cl.

In three of four tropical savanna pasture species studied, Ford and Wilson (1981) found substantial increases in certain solutes, especially Na, K, Cl, and sucrose, when plants were subjected to a 35-day drying cycle. Wilson et al. (1980) reported the data for water potentials of the plants in the Ford and Wilson (1981) study. The three grass species with increased solute concentrations had decreased water potential, but osmotic adjustment was adequate for turgor maintenance that aided in maintaining photosynthesis throughout the period of water stress. Nevertheless, leaf elongation ceased after two weeks of drying. The fourth species, a legume, was able to maintain turgor and higher water potential throughout the drying cycle by regulating stomatal opening.

Following the studies by Wilson et al. (1980) and Ford and Wilson (1981), Wilson and Ludlow (1983) studied the effects of K fertilization on water relations characteristics of the three grasses that adjusted osmotically. They concluded that high K did not generally promote greater osmotic adjustment of water-stressed leaves and that higher tissue K concentrations, which might have increased osmotic adjustment, were counterbalanced by lower concentrations of other solutes. Thus, although K is important in plant osmotic regulation, Wilson and Ludlow (1983) concluded that an increased supply of K to the plant may not improve the ability of the plant to osmotically adjust. Their low K treatment, however, had quite high K availability (M. M. Ludlow, personal communication) so that further comparisons with plants grown with low K availability are warranted.

Many other studies confirm the importance of K in regulating osmotic and water potentials. Dhindsa et al.

(1975) stated that K and malate can account for 50% of the osmotic potential in the cells of cotton fiber and that the concentrations of these ions are at their peak during periods of maximum cell extension. Smid and Peaslee (1976) found higher concentrations of K in younger leaves and plants. This, they thought, affected the water potential gradient in such a way as to increase water transport to growing tissues.

In summary, fourwing saltbush accumulates a large amount of K in its leaves and stems, it probably uses this to some extent for osmotic adjustment, and it "fertilizes" the soil beneath its canopy with this nutrient to a much greater extent than sagebrush. If K is limiting in the bulk soil (the levels determined on bulk soil at the Nephi Experiment Station, 430 ppm, are not considered limiting), crested wheatgrass plants neighboring fourwing saltbush could theoretically obtain this extra K and use it for osmotic adjustment. This might lead to a longer growing period because of sustained growth, photosynthesis, and water extraction.

Summary and Objectives

There are many possible reasons for the different reactions of crested wheatgrass to sagebrush and fourwing saltbush. A summary of alternative hypotheses examined in this study is given below.

1. Island of Fertility

Potassium is added to the soil by fourwing saltbush and influences growth rate or water stress tolerance of associated grasses. If K is limiting in the soil, this may be a major factor in the increased growth of crested wheatgrass under fourwing saltbush. Potassium is used by many plants to increase water stress tolerance through osmotic adjustment, but it is not know if this occurs in crested wheatgrass. Although reasonable, these interactions would probably not explain the increased growth of crested wheatgrass with fourwing saltbush in the study by Rumbaugh et al. (1982), because of the non-limiting background K (430 ppm). at their site. It is possible, however, that the very high levels of K (1600 ppm) in the soil under the fourwing saltbush at the Nephi site caused the increased crested wheatgrass yield. These possible causes of increased crested wheatgrass production will be examined in Objectives 1, 2, and 3 below.

2. Root Growth and Water Extraction

Better niche partitioning occurs in the root zone in grass-fourwing saltbush associations and results in greater total resource utilization than in grass-sagebrush associations. Greater total production from crested wheatgrass and fourwing saltbush over crested wheatgrass and sagebrush would not be expected if fourwing saltbush roots only exploited a larger soil volume for water than sagebrush. If this mechanism is operating, increased production of crested wheatgrass under fourwing saltbush would imply that crested wheatgrass could be using water more efficiently, perhaps through the effects of osmotic adjustment. Alternatively or in addition, crested wheatgrass could be extracting more water through greater root activity when fourwing saltbush is present. Objective 4 will examine seasonal patterns and the amount of water extraction by each species in monoculture and in two-way mixtures.

Other mechanisms could also be operating, such as differences in microclimates, associated fauna, and soil microflora. However, considering the evidence available in the literature, the possibilities discussed above appear the most reasonable.

The following specific objectives address these possibilities:

1.a. Determine the peak nutrient {nitrogen (N), phosphorous (P), and potassium (K)} standing crops in crested wheatgrass in monoculture and in mixture with sagebrush and fourwing saltbush.

b. Determine the peak nutrient (N, P, and K) standing crops in fourwing saltbush and sagebrush in monoculture and in mixture with crested wheatgrass.

2. Quantify release of nutrients from standing biomass and litter of fourwing saltbush and sagebrush.
3. Determine if K is limiting to crested wheatgrass under well-watered and water-stressed conditions.
4. Determine water-use patterns and plant water potentials for the shrubs and grass in monoculture and in mixtures.

Because of the breadth of these objectives, it was hoped that the study results would provide a basis for determining the direction of future research in the area of grass-shrub interactions.

CHAPTER II

STUDY AREA AND METHODS

Study Area

The majority of this study was conducted at the Green Canyon Ecology Center Research Area about 4 km north of the Utah State University campus as part of a Utah Agricultural Experiment Station project (AES-779) during 1983 and 1984. Soils at the Ecology Center are typic haploxerolls formed from alluvium, and the vegetation formerly occupying the area was dominated by sagebrush and bluebunch wheatgrass (Hull and Hull, 1974; Southard et al., 1978). Caldwell et al. (1981) and Richards and Caldwell (1987) have further described the soils and climate at this location.

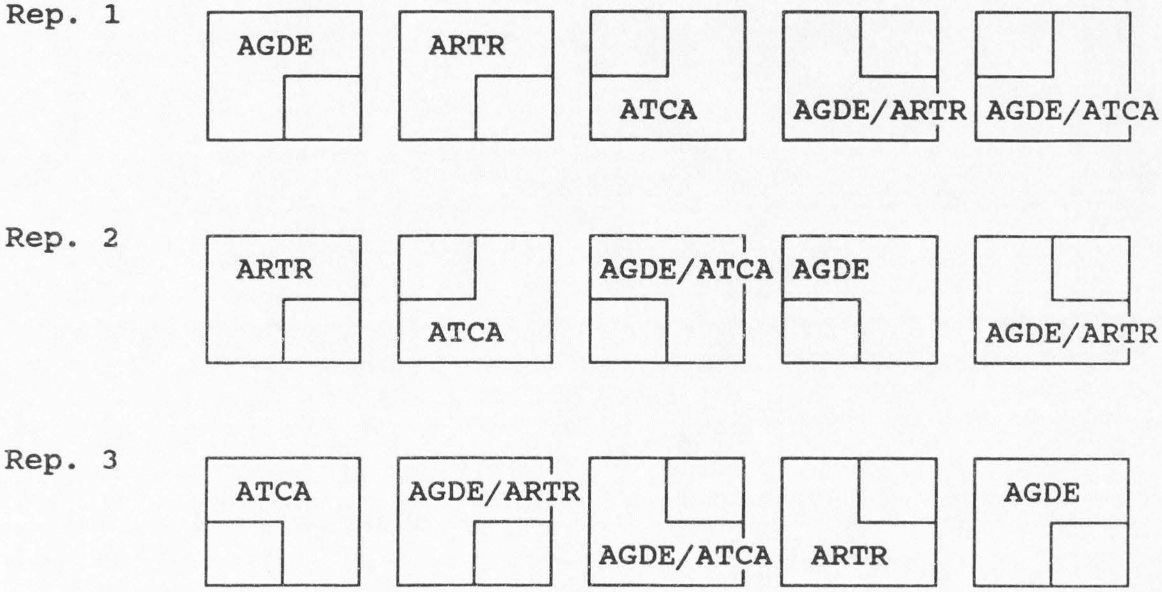
Precipitation in 1984 at Green Canyon was 619 mm, slightly below the six-year (1980-1985) average of 668 mm but well above the long-term average of 468 mm in nearby North Logan. Precipitation in June, July, and August was 85, 59, and 16 mm, mostly above the six- and seven-year averages of 44, 33, and 30 mm. These months of above-normal precipitation substantially influenced some of the results, especially research conducted under Objective 4.

The field experiments at Green Canyon were set up as a randomized, complete-block design with 14 treatments with three replications. These same plots were studied by Pendery and Provenza (1987). Only five of the treatments were used for the current experiments (Figure 1a). These were: sagebrush monoculture, fourwing saltbush monoculture, crested wheatgrass monoculture, sagebrush-crested wheatgrass mixture (50-50), and fourwing saltbush-crested wheatgrass mixture (50-50). Figure 1b shows the arrangement of plants in the plots. All plots had the same total density. The experimental layout prevented confoundment by differential deposition of wind-transported soil or organic matter.

Plots were sectioned into quarters and one-quarter from each plot was chosen randomly for sampling (Figure 1a.) . A neutron probe access tube (85 cm depth) was installed in each quarter plot used. Soil psychrometers were installed in two replicates of each treatment.

Fourwing saltbush plants for this study were grown from seed collected from the plants used in the study by Rumbaugh et al. (1982). Sagebrush plants were transplanted from an area near the study site. Crested wheatgrass plants were taken from an established stand near Tintic, Utah.

a.



b.

X O X O X O X O X
O X O X O X O X O
X O X O X O X O X
O X O X O X O X O
X O X O X O X O X
O X O X O X O X O
X O X O X O X O X
O X O X O X O X O
X O X O X O X O X

Figure 1. Green Canyon Ecology Center study plots.

1a. Schematic representation of the plots and quarter plots used in this study. AGDE = crested wheatgrass, ARTR = sagebrush, ATCA = fourwing saltbush

1b. Arrangement of plants within a grass-shrub mixture. Rows and columns are 0.5 m apart. This shows one-fourth of a 17 X 17 plant plot. The X's represent shrubs and the O's indicate grasses.

Methods

Objective 1: Nutrient Standing Crop

On 31 May, 18 June, 9 July, and 28 July 1984, three grass plants from each of the plots containing crested wheatgrass were harvested. The grasses from the monoculture plots were separated into inflorescences, stems and sheaths, leaf blades, and root crowns. These were weighed and analyzed for N, P, and K, as described below, to determine the time of the peak standing crop. These methods allowed direct comparison with the N standing crop data of Caldwell et al. (1981), determined in crested wheatgrass plants at the same site. Caldwell et al. (1981), however, did not include inflorescences in their analyses. Crested wheatgrass plants from the mixture plots were only separated into shoots and root crowns, until inflorescences appeared when they were also analyzed separately.

Three individual plants of the sagebrush and fourwing saltbush from each plot where the respective species occurred were harvested on 22 June, 6 August, and 11 September 1984. These were separated into two components (stems and inflorescences; leaves), dried, weighed, and analyzed for N, P, and K.

Plant tissues were ground to pass a 20 mesh screen. Potassium was determined by atomic absorption spectrophotometry following hot water extraction (24 hr at 75°C). Nitrogen and phosphorous were determined with a colorimetric assay following sulfuric acid digestion (USDA, 1954).

Water extractable soil K was determined by atomic absorption spectrophotometry by the Utah State University Soil, Plant, and Water Analysis Laboratory. Soil water was vacuum filtered from saturated paste for analysis.

Canopy coverage and number of individual plants in each plot were determined using photographs taken on 1 and 16 November 1984 with a camera suspended 7 m above the plots on a portable stand (Owens et al., 1985).

Relative yields per plant (RYP) and relative yield totals (RYT) were calculated based on Fowler (1982). The RYP term estimates how a plant performs in mixture with another species compared to its performance in monoculture. The RYT term estimates the total yield of two species in a mixture compared to how they perform in monocultures.

Randomized, complete-block analysis of variance was followed by orthogonal decomposition of the treatment sums of squares to determine differences in factor effects at 95% confidence.

Objective 2: Nutrient Deposition

Litter traps consisting of 0.5 X 0.5 m sheets of nylon mosquito netting were anchored to the ground beneath one-quarter of the canopies of four shrubs on 15 April 1984. Five of these traps were placed in each shrub monoculture plot, and the litter was collected, dried, and weighed at monthly intervals until November, 1984. Litter was not collected through the winter. Previous studies by Mack (1977) reported that the total quantity of litterfall from sagebrush was much less in the winter and fall than in the summer.

In November, 1983, and again in July and October, 1984, "fresh" litter was obtained from five shrubs in each treatment by gently shaking the branches of each shrub. A portion of these leaves was analyzed for N, P, and K, and the rest was placed in bags made of nylon mosquito netting sewn with nylon thread and placed on the ground in the plots from which they were harvested. For the leaves collected in November, 1983, this was done on 8 March 1984, when about 1 m of snow remained on the plots. For the leaves collected in 1984, litter bags were positioned on 21 November 1984. Samples from the first group of bags were collected on 4 April 1984, just after the snow had melted; on 2 July 1984;

and on 15 October 1984. The second group of samples was collected on 9 April 1985 after the snow had melted. The purpose of the second group of samples was to confirm the results for loss of nutrients through winter obtained from the first. All of these samples were analyzed for N, P, and K.

Precipitation collectors made of PVC pipe cut lengthwise with openings 15 X 30 cm were placed beneath three shrubs in each shrub monoculture treatment and in adjacent clear areas. The amount of precipitation and throughfall, and nutrient concentrations in each were determined during the 1984 growing season.

Percent cover from the photographs of the plots, throughfall and litter data were used according to Equation 1 to calculate the total nutrient return (TNR) to the soil from above-ground portions of the two shrubs:

$$TNR = (Pt)(Nt)(Ft) + (L)(Nl)(Ll) - (Pp)(Np) \qquad (1)$$

Where Pt is precipitation per unit area falling through shrubs, Pp is precipitation per unit area in clear areas, Nt is nutrient concentration in throughfall precipitation, Np is nutrient concentration in precipitation not falling through shrubs, Nl is nutrient concentration in fresh litter, Ft is the proportion of plots covered by the shrub canopy, Ll is the proportion of nutrient lost from the litter, and L is the mass of litter falling per unit area.

Objective 3: Effects of Potassium Fertilization on Water Relations of Crested Wheatgrass

Arcillite, a montmorillonitic clay material, and silica sand (1 kg each) were placed in each of thirty 30-cm-long sections of 10-cm diameter PVC pipe capped at one end. Caps had adequate drainage holes. This "soil" was leached with 4 L of distilled water to assure low initial K availability. Ten tillers of crested wheatgrass were planted in each pot and grown in a greenhouse for 35 days before a 17-day drying cycle was initiated by withholding water from half of the plants. Control plants continued to receive normal watering.

During the establishment period, pots were watered alternately with either distilled water or a full-strength modified Hoagland's solution (Table 2). Potassium levels were varied in the fertilizer solution to give 3 K treatment levels with 5 replicate plants in each water level-fertilization treatment. Water-soluble K was 41, 93, and 150 ppm in the low, medium, and high fertilization treatments, respectively, when the drying cycle began.

At the beginning and end of the drying cycle, the last fully-expanded leaf was sampled from a tiller in each pot. These were each weighed, placed in chambers with individually calibrated screened end-window psychrometers (J. R. D. Merrill Specialty Equipment, Logan, UT) and

Table 2. Concentrations of nutrients used in the potassium fertilization experiment (Objective 3). The level of K_2SO_4 was varied to give 61 ppm K for the medium K treatment and 0 ppm K for the low K treatment. S levels also varied because of the variation in levels of K_2SO_4.

		µM	ppm
K	(in K_2SO_4)	3120	122
N	(in $Ca(NO_3)_2 \cdot 4H_2O$, $NH_4H_2PO_4$, and NH_4NO_3)	16000	224
Ca	(in $Ca(NO_3)_2 \cdot 4H_2O$)	4000	160
P	(in $NH_4H_2PO_4$)	2000	62
S	(in K_2SO_4, $MgSO_4 \cdot 7H_2O$, $MnSO_4 \cdot H_2O$, $ZnSO_4 \cdot 7H_2O$, and $CuSO_4 \cdot 5H_2O$)	2560	82
Mg	(in $MgSO_4 \cdot 7H_2O$)	1000	24
B	(in H_3BO_3)	25	0.27
Mn	(in $MnSO_4 \cdot H_2O$)	2.0	0.11
Zn	(in $ZnSO_4 \cdot 7H_2O$)	2.0	0.13
Cu	(in $CuSO_4 \cdot 5H_2O$)	0.5	0.032
Mo	(in H_2MoO_4)	0.5	0.050
Fe	(EDTA chelated)	20	1.1

allowed to equilibrate at 25°C. A microvoltmeter (Wescor, Inc., Logan, UT) measured psychrometer output using a 30 s, 8 mA cooling current, and the total water potential was determined. The leaves were then frozen in liquid nitrogen and allowed to reequilibrate; osmotic potential was then determined. These leaves were removed from the chambers, dried, and weighed again. From these data, water content and turgor pressure (total less osmotic potential) were calculated.

To determine osmotic potential at full turgor, a similar leaf was taken from another tiller in each pot, weighed, and placed in a test tube with water and filter paper to allow the leaf to reach full turgor under 100% humidity conditions. Rehydration occurred in a refrigerator for 6 hours at 2°C with illumination at about the compensation point for crested wheatgrass, 40-50 $E \cdot m^{-2} \cdot s^{-1}$ (400 to 700 nm). The leaves were removed, blotted, weighed, and placed in chambers with psychrometers. After equilibration, water potential was determined, the samples were frozen in liquid nitrogen, and osmotic potential was determined as before. Leaf dry weight was then determined. These measurements gave water and osmotic potential at full turgor, turgor potential at full turgor, and relative water content. Osmotic adjustment was calculated as the difference between osmotic potential at full turgor at the beginning and end of the drying cycle. Increased osmotic adjustment over that of the control plants was considered to be a result of treatment, either fertilization or water stress or both.

The drying cycle ended when the first fully expanded leaves of two grasses that had not received water but were not otherwise in the experiment had xylem water potentials averaging -4.0 MPa as measured by a pressure bomb at mid-day. After the drying cycle was completed, all of the above-ground portions of the plants were harvested, separated into live and dead portions, dried, weighed, and analyzed for K concentration. Data were analyzed using a two-way analysis of variance with two water and three fertilization treatments. The Tukey multiple comparison procedure was used for mean comparisons.

Objective 4:
Soil and Plant Water Relations

Neutron probe (Campbell Pacific Nuclear, Model 503) measurements to determine soil volumetric water content were taken weekly or biweekly from early May through mid-September, 1984, at depths of 20, 40, 60, and 80 cm in the field plots. Psychrometer readings of soil water potential were taken at the same times at depths of 40 and 80 cm through mid-August using the methods and instrumentation described in Objective 3 above. Readings were corrected to 25°C.

Predawn (1:00 to 4:00 standard time) and mid-day (12:00 to 15:00 standard time) xylem water potentials were determined with a pressure bomb (PMS Instrument Corp., Corvallis, OR) for three samples from three plants of each species in each plot on 2 July, 19 July, 6 August, and 27 August 1984, or within a day of these dates when time did not allow complete sampling in one day. Crested wheatgrass leaves were chosen randomly from throughout the plants for the 2 and 19 July measurements. Beginning on 6 August, crested wheatgrass inflorescences were used. Sagebrush and fourwing saltbush terminal stem pieces were sampled for all shrub measurements.

In 1984, a large amount of precipitation was received during the period when the neutron probe readings were taken. Estimation of the amount of water added to each layer of the soil profile from rainfall and drainage between neutron probe readings is a difficult and error-laden procedure (Rambal, 1984). However, because of the large amount of precipitation received, estimation was necessary. The amount of drainage to each soil layer was calculated as the excess not held by the overlying soil layer at field capacity. The field capacity was estimated to be 0.28. Some inaccuracies undoubtedly resulted because the field capacities of all soil layers were not identical and evaporation was not included. However, most of the precipitation, especially in the latter part of the summer, did not reach below 30 cm so that calculations of water use below that level would not have been affected by the estimation procedure.

Average daily water use calculations were based on the highest and lowest volumetric water contents measured plus the total precipitation and drainage for each soil level.

CHAPTER III

RESULTS

Nutrient Standing Crop

Standing crops of N, P, and K for monocultures of crested wheatgrass for the first three harvests are shown in Figure 2. No significant differences were found between the first two sampling times for any of these nutrients. According to the results of Caldwell et al. (1981) for crested wheatgrass at the same site, peak standing crop of nitrogen, **excluding** inflorescences, occurred in mid-May to early June (Figure 3). In the present study, the first harvest probably represented peak standing crop. Inflorescences made only a small contribution to standing crop at the end of May in my study because the plants were in the "boot" stage of phenological development and inflorescences were small (Figure 2). By mid-June, there was no net addition to the standing crops as the inflorescences matured because of concomitant nutrient loss from other plant parts, mainly leaf blades.

At the time of peak standing crop (31 May), no significant differences were detected for N, P, or K pools

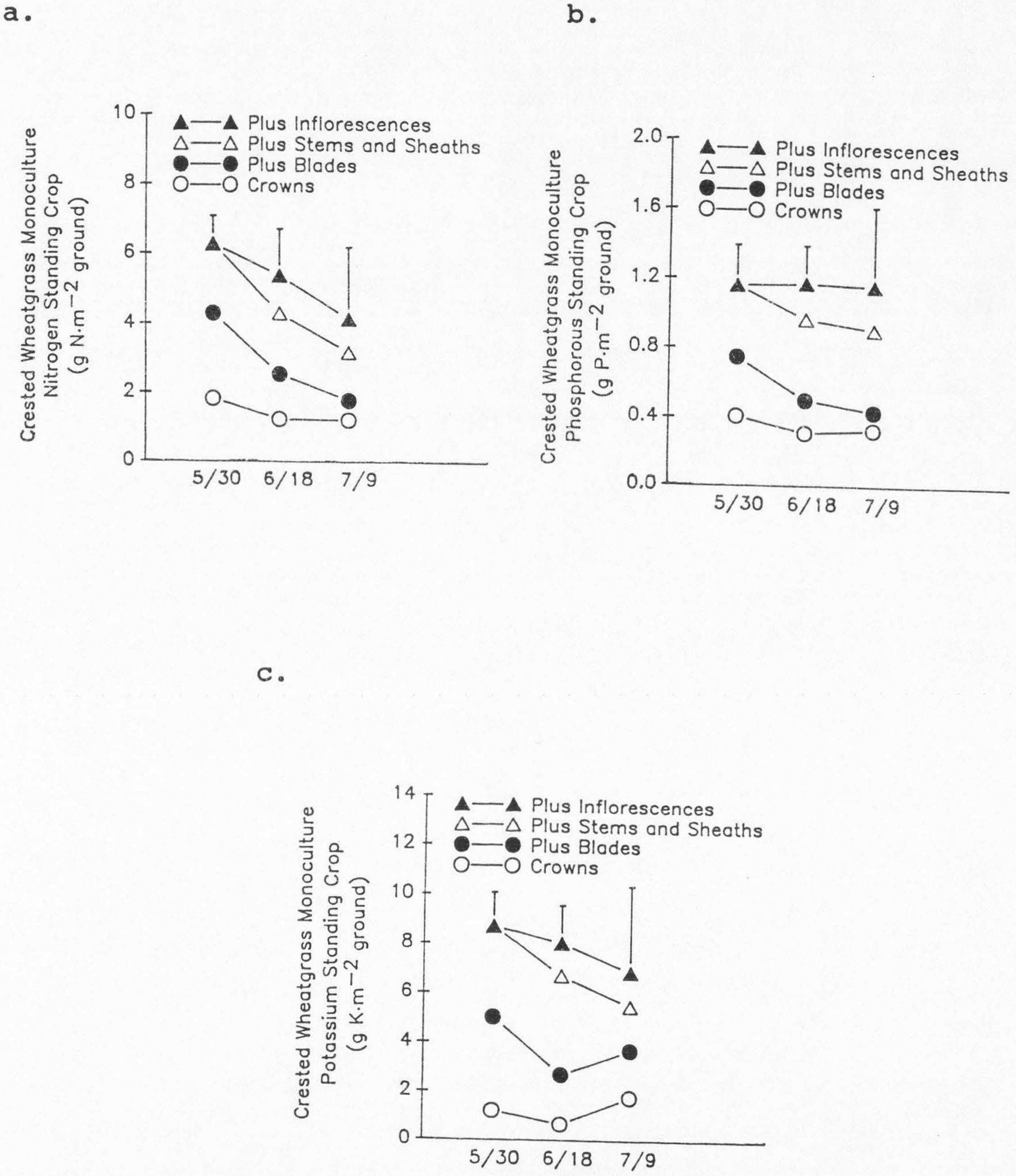


Figure 2. Standing crop of N (a), P (b), and K (c) for crested wheatgrass growing in monoculture. Error bars indicate one standard error of the total standing crop.

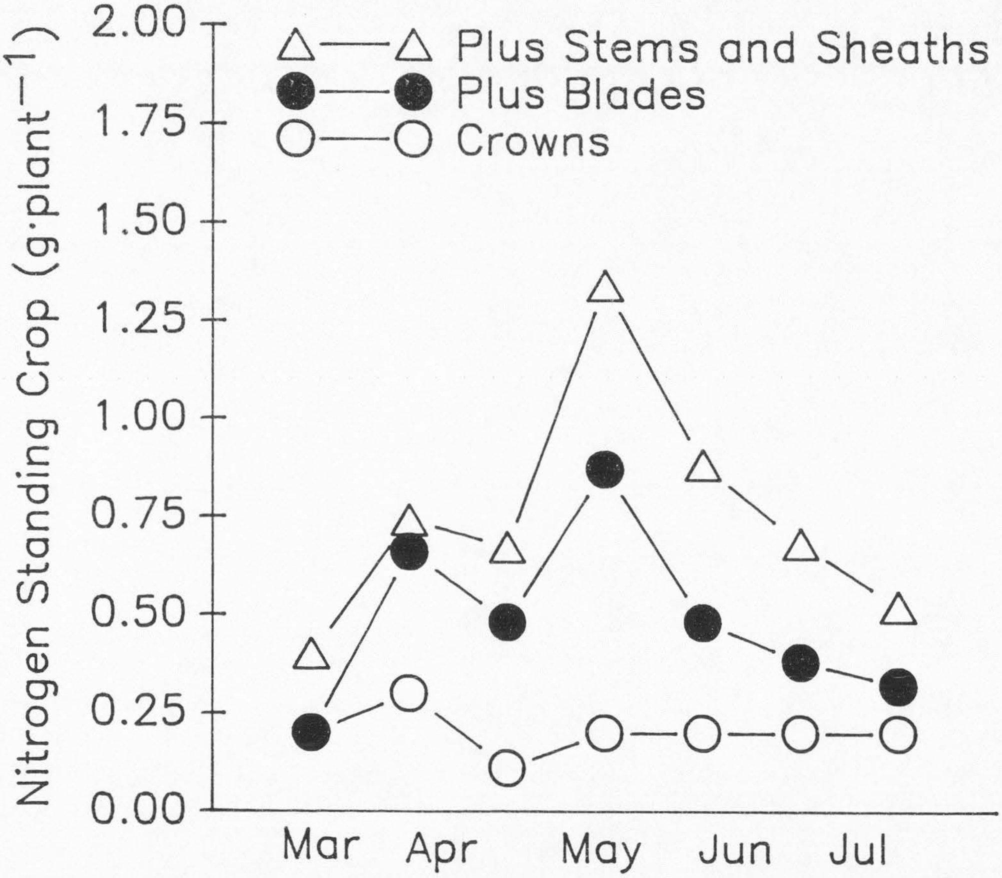


Figure 3. Nitrogen standing crop in crested wheatgrass. Adapted from Caldwell et al. (1981).

between crested wheatgrass in monoculture and in mixture with sagebrush (Tables 3 and 4). There was significantly less K, and on a canopy basis N, in the crested wheatgrass growing in mixture with fourwing saltbush. Because plant weights of crested wheatgrass were not significantly different in the various treatments, this decrease was due to lower concentrations.

With the exception of N in plants in the fourwing saltbush mixture, nutrient standing crops peaked on 6 August for both shrub species in all treatments (Figures 4 and 5). Nutrient concentrations were not significantly different

Table 3. Mass of nutrients in crested wheatgrass ($g \cdot plant^{-1}$) at the time of peak nutrient standing crop (31 May). Within a row, values followed by different letters are significantly different at $P<.05$.

	Crested Wheatgrass Monoculture	with Sagebrush	with Fourwing Saltbush
N	1.42 a	1.40 a	1.15 a
P	0.26 a	0.32 a	0.26 a
K	1.98 a	1.94 a	1.16 b

Table 4. Mass of nutrients ($g \cdot m^{-2}$ canopy) of crested wheatgrass at the time of peak standing crop (31 May). Within a row, values followed by different letters are significantly different at $P<.05$.

	Crested Wheatgrass Monoculture	with Sagebrush	with Fourwing Saltbush
N	33.26 a	29.00 ab	21.87 b
P	6.14 a	6.34 a	4.90 a
K	46.09 a	37.40 a	22.03 b

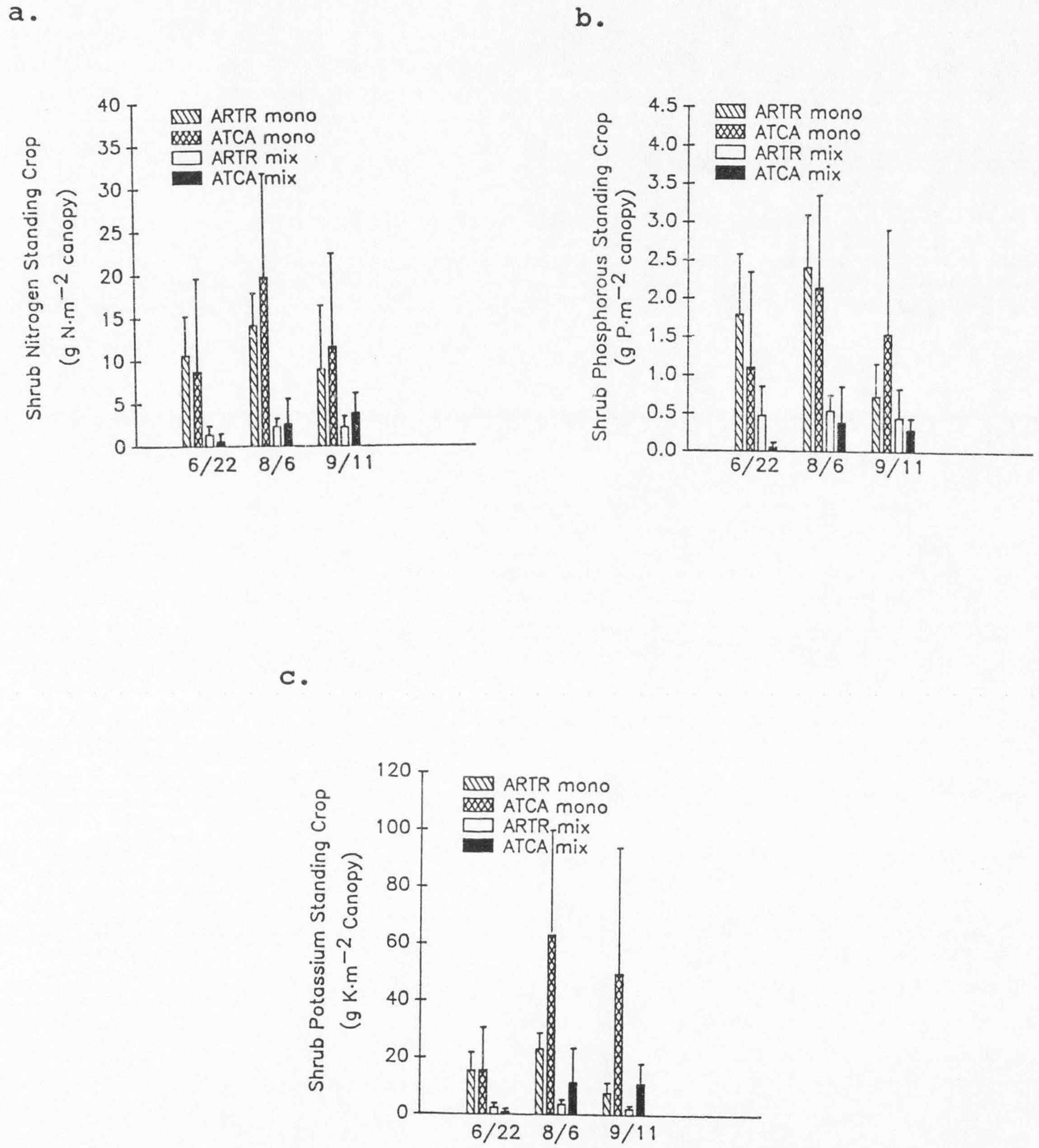


Figure 4. Shrub N (a), P (b), and K (c) standing crops (g·m-2 canopy). AGDE = crested wheatgrass, ARTR = sagebrush, ATCA = fourwing saltbush

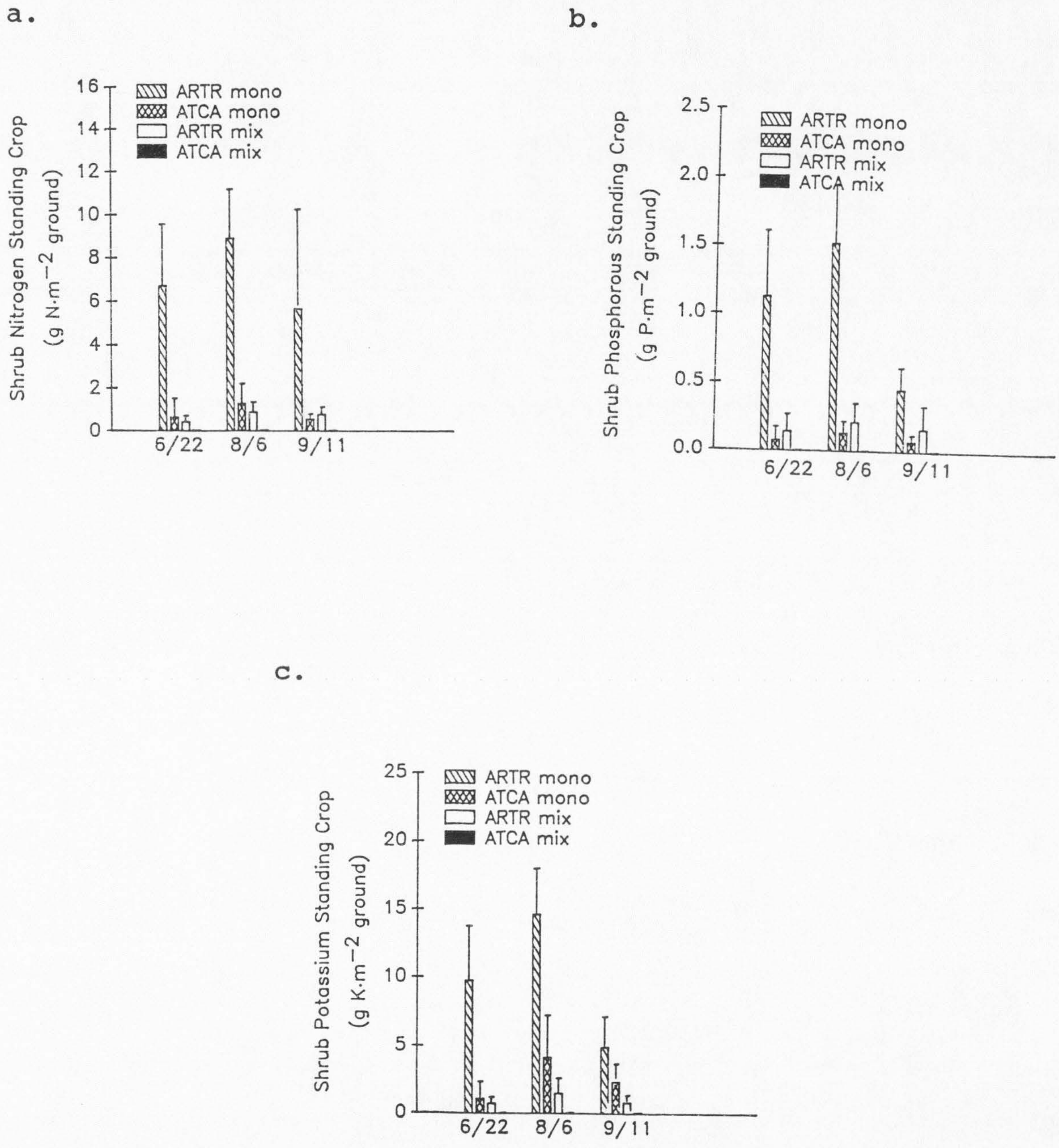


Figure 5. Standing crops of N (a), P (b), and K (c) ($g \cdot m^{-2}$ ground). The fourwing saltbush mixture values are nearly zero. AGDE = crested wheatgrass, ARTR = sagebrush, ATCA = fourwing saltbush

between treatments for the shrub species, except for a higher P concentration in sagebrush growing in mixture (Table 5). As expected, a large difference in K concentration was observed between the shrub species. Even though sagebrush plants had nearly a fourfold greater dry weight than fourwing saltbush in the same treatments, no differences in K accumulation per plant were detected between the species within a treatment (Table 6). The accumulation of K in fourwing saltbush is particularly noticeable when expressed as standing crop per unit area of canopy coverage (Table 7).

Table 5. Nutrient concentrations (%) in shrubs on 6 August. Within a row, values followed by different letters are significantly different at $P<.05$.

	Sagebrush		Fourwing Saltbush	
	Monoculture	with Crested Wheatgrass	Monoculture	with Crested Wheatgrass
N	1.03 a	1.34 a	1.34 a	1.20 a
P	0.18 a	0.30 b	0.14 a	0.14 a
K	1.71 a	2.01 a	4.13 b	4.81 b

Table 6. Mass of nutrients in shrubs (g·plant^{-1}) on 6 August. Within a row, values followed by different letters are significantly different at $P<.05$.

	Sagebrush		Fourwing Saltbush	
	Monoculture	with Crested Wheatgrass	Monoculture	with Crested Wheatgrass
N	1.97 a	0.23 b	0.67 c	0.06 d
P	0.35 a	0.06 b	0.06 b	0.01 b
K	3.40 a	0.39 b	2.16 a	0.28 b

Table 7. Mass of nutrients in shrubs ($g \cdot m^{-2}$ canopy) on 6 August. Within a row, values followed by different letters are significantly different at $P<.05$.

	Sagebrush		Fourwing Saltbush	
	Monoculture	with Crested Wheatgrass	Monoculture	with Crested Wheatgrass
N	14.14 a	2.33 b	19.80 a	2.65 b
P	2.41 a	0.54 b	2.14 a	0.38 b
K	23.16 a	3.67 b	63.06 c	11.42 ab

None of the relative yield per plant (RYP) values for nutrients in crested wheatgrass were different from one (Table 8). A RYP value of one indicates that a plant performs as well in mixture with another species as in monoculture; values less than or greater than one indicate reduced or enhanced performance, respectively. Consequently, the crested wheatgrass nutrient acquisition was little-affected by the shrubs, although K content of crested wheatgrass in mixture with fourwing saltbush was apparently suppressed (Table 4).

All of the nutrient RYP values for the shrubs were less than one, indicating decreased performance in mixture with crested wheatgrass (Table 9). Because nutrient concentrations in the shrubs in monoculture and in mixture were not different, this yield suppression in the shrubs must be attributable to a lower biomass.

Relative yield total (RYT) (Table 10) measures productivity of all species in a mixture according to

Table 8. Values of RYP of nutrient standing crops of crested wheatgrass in mixture with sagebrush and fourwing saltbush.

	Crested Wheatgrass	
	with Sagebrush	with Fourwing Saltbush
N	1.23	0.98
P	1.04	0.81
K	0.98	0.59

Table 9. Values of RYP of nutrient standing crops of sagebrush and fourwing saltbush in mixture with crested wheatgrass.

	Sagebrush	Fourwing Saltbush
N	0.11	0.09
P	0.16	0.14
K	0.11	0.13

Table 10. Values of RYT of nutrient standing crops of crested wheatgrass in mixture with sagebrush or fourwing saltbush. The values used are from the peak standing crops for each species.

	Crested Wheatgrass/Sagebrush	Crested Wheatgrass/Fourwing
N	0.67	0.54
P	0.60	0.48
K	0.55	0.36

Equation 2.

$$RYT = \frac{RYP_1 + RYP_2 + \ldots + RYP_n}{n} \qquad (2)$$

Where n is the total number of species in a mixture.

Although nutrient RYP values for sagebrush were less than one, nutrient RYT values for the crested wheatgrass/sagebrush mixture plots were not different from one. This suggests a slightly increased performance (compared to monoculture) of crested wheatgrass when grown in mixture with sagebrush. Nutrient RYT values for the crested wheatgrass/fourwing saltbush mixture plots were all significantly less than one, reflecting both the small size of fourwing saltbush in the mixture plots and the reduced yield of crested wheatgrass in mixture with fourwing saltbush (Tables 3 and 4).

Nutrient Deposition

Litter deposition from sagebrush and fourwing saltbush peaked in September and October respectively (Figure 6). Leaf fall did not increase in sagebrush in early summer, as found by others (Mack, 1977; Miller and Schultz, 1987). Litterfall decreased markedly for both sagebrush and fourwing saltbush following peak litter deposition.

Cumulative litter deposition from May through November was 93 and 90% of total live leaf biomass for sagebrush and fourwing saltbush, respectively. In both species, most of the leaves are apparently recycled in a season. This is in agreement with observations of others (Deittert, 1938; Miller and Schultz, 1987) and suggests minimal winter leaf losses.

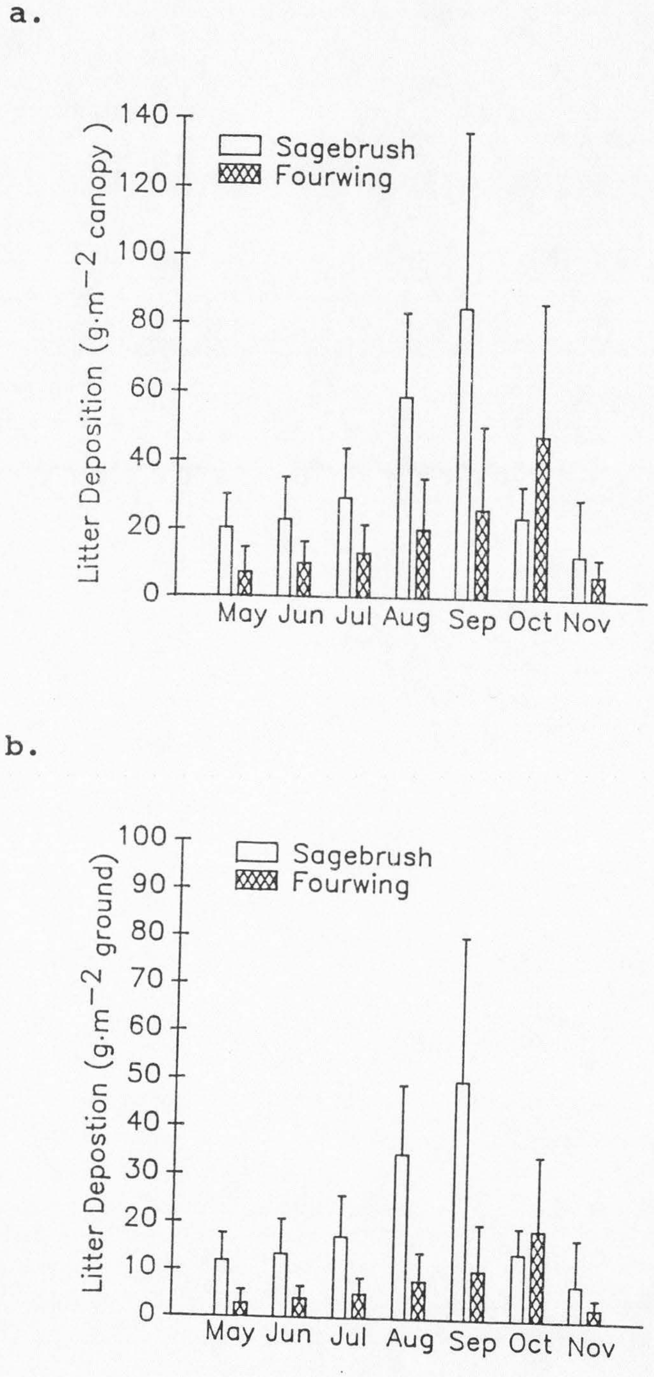


Figure 6. Litter deposition·m^2 canopy (a) and ground (b) for fourwing saltbush and sagebrush.

Mass and nutrient loss from the first group of litter bags are shown in Figure 7. Results from the second group of bags (data not shown) were comparable to the first sampling of the first group, except that fourwing saltbush litter exhibited a greater K loss.

Pools of N in litter bags increased up to 8165% of the beginning values with very large standard errors. This, clearly, did not show nutrient return but was probably a result of microbial activity and shows one of the limitations of the litter bag technique.

Phosphorous contents of fourwing saltbush litter also increased after the initial loss, but not as much as N. Litter bag estimates of K loss are probably more reliable due to rapid leaching and less biological fixation than for N and P. Contents of K decreased to very low levels (Figure 7). October litter samples of fourwing saltbush had <1% of initial K contents.

Data from the litter traps and litter bags are combined in Tables 11 and 12 to provide estimates of the total amount of nutrients deposited and released based on the percentages of nutrients remaining in the litter bags in October. Calculations were not made for N in Table 12 because they would show negative input to the soil. The total amount deposited should be, over an extended period, what is actually returned to the soil via litterfall. Potential and actual additions of N and P were less for fourwing saltbush

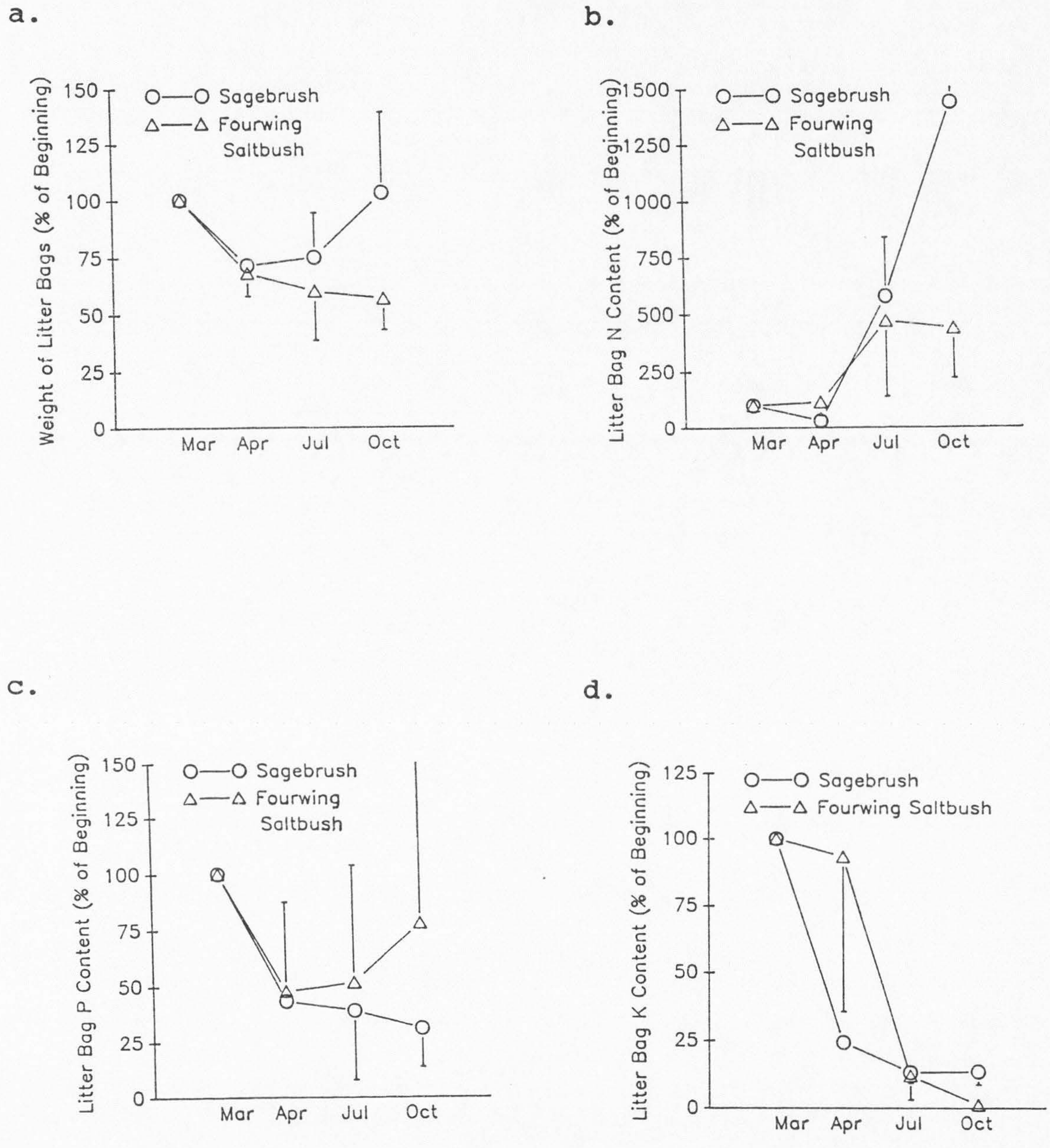


Figure 7. Decreases in litter bag content weights (a) and nutrient percentages (b, c, and d) through time. Error bars indicate one standard error. When not shown, the standard errors were smaller than the symbols. The standard error for the final N content for sagebrush was 2406.

than sagebrush, but K returns were much greater for fourwing saltbush.

Samples of rain were not collected for every storm during the summer, but there were good correlations by Equations 3 and 4 ($r^2 = 0.88$ and 0.87 for sagebrush and fourwing saltbush, respectively) between precipitation amounts measured at a rain gauge within the research facility and the amount of water in the throughfall traps.

Table 11. Potential litterfall nutrient additions from combined litter trap and litter bag nutrient content data. Numbers in parentheses represent standard errors.

Total Litter ($g \cdot m^{-2}$ canopy)	Beginning Litter Bag Nutrient Content		Total Nutrient Deposited ($g \cdot m^{-2}$ Canopy)
Sagebrush (n=10)			
	N	0.62% (0.38)	1.57 (0.97)
254.2 (77.0)	P	0.12% (0.04)	0.31 (0.11)
	K	0.49% (0.05)	1.23 (0.13)
Fourwing Saltbush (n=15)			
	N	0.47% (0.24)	0.62 (0.32)
133.4 (85.7)	P	0.06% (0.05)	0.08 (0.06)
	K	4.47% (1.30)	5.98 (1.74)

Table 12. Calculated nutrient release based on quantities of litter in the litter traps from April to November and the proportion of nutrients remaining in the litter bags in October. Numbers in parentheses represent standard errors.

	Sagebrush (n=10)			Fourwing Saltbush (n=15)		
	($g \cdot m^{-2}$ canopy)		% of total	($g \cdot m^{-2}$ canopy)		% of total
P	0.10	(0.37)	33.7	0.02	(0.01)	21.4
K	1.06	(0.49)	86.4	5.91	(3.68)	98.9

$$\hat{y} = 42.5x - 24.4 \quad (3)$$

$$\hat{y} = 40.9x + 11.6 \quad (4)$$

Where $\hat{y}$ is precipitation (mm) and x is the amount of water (ml) in sagebrush (3) and fourwing saltbush (4) throughfall traps.

Concentrations of K in the water also correlated (r^2 = 0.26 and 0.61, significant at $\underline{P}<.05$ and .01 for sagebrush and fourwing saltbush, respectively), in a non-linear fashion, with amounts of water in the traps (Equations 5 and 6).

$$\hat{y} = 137.0 - 0.49x + 0.00076x^2 \quad (5)$$

$$\hat{y} = 278.0 - 0.66x + 0.00041x^2 \quad (6)$$

Where $\hat{y}$ is K concentration (ppm) and x is the amount of precipitation (ml) in traps for sagebrush (5) and fourwing saltbush (6).

For storms where precipitation was not collected, quantities of water in the traps were predicted by the regression equations and combined with expected K concentrations to give total expected quantities of K returned by throughfall from June through September. These values were 20.6 $g \cdot m^{-2}$ canopy for fourwing saltbush and 13.6 $g \cdot m^{-2}$ canopy for sagebrush. The contribution to each of these from rainfall is 0.8 $g \cdot m^{-2}$.

Combining the throughfall, litterfall, and litter bag data, and subtracting the input from precipitation, total K return is estimated to be 13.9 and 25.7 $g{\cdot}m^{-2}$ canopy for sagebrush and fourwing saltbush, respectively. Inasmuch as the values for throughfall are estimates, no statistical comparison can be made.

Effects of Potassium Fertilization on Crested Wheatgrass Water Relations

Selected measurements and calculations for the potassium fertilization/water stress experiment are presented in Table 13. There was only one statistically significant difference between osmotic adjustment measurements, but a trend was observed for greater osmotic

Table 13. Water relations measurements of crested wheatgrass leaves at the end of the greenhouse experiment. Water potential measurements are in MPa and dry weights are in g. Values in columns with different letters are significantly different at $P<.05$.

	Osmotic Potential at Full Turgor ($\psi^{\pi100}$)	Osmotic Adjustment ($\Delta\psi^{\pi100}$)	Mid-day Total Water Potential (ψ_w)	%K	Weight
Wet					
Low K	-2.93 a	0.53 ab	-2.60 a	2.88 a	1.57 a
Med K	-1.94 a	-0.51 a	-3.44 ab	3.43 b	1.30 ab
High K	-2.98 a	1.19 ab	-4.30 ab	3.28 ab	0.90 bc
Dry					
Low K	-2.27 a	0.45 ab	-5.47 b	2.76 a	0.76 bc
Med K	-3.50 a	1.13 ab	-5.56 b	3.43 b	0.91 ac
High K	-3.45 a	2.09 b	-4.77 ab	3.40 b	0.53 c

adjustment with higher soil K contents. No differences were found between measurements of osmotic potential at full turgor.

No differences were detected between the tissue K concentrations of the medium and high K treatments, but the low K treatment plants had significantly lower K than the other two fertilization treatments. Weights of the water-stressed plants were generally less than those that continued to receive water. While the differences between the weights of the water-stressed plants were not significant, the water-stress, high K treatment plants weighed less than those in any other treatment, and the watered high K treatment plants also had the lowest weights of the watered plants.

Soil Water Relationships

Rates of water extraction from the soil did not show clear patterns of seasonality and depth as observed by Thorgeirsson (1985) (Figure 8). Water extraction rates varied considerably, especially at the beginning of the summer when there was a large amount of precipitation. Precipitation of 25 mm was recorded in the three days prior to the first readings in June (the third symbols in Figure 8) when water use rates were high. There was even more precipitation (33 mm) before the next readings when almost

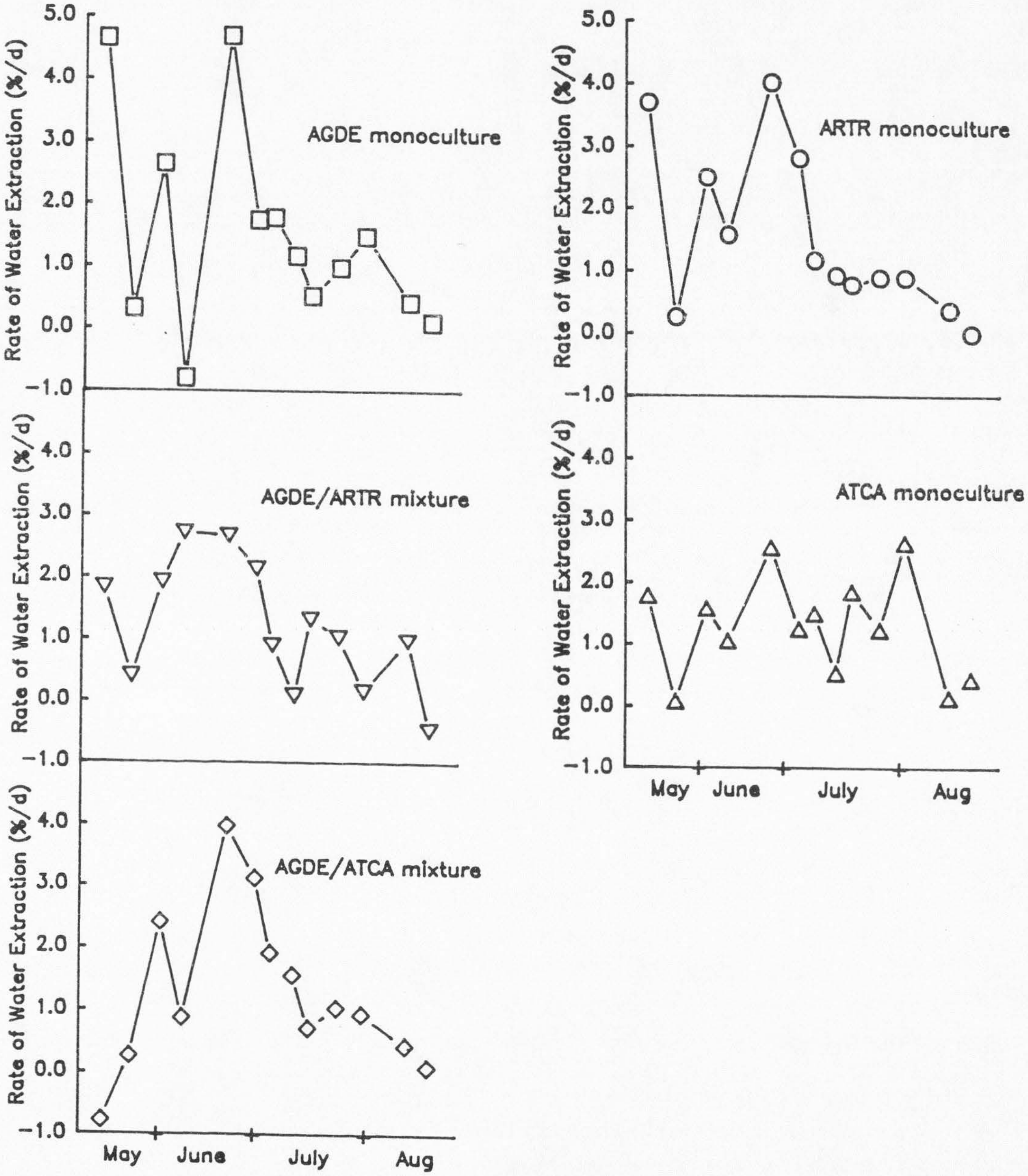


Figure 8. Daily rates of available water extraction averaged through all depths. Estimated contributions of precipitation are included. AGDE = crested wheatgrass, ARTR = sagebrush, ATCA = fourwing saltbush

all of the treatments had decreased water use. Another 20 mm of precipitation fell before the next readings, when there was another sharp increase in water extraction rate.

Fortunately, little rainfall was received to confound the results from mid-June to late July, and more uniform patterns of decreasing water use became clear. Late July and early August rains had the effect of increasing water use in the last part of the summer when it would normally continue to decline.

The effects of both the early and the late summer precipitation are also evident in the soil water potential data (Figure 9). The crested wheatgrass monoculture plots, with twice the density of crested wheatgrass plants compared to the mixture plots, were clearly drier at 40 cm than any of the mixture plots. Minimum soil water potential measurements at 40 cm were -3.4, -2.6, and -2.4 MPa for crested wheatgrass monoculture, sagebrush mixture, and fourwing saltbush mixture plots, respectively. Minimum values at 40 cm for the shrub monoculture plots were -3.0 and -2.0 MPa for sagebrush and fourwing saltbush.

No significant differences in predawn xylem water potentials of crested wheatgrass were found among treatments through the 2 July measurements (Figure 10a). Starting on 19 July, crested wheatgrass in mixture with fourwing saltbush had lower predawn water potentials than those in the other two treatments, but treatments did not differ on 27 August.

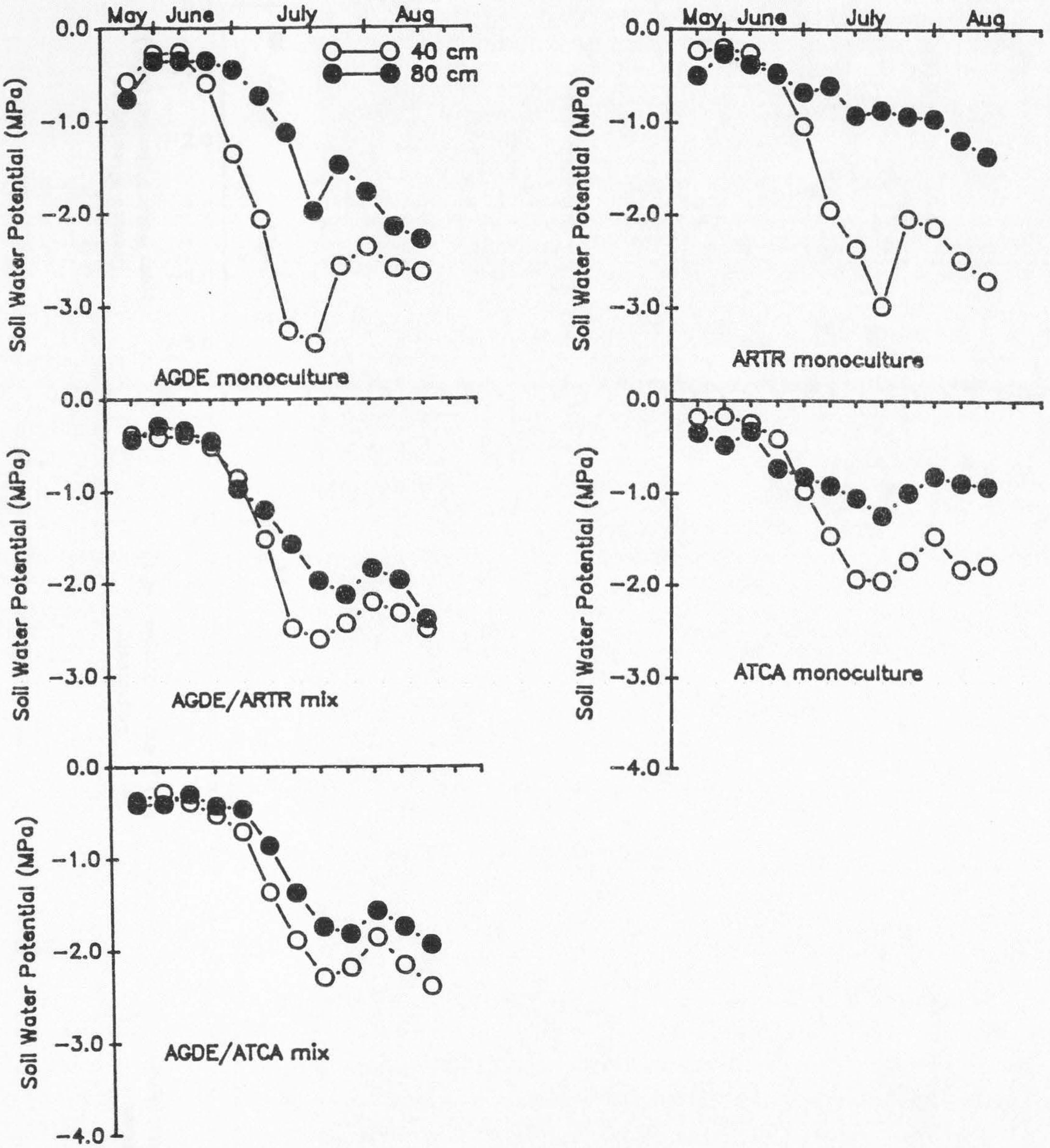


Figure 9. Soil water potentials of the treatment plots. These measurements were taken at the same time as the volumetric water content measurements in Figure 8. AGDE = crested wheatgrass, ARTR = sagebrush, ATCA = fourwing saltbush

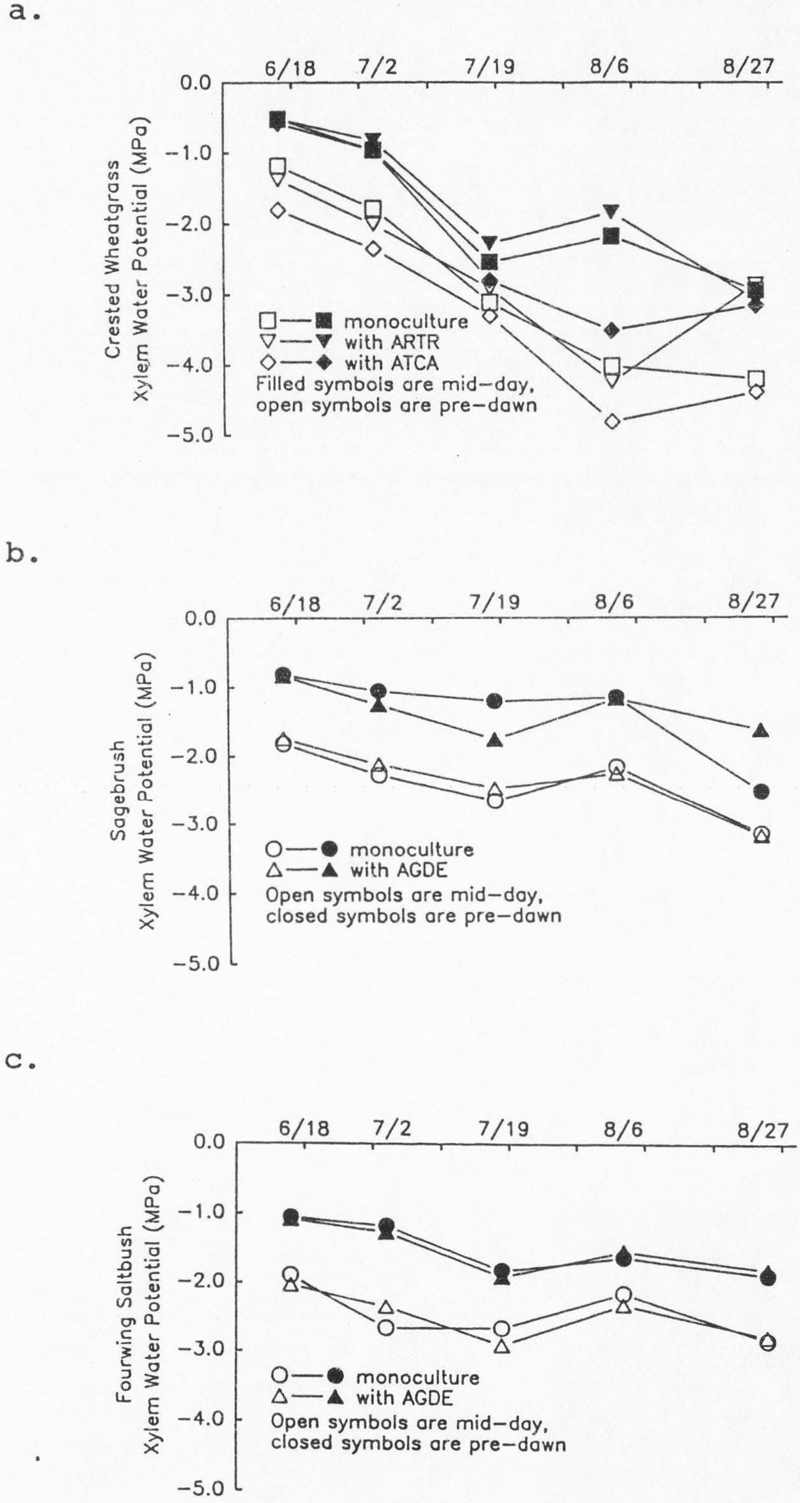


Figure 10. Predawn (filled symbols) and mid-day (open symbols) crested wheatgrass (a), sagebrush (b), and fourwing saltbush (c), xylem water potentials.

Mid-day measurements of xylem water potential for crested wheatgrass showed no difference on 19 July, but the fourwing saltbush mixture plants had lower potentials by the end of the summer. The increase in crested wheatgrass xylem water potentials on 2 August may be attributable to the change to using inflorescences for the measurements or to rain.

Few differences were observed between treatments for the shrub xylem water potentials (Figures 10b and c). On 27 August predawn xylem water potentials for sagebrush growing in monoculture were significantly lower than those of sagebrush growing in mixture with crested wheatgrass. Sagebrush plants probably continued to transpire in mixture with senesced crested wheatgrass and had little competition for water, but monoculture plants may have had greater intraspecific competition.

CHAPTER IV

DISCUSSION

Nutrient Relationships

High K concentrations in leaves and high return to soil from fourwing saltbush were expected to lead to increased K concentration and biomass yield of crested wheatgrass when the two species were growing in mixture. Crested wheatgrass in mixture with sagebrush was expected to have decreased yields compared to crested wheatgrass monoculture plots. Return of K to the soil from sagebrush was anticipated to be less than from fourwing saltbush, but no difference was expected in return of N or P.

Soil K concentrations in crested wheatgrass/fourwing saltbush mixture plots probably had not been influenced by additions from fourwing saltbush when this study was undertaken because shrubs had only been growing there one year. In contrast to the expected increase, the reduced K concentration in crested wheatgrass in mixture with fourwing saltbush suggests a competitive effect caused by the fourwing saltbush (Tables 3 and 4). This is surprising because of the small size of the fourwing saltbush plants in those plots. Other possible explanations, however, such as effects of soil conditions that might have appeared as block effects, were not significant.

The lower K concentrations in crested wheatgrass in mixture with fourwing saltbush did not limit biomass production. Pendery and Provenza (1987) also found no significant differences between the biomass yields of crested wheatgrass with fourwing saltbush compared to the other shrub mixtures. However, there was no increase in crested wheatgrass yield in mixture with fourwing saltbush, as found by Rumbaugh et al. (1982).

Crested wheatgrass nutrient RYP values (Table 8) are less than the significant biomass RYP value (1.89) which Pendery and Provenza (1987) reported for crested wheatgrass in two-way mixtures. Crested wheatgrass biomass or nutrient pools were not increased in shrub mixture plots. Pendery and Provenza's results include samples from treatments not used in my study, and they did not include crowns.

Differences between sagebrush and fourwing saltbush in nutrient standing crops are consistent with my island of fertility hypothesis and with the work of Romney et al. (1973) and Wallace et al. (1973) that indicated that fourwing saltbush accumulated large amounts of K. Accumulation of nutrients by both shrub species continued through late summer, before translocation and leaching decreased standing crops. This pattern contrasts with the lack of accumulation in crested wheatgrass after the end of

May (Figure 3).

The amount of K returned to the soil by throughfall was much greater than that returned by litterfall or by inputs from precipitation alone. This implies that much of the K in leaves was leached before they fell, in agreement with Chapin (1980). Some of the K from throughfall was undoubtedly from dust collected on the leaves and may or may not represent an actual gain. Ellis et al. (1983) decided not to consider throughfall in their study of nutrient gain in southern California chaparral because of the difficulty in deciding whether or not accumulated dust on leaves and branches was of local origin. Because of similar morphology, it is unlikely that dry deposition could account for the large difference in K cycling between the shrub species.

The difference between the species in the amount of K returned to the soil, 7.0 $g \cdot m^{-2}$ canopy, is large and represents a 55% increase for fourwing saltbush over sagebrush as hypothesized. These K return results support other studies (Fairchild and Brotherson, 1980; Romney et al., 1980) showing greater soil K concentrations under fourwing saltbush than sagebrush. If the response of crested wheatgrass to fourwing saltbush is nutrient-related, this study shows that, of the three nutrients studied, K relations differ most strongly between sagebrush and fourwing saltbush. Study of the effects of very high levels of K, such as were found in soil under fourwing saltbush at the Nephi Experiment Station (1600 ppm), on crested wheatgrass may be of value in elucidating the grass/fourwing saltbush interaction. Other cations may be freed from soil colloids by the mass effects of high K concentrations.

Pendery and Provenza (1987) discussed some of the difficulties with transplanting shrubs into established stands of crested wheatgrass as was done at the Green Canyon Research Center for this study. They found both mortality and biomass yield of prostrate kochia, Kochia prostrata, sagebrush, and fourwing saltbush adversely affected by interference from previously established crested wheatgrass and concurrently-planted alfalfa compared to shrub monoculture plots. If the benefits of interplanting shrubs with grasses are to be accrued within a practical time frame, more effort must be made to allow shrubs to become established before they are required to compete with grasses.

As expected, return of K to the soil from fourwing saltbush was greater than from sagebrush. Effects of mature shrubs on crested wheatgrass were probably not expressed in this study, however, and crested wheatgrass nutrient standing crops were neither increased in fourwing saltbush mixture plots nor decreased in sagebrush mixture plots as expected from previous studies.

Soil Water Relationships

Anticipated high soil and crested wheatgrass tissue K concentrations in fourwing saltbush mixture plots were expected to lead to osmotic adjustment and an extended period of growth for crested wheatgrass. Differential patterns of depth and timing of water use by crested wheatgrass, sagebrush, and fourwing saltbush were also anticipated to result in less water stress in crested wheatgrass growing in mixture with fourwing saltbush than when growing with sagebrush or in monoculture.

Contrary to expectations, crested wheatgrass plants growing in mixture with fourwing saltbush were more water stressed in the latter part of the summer than those in the other plots (Figure 10a). Soil water potentials in the fourwing saltbush mixture plots were similar to those for the other two plots with crested wheatgrass. The reason for these apparently contradictory results is not clear and could be addressed in further studies.

The increased water stress and decreased N and K concentrations of crested wheatgrass in mixture with fourwing saltbush indicate interspecific competition. The significant measured influence of fourwing saltbush on crested wheatgrass in these plots contrasts with the previous reports of improved growth of crested wheatgrass when growing with fourwing saltbush. Also, the effects of fourwing saltbush on crested wheatgrass are surprising because the shrubs were so small (Figures 4 and 5).

Despite the variability in the water extraction rates (Figure 8), a few patterns could be distinguished. Fourwing saltbush monoculture plots had the most uniform rate of water extraction throughout the growing season. Rates of extraction for every other plot, including sagebrush monocultures, peaked in mid-June. This suggests that the timing of water uptake for sagebrush and crested wheatgrass overlap and are concentrated in late spring, while fourwing saltbush uses water throughout the season. In addition to the possible vertical spatial separation between the bulk of crested wheatgrass and fourwing saltbush root systems (Wallace and Romney, 1972; Fairchild and Brotherson, 1980; Wallace et al., 1980), a temporal separation in competition for water may also exist. Caldwell et al. (1977) found that while <u>Atriplex</u> <u>confertifolia</u> exhibited maximum photosynthetic rates in the spring, it had a prolonged period of low photosynthetic activity in the dry late summer. <u>Ceratoides</u> <u>lanata</u>, a co-occurring C_3 species, had higher photosynthetic rates in the spring and was largely inactive during the late summer. This appears to be a similar pattern to that of fourwing saltbush, a C_4 species, and sagebrush, a C_3 species.

The difference in timing could be very important in certain parts of the distribution of fourwing saltbush in the southern Intermountain Area where substantial precipitation is received in July and August. Crested wheatgrass could use available soil moisture in the spring and early summer while fourwing saltbush could rely more on late summer rains. Precipitation in Cedar City in southern Utah increases 156% in July and August compared to June. Logan and Nephi, in the northern and central parts of the state, do not experience the phenomenon of late summer rains to the extent that more southerly areas do. While this does not explain increases in crested wheatgrass production, it does indicate less of a negative interaction than with sagebrush.

There were no effects on crested wheatgrass water potentials caused by increased K concentrations which were expected to result from high additions of K to the soil from fourwing saltbush. A difference between sagebrush and fourwing saltbush in timing of water extraction indicates a lack of competition between crested wheatgrass and fourwing saltbush compared to sagebrush.

Potassium in Soil and Water Relationships

Soil K concentrations of less than 100 ppm are generally considered to limit plant production (D. Whiting, personal communication). The initial low soil K treatment concentration of 41 ppm in the low-K treatment of the greenhouse experiment was expected to limit crested wheatgrass growth, especially under conditions of water stress. Increased K concentrations in the soil were expected to increase the ability of crested wheatgrass to osmotically adjust and continue growth under water stress.

Crested wheatgrass accumulated K when it was provided in the soil in larger quantities (Table 13) and it may have used K for osmotic adjustment. Although few significant differences in osmotic adjustment were observed among treatments, a trend toward greater osmotic adjustment with higher soil K levels was exhibited in the water-stressed plants. The degree of adjustment (up to 1.56 MPa higher than in the watered low K plants) is much greater than that reported by Wilson and Ludlow (1983) (maximum of 0.66, 0.66, and 0.71 MPa) in their field study of K fertilization of three tropical grasses.

The water-stressed high K plants weighed the least of any treatment. High K levels may have been toxic in this particular environment. Soil levels much higher than those in this experiment, however, are common in field situations. For example, the soil at the Nephi Experiment Station had higher soil K levels (1600 ppm) without any apparent toxicity problems.

If the degree of osmotic adjustment that apparently took place in this experiment occurs in the field where high soil K concentrations occur, the addition of a K accumulator, such as fourwing saltbush, to grass plantings may increase the production and quality of crested wheatgrass and possibly other plants. Further studies need to be conducted to confirm these results to show that osmotic adjustment in crested wheatgrass is, indeed, leading to a maintenance of turgor, leaf elongation, and photosynthesis and to a subsequent increase in productivity.

Conclusions and Recommendations

Many of the results of this study demonstrate differences between sagebrush and fourwing saltbush and possible effects on crested wheatgrass. The results show the need for further research, especially with regard to water use by fourwing saltbush and the effects of K on crested wheatgrass.

The data in this study show strong competition, even by very small fourwing saltbush plants, for water and nutrients (N and K). Although fourwing saltbush was able to compete well with the crested wheatgrass for water and nutrients it did not respond with increased growth, a result that remains unexplained. The results contrast with those of Rumbaugh et al. (1982) which showed increased crested wheatgrass yield when it was grown in association with fourwing saltbush. A more detailed study of timing and depth of water use by fourwing saltbush and crested wheatgrass in well-established and new stands needs to be performed.

Potassium fertilization of soil with limiting amounts of K was shown to increase crested wheatgrass K concentrations and osmotic adjustment under water stress. Osmotic adjustment did not lead to an increase in biomass production. Additions of K from fourwing saltbush may lead to osmotic adjustment in crested wheatgrass under conditions of low soil K availability.

It is clear from this and other studies that fourwing saltbush accumulates large amounts of K and rapidly returns this to the soil. In this study, yield, nutrient pools, and water status of crested wheatgrass were reduced rather than increased as expected.

Fourwing saltbush and other species of Atriplex are considered to be genetically very diverse with numerous locally adapted ecotypes (Stutz, 1982). Conclusions drawn on results of studies of one ecotype might not apply in different situations where that ecotype was not adapted.

Future research should be conducted to further define physiological differences between sagebrush and fourwing saltbush and the associated responses of crested wheatgrass. Increased forage yield and quality at times when the availability of other plants for livestock or wildlife may be low, make the inclusion of fourwing saltbush and, to some degree, sagebrush in mixed plantings with crested wheatgrass desirable.

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