AN ABSTRACT OF THE THESIS OF

James T. Romo for the degree of Doctor of Philosophy
in Rangeland Resources presented on October 5, 1984 .

Title: Water Relations in *Artemisia tridentata* subsp. *wyomingensis*, *Sarcobatus vermiculatus* and *Kochia prostrata*

Redacted for Privacy

Abstract approved: Marshall R. Haferkamp

Responses during germination and plant growth of prostrate kochia (*Kochia prostrata*), greasewood (*Sacrobatus vermiculatus*) and Wyoming big sagebrush (*Artemisia tridentata* subsp. *wyomingensis*) were measured under varying levels of water stress, temperature, and specific ions to evaluate the adaptability of prostrate kochia for revegetating greasewood communities.

Prostrate kochia and greasewood seeds were incubated at 10 and 20C on substrates of salt affected soils. Germination of both species was reduced by low temperatures, but neither was affected by chemical properties of soils.

Germination of prostrate kochia was further evaluated in varying levels of temperature, water potentials, and

approximately 10 $\mu g.cm^{-3}$. Maximum g_s decreased and resistance to liquid water flux increased as predawn leaf water potentials declined in sagebrush. Maximum g_s of greasewood was reduced by nighttime temperatures near freezing and daytime vapor pressure deficits above 10 $\mu g.cm^{-3}$.

Water Relations in *Artemisia tridentata* subsp. *wyomingensis*, *Sarcobatus vermiculatus*, and *Kochia prostrata*

by

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A THESIS
submitted to
Oregon State University

in partial fulfillment of
the requirements for the degree of

Doctor of Philosophy

Completed October 5, 1984

Commencement June 1985

Approved:

Redacted for Privacy

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Date Thesis is presented: October 5, 1984

Typed by: Modern Office Management Systems

For: James T. Romo

Acknowledgements

I extend my appreciation to the staff of Squaw Butte Experiment Station for financial support, use of equipment and facilities, and hospitality throughout my graduate program.

I express appreciation to my major professor, Marshall Haferkamp, who provided constructive criticism during the development and execution of these studies and preparation of this thesis. Many of our discussions were very thought provoking.

My thanks to my committee members, Drs. Lee Eddleman, Don Grabe, Bill Krueger, Richard Miller, and Dale Moss for constructive comments and discussion throughout my program.

Appreciation is extended to staff and graduate students in the Department of Rangeland Resources.

To my parents, Phyllis and Clarence Romo, I thank you for your encouragement throughout my college education.

And finally, but most important, I dedicate this thesis to my wife Cindy. Cindy assisted in all phases of my studies, prepared all graphic arts, and gave unending moral support during the past three years. Thank you.

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Introduction

Germination, growth, survival, and reproduction of plants are directly or indirectly influenced by water. Distribution of plants is often regulated more by the availability of water during critical periods than other environmental factors (Kozlowski 1968). On rangelands, plant water deficits are daily and seasonal events, and it is important to understand plant responses to a limited water supply at all stages of growth. It is equally important to understand responses of plants during periods of high moisture availability. Depending on the intensity and duration of water stress, nearly all plant constituents and processes are altered (Hsiao 1973).

Survival of plants in arid regions depends on structural and functional adaptations that enable spatial and temporal exploitation of water. The frequency, intensity, and duration of water stress, or conditions favorable for growth, in combination with other abiotic and biotic factors, influence the competitiveness of plants and composition of communities. Because low water availability often limits survival, selective pressure for adaptations for drought resistance may be high (Pallardy 1981). However, survival does not provide precise comparative information regarding water relations and drought resistance.

Knowledge of the physiological requirements of plants is central to range management. Determining adaptations and physiological characteristics of plants inhabiting harsh environments may be useful for a variety of applications. Information derived from physiological studies may be useful for selecting superior plant materials for revegetating rangelands, and it may be useful for control of undesirable species. Assessing and interpreting plant water status, in relation to environmental factors or physiological characteristics, are useful for understanding distributional patterns of plants (Ritchie and Hinckley 1975). Physiological studies also yield information that is crucial for the analysis of the structure and function of ecosystems.

Tolerance of water stress is an important consideration when selecting plants for revegetating rangelands in arid and semiarid regions. Climate and soils are criteria most often used for selecting species. However, methods for quantifying aridity on a particular site are poorly defined. Droughtiness may be reflected in the intensity of seasonal and diurnal water stress in species inhabiting a site. Information derived from studies of water relations in the species inhabiting a site may be useful for selecting improved species. This procedure would be possible only if requirements and responses to water stress are known for both native and improved species.

This research was conducted to evaluate the suitability of prostrate kochia (_Kochia prostrata_ (L.) Schrad.) for improving sites in the shrub steppe that are dominated by greasewood (_Sarcobatus vermiculatus_ (Hook.) Torr.). It was hypothesized adaptability of prostrate kochia could be measured by comparing its response to water stress with responses in native shrubs. High salt concentrations and low soil water potentials limit germination, growth, establishment, and persistence of many desirable species on sites occupied by greasewood. Therefore, studies were conducted to compare germination responses to temperature, water stress, and specific ions in prostrate kochia and greasewood. Studies were also conducted to determine whether greasewood or Wyoming big sagebrush (_Artemisia tridentata_ Nutt. subsp. _wyomingensis_) are suitable indicators of the soil moisture regime on a particular site. This evaluation was complemented by determining seasonal and diurnal characteristics of water relations in prostrate kochia.

The specific objectives were to:

1. Evaluate the potential for using soils as an *in vitro* technique for assessing the effects of specific ions on germination.
2. Evaluate the effects of temperature, water stress, and various concentrations of potassium chloride and sodium chloride on germination of prostrate kochia under controlled environmental conditions.
3. Evaluate the effects of water stress and several concentrations of potassium chloride and sodium chloride on germination of three collections of greasewood.
4. Evaluate the seasonal and diurnal course of leaf water potential, stomatal conductance, transpiration rates, and resistance to water flux in prostrate kochia in the field.
5. Evaluate seasonal and diurnal leaf water potentials, stomatal conductance, transpiration rates, and resistance to water flux in Wyoming big sagebrush and greasewood in a side-by-side comparison in the field.

Literature Review

The Physical Environment

The environment of the cool shrub steppe is characterized by extreme flucuations in temperature and precipitation (Caldwell 1974). Winter temperatures are often below freezing for prolonged periods, and summer temperatures can reach 40C. Precipitation is quite variable throughout the area, and ranges from 150 to 350mm annually. Most precipitation is received as snow in late fall, winter, and early spring when temperatures are too low for growth of most species (Harris 1967; Daubenmire 1972). Moisture availability and temperatures favorable for growth are poorly synchronized, thus, germination and growth of most plants are restricted to a short period in spring and early summer. Plants grow as temperatures rise in the spring, but they enter dormancy when soil moisture is depleted and temperatures are high (Harris 1967; Moore et al. 1972a; DePuit and Caldwell 1973, 1975; Caldwell et al. 1977). Plants must also endure dormancy induced by low winter temperatures.

Chemical and physical properties of soils locally exacerbates climatic conditions (Shantz and Piemeisel 1940; Gates et al. 1956). Chemical and physical properties of soils vary with topographic position (Shantz and Piemeisel 1940), parent materials (Fireman and Hayward 1952) and the type of vegetation (Roberts 1950; Rickard 1965a). Within the shrub steppe, considerable areas have soils that are fine-textured with high salt content. Although fine textured soils have high water holding capacity, water availability may be limited by low infiltration rates (Gates et al. 1956; Rollins et al. 1968; Branson et al. 1970) and low osmotic potentials caused by salt accumulations (Gates et al. 1956; Branson et al. 1967, 1970). Branson et al. (1970) found water potentials of surface soils ranging from -0.01 MPa to less than -75.0 MPa from spring to fall. Thus, the general climate of the shrub steppe and the physical and chemical properties of soils are of primary importance when selecting sites and species for revegetation efforts in the shrub steppe (Bleak et al. 1965; Eckert et al. 1978).

In a study of relationships between edaphic factors and shrub distribution in Utah, Gates and associates (1956) found total soluble salts (TSS), electrical conductivity, exchangeable sodium percentage (ESP), and soluble sodium were correlated with plant associations. These factors directly or indirectly influence water availability in soils and growth of plants. In another study, Branson et al. (1967) hypothesized shrub distribution is related to the capacity of different species to remove soil moisture at low soil water potentials. The chemical and physical properties and water regime of soils may, however, be altered by species occupying the site. Plant induced changes in soil properties may influence the distribution of plants within a community by affecting germination and establishment.

Evidence suggests changes in chemical properties may be related to specific taxa (Moore et al. 1972b; Weibe and Walter 1972; Wallace et al. 1973; Rickard 1982). Shrubs apparently influence the chemical and physical mosaic of soils in at least two ways. Shrubs sequester ions in their leaves, and through leaf drop and decay, they enrich the nutrient status of soils beneath shrubs. Modification of physical properties is most pronounced in sparsely vegetated communities. In many areas, small coppice dunes of coarse-textured soils form around the base of shrubs. Often shrub interspaces are stripped of coarse materials by wind erosion, leaving fine-textured and crusted soils (Rollins et al. 1968; Eckert et al. 1978).

Roberts (1950) found sodium and TSS were higher under *Sarcobatus vermiculatus* and *Atriplex confertifolia* than in interspaces. He also reported sodium and TSS decreased with depth and distance from shrubs. Fireman and Hayward (1952) found pH, TSS, and ESP were higher under *S.*

vermiculatus and *A. confertifolia* and in interspaces than under *Artemisia tridentata*. Patterns of chemical properties were also better developed under larger and presumably older shrubs. Rickard (1965b) found potassium, calcium, and magnesium were higher under *Grayia spinosa* than in interspaces; sodium, potassium, and calcium were higher under *S. vermiculatus* than in interspaces. The observations of Rollins et al. (1968) do, however, show a deviation from other research. They reported TSS and ESP were lower beneath *S. vermiculatus* than in interspaces. They concluded lower levels of ions under shrubs were related to leaching from coarse-textured coppice dunes.

Soils of the shrub steppe are quite variable and the heterogeneity of soils influences seed germination and seedling establishment. Differences in seed germination and seedling establishment may be related to amelioration of the microenvironment (Schlatterer and Hironaka 1972; Young and Evans 1975) or to the effects of physical and chemical properties of soils (Rollins et al. 1968; Eckert et al. 1973). Young and Evans (1975) concluded *Bromus tectorum* germinated and established better under shrubs than in interspaces because the canopy and litter moderated temperature and moisture conditions, and maintained them within the range required for germination. Schlatterer and Hironaka (1972) felt increased fertility and a more favorable microenvironment favors establishment of Sitanion hystrix under shrubs. Agropyron elongatum established better where S. vermiculatus had grown than on interspace soils (Rollins et al. 1968). They concluded high concentrations of sodium, boron, and TSS limited establishment of A. elongatum on interspace soils. Roundy (1983) also found soils of coppice dunes were more penetrable than interspace soils and therefore, mechanical resistance to emerging seedlings was lower and establishment of A. elongatum and Elymus cinereus was higher on coppice dunes.

For establishment in the shrub steppe, seeds and seedlings must tolerate extremes in temperature, moisture availability, and chemical and physical properties of soils. Irregular rainfall, extreme temperatures, and rapid loss of water through evaporation and plant consumption, may cause high seedling mortality (Bleak et al. 1965; Wein and West 1971). Establishment may be related to a sequence of years that favor seed development, germination, and seedling survival (Went 1955). Cluff et al. (1983) also hypothesized that plants possessing specific germination requirements probably establish periodically. However, most widespread native and naturalized plants can germinate over a wide range of environmental conditions. Through natural selection, native plants have evolved structural and functional adaptations enabling survival and regeneration despite rigors of the physical environment. By identifying adaptations, scientists can select superior plant materials with similar characteristics.

Seed Germination

When selecting species for use in revegetation, the climate and soils should be considered. With this knowledge, the effects of abiotic factors on germination and growth can be assessed and best adapted species selected. Knowledge of the effects of temperature, light, water stress, and specific ions on germination and seed vigor is particularly valuable for land managers. By understanding requirements for each species, managers can select species or cultivars to match environmental conditions expected in the field.

Germination Characteristics of Native and Naturalized Plants

Seeds of *Grayia spinosa*, collected in Nevada and southern California, germinated at temperatures ranging from 0 to 40C (Wood et al. 1976). Optimum germination occurred at alternating temperatures of 5C with 10 to 30C, and at constant temperatures, germination was highest at

10 and 15C. They concluded the ability of *G. spinosa* to germinate at cool temperatures reflects a requirement for species of cold-arid environments to germinate in late fall or early spring when soil moisture is available. This is particularly important in the Intermountain Region because the coincidence of warm seedbed temperatures and adequate moisture is rare.

Germination requirements for *Artemisia tridentata* have been reported by Weldon et al. (1959), McDonough and Harniss (1974), Harniss and McDonough (1976) and Eddleman (1977). Weldon and associates (1959) found germination was affected by the interaction of temperature and light. At 3C, germination was approximately five-fold higher in light than in dark, but at 21C, germination was stimulated about three-fold by light. McDonough and Harniss (1974) and Harniss and McDonough (1976) reported germination of the subspecies *tridentata*, *vaseyana*, and *wyomingensis* was similar at temperatures between 2 and 20C. Cold stratification improved germination of *vaseyana*, but its effect was variable in *wyomingensis* and *tridentata*. McDonough and Harniss (1974) felt a stratification requirement for *vaseyana* is an adaptive mechanism for its habitat, which often maintains snow cover for extended periods. Eddleman (1977) reported new seed of the subspecies *wyomingensis* germinated best after 60 to 90 days of cold stratification; older seeds did not require stratification. Stratification occurs naturally in the field during the winter, and it may enable seeds to germinate in the spring when soil moisture is near optimal for seedling growth (McDonough and Harniss 1974).

Sitanion hystrix germinates well over a wide range of temperatures (Eddleman 1977; Young and Evans 1977). Eddleman (1977) concluded dry storage of seeds at 4C, followed by warm incubation temperatures, was the only treatment that reduced germination. Young and Evans (1977) reported 15C, and alternating 10-15C and 10-20C, were optimal for germination. They felt the lack of afterripening requirements and the ability to germinate at cold temperatures are important for seedling establishment in sagebrush-bunchgrass communities.

Young and Evans (1981) studied germination of Elymus cinereus at constant temperatures ranging from 2 to 40C. Seeds germinated at temperatures lower than 40C, and germination was highest at 15C. Eddleman (1977) also reported germination of E. cinereus was reduced at temperatures above 20C. Furthermore, Eddleman concluded light was not required for germination. Young and Evans (1981) concluded E. cinereus probably does not germinate the year of seed maturation because the seedbed may be initially too dry for germination, and when moisture is sufficient, temperatures may be too low. Thus, seeds may overwinter and germinate in the spring when moisture is high and temperatures are favorable.

Harris (1967) and Eddleman (1977) reported *Agropyron spicatum* germinated best at 20C, but seeds also germinated at higher and lower temperatures. In a subsequent study, Young and coworkers (1981a) found *A. spicatum* germinated best at temperatures ranging from 5 to 40C; optimal incubation temperatures were alternating 15-20C through 15-40C. Harris (1967) felt the inability of *A. spicatum* to germinate and grow at low temperatures limits growth where winter precipitation predominates.

Hulbert (1955) and Steinbauer and Grigsby (1957) reported germination requirements for *Bromus tectorum* were quite variable; optimal temperatures for germination changed and broadened as seeds aged. Optimum temperatures for germination was 10C for freshly harvested seeds, 15C for 4 week old seeds, and 20C for seeds that were 1 year old (Hulbert 1955). Steinbauer and Grigsby (1957) found seeds 1 week old germinated best at 15C, but if seeds were stratified at 4C, they germinated best at 20C. Thill et al. (1980) found warm stratification improved germination at 30C, but it had little effect on germination at 15 and 20C. Hulbert (1955) concluded the ability of *B. tectorum* to germinate at the most favorable time for seedling establishment was related to changing requirements for germination and changing environmental conditions. Mack and Pyke (1983) found recruitment of seedlings was concentrated in late summer and autumn after rains were received. Harris (1967) felt the ability of B. tectorum to germinate in the autumn and grow in the winter are important for establishment in regions with winter percipitation. The ability to grow at low temperatures may also be an important consideration when selecting species for revegetating saline sites.

Sarcobatus vermiculatus, collected in eastern Montana, germinated best at 4 and 10C without stratification and at constant 30C with stratification (Eddleman 1979). Sabo et al. (1979) reported S. vermiculatus, collected in New Mexico, also germinated best at cold temperatures; germination was substantially reduced at temperatures above 15C. Romo and Eddleman (1985) reported S. vermiculatus germinated at temperatures between 5 and 40C, and germination was highest at constant temperatures of 5 through 25C. Eddleman (1979) concluded some seeds of S. vermiculatus may germinate in the fall, but freezing temperatures may cause high seedling mortality. An afterripening requirement, and the ability to germinate at low temperatures, probably restricts most germination of S. vermiculatus to spring (Romo and

Eddleman 1985). Seedling resistance to damage by low temperatures may be an important factor to consider when selecting plants to germinate at low temperatures (Bleak et al. 1965).

Balyan (1972) reported germination requirements of *Kochia prostrata* were related to habitats where seeds were collected. Ecotypes collected from mountainous areas in the Soviet Union, germinated best at temperatures between 24 and 28C. Some seeds germinated at temperatures as low as 4C and as high at 35C. Seeds collected in the semidesert and desert regions required higher temperatures for germination; optimal incubation temperatures were between 30 and 35C. Minimum and maximum temperatures for germination were 6 and 40C, respectively. Balyan (1972) also noted germination occurred in the field when daily temperatures averaged 2 to 3C; temperatures to -4C did not adversely affect germination. Young et al. (1981b) evaluated germination requirements of 23 accessions of *K. prostrata*. All accessions germinated best at 20C. Optimal germination of accession PI 314929, recently released as 'Immigrant', occurred at 15, 20, and 25C and at alternating 15-20C. They concluded widely fluctuating seedbed temperatures are important in the seedbed ecology of *K. prostrata*.

Effects of Water Potential and Specific Ions on Germination

Germinability under moisture stress is an important consideration when selecting species for revegetating sites in the shrub steppe. Decreasing water potentials or increasing ionic concentrations delay and reduce germination. Depending on the species, water potential may limit germination more than ions, or ions may inhibit germination more than water potential (Ungar 1973). Usually the interaction of temperature and water potential, or temperature and specific ions are significant, and germination is least inhibited at optimal incubation temperatures (Springfield 1966; Tadmor et al. 1969; Ungar 1978, 1982).

Germination of Distichlis spicata was similar in solutions of NaCl and polyethylene glycol (PEG) at comparable water potentials (Cluff et al. 1983). In both solutions, germination was significantly reduced at water potentials lower than -0.1 MPa, and no seeds germinated at water potentials lower than -1.5 MPa. Sabo et al. (1979) germinated seeds of D. spicata collected in New Mexico. They found seeds germinated well to -1.6 MPa, but germination was significantly reduced from control at -1.0 MPa. Cluff et al. (1983) found D. spicata required alternating temperatures of 30 to 40C for optimal germination. Sabo et al. (1979) reported alternating temperatures of 36-40C were necessary for optimal germination. These results indicate D. spicata germinates if temperature and water potentials are high. The coincidence of these conditions is rare in the shrub steppe, thus, establishment may be episodic (Cluff et al. 1983).

Agropyron spicatum, Artemisia tridentata, Lepidium perfoliatum, and Elymus cinereus germinated better in NaCl and Na_2SO_4 than in PEG; Na_2CO_3 was toxic to all species except E. cinereus (Choudhuri 1968). Choudhuri (1968) concluded all species were less tolerant of salinity during germination than during the seedling stage if salinization was gradual. An abrupt increase in salinity caused death in all species. In a similar study, Young and Evans (1981) reported their collections of E. cinereus germinated poorer in NaCl than in PEG. They concluded seeds of E. cinereus collected from saline sites were less adapted to germinate in saline conditions than seeds from non-saline sites. However, Choudhuri (1968) found no significant differences in germination of E. cinereus from saline and non-saline habitats. Young and Evans (1981) postulated low germinability of seeds from saline environments may represent an adaptation that prevents germination except when surface soils are leached of salts and moisture conditions are favorable, or seeds may be preconditioned while lying in the soil and they are better able to germinate at low osmotic potentials. These requirements may restrict most germination of *E. cinereus* to spring.

In the laboratory, germination of *Agropyron spicatum* and *Bromus tectorum* was related to the interaction of temperature and water potential (Harris 1967). Both species germinated best at 20C and germination was lower at 10 and 30C. At 10C, *B. tectorum* germinated more rapidly and root growth was greater than *A. spicatum*. Under field conditions *B. tectorum* also germinated faster than *A. spicatum*. Plants that germinate early, and rapidly extend roots, have the best opportunity for growth and establishment before the onset of low winter temperatures or summer drought (Harris 1967). Early germination and rapid root growth may be equally important for seedling establishment on salt affected soils.

Weldon et al. (1959) reported germination of *Artemisia tridentata* was higher at all water potentials at 21C than at 3C. Germination was inhibited more by water potentials at 21C. At 3 and 21C, germination was significantly lower at -0.4 MPa than at 0 MPa. Germination was significantly reduced between -0.4 and -0.8 MPa at 21C, but not at 3C. *A. tridentata* has apparently developed the capacity to germinate at cool temperatures when moisture deficits are likely least severe.

Springfield (1968) found germination of Eurotia lanata was reduced more by water potentials at high than at low temperatures. He concluded soil moisture near field capacity is necessary for germination at high temperatures, and water stress inhibits germination less at lower temperatures. This adaptation may increase germination when temperatures are low and thus maximize the growth period for seedlings. Species which germinate at low temperatures, and under moderate moisture stress, may establish best on saline soils.

Germination of Grayia spinosa is reduced more by ions than water potential (Wood et al. 1976). Germination was approximately 40 percent at -1.6 MPa in PEG, but in NaCl, seeds did not germinate at water potentials lower than -1.3 MPa. They felt the severe reduction of germination in NaCl reflected ion toxicity. Furthermore, high concentrations of NaCl may not be a problem on sites supporting G. spinosa.

Romo and Eddleman (1985) reported a significant ion X water potential X temperature interaction in germination of Sarcobatus vermiculatus. Germination was highest at 10 and 20C and lowest at 30C, and more seeds germinated in

NaCl than in Na_2SO_4 or PEG. At 10 and 20C, seeds germinated to -3.6 MPa in NaCl and Na_2SO_4. When incubated at 30C, seeds germinated to -3.0 MPa in NaCl and -2.4 MPa in Na_2SO_4. In PEG solutions, seeds germinated at water potentials higher than -2.7 MPa at all temperatures. Sabo et al. (1979) found their New Mexico source of S. vermiculatus germinated more than 80 percent at water potentials higher than -1.6 MPa. Romo and Eddleman (1985) felt an afterripening requirement, combined with high germination at low temperatures, limits most germination to the spring when salts in soils are most likely diluted.

The germination response of Kochia prostrata to water stress and specific ions is poorly documented. Balyan (1972) stated "a great quantity of moisture is needed during germination" of K. prostrata. Balyan further reported seeds require 36 to 44 percent of their weight or 8 to 10 percent soil moisture for germination. Semushina and Morozova (1980) attempted to better quantify moisture requirements for germination at 24C and alternating 20-30C. Germination was highest at 24C and ranged from 66 to 96 percent at -0.5 MPa and 24 to 70 percent at -1.2 MPa. At the higher temperatures germination ranged from 48 to 88 percent and 0 to 35 percent at -0.5 and -1.2 MPa, respectively. They concluded seeds of ecotypes from more saline soils were more salt tolerant during germination than ecotypes from less saline soils. Because of the genetic variability in *K. prostrata* (Balyan 1972), specific ecotypes or accessions should be characterized for their response to water stress and specific ions. Knowledge of germination requirements of these ecotypes is useful for selecting cultural practices and sites to insure establishment.

Plant Water Relations

The study of water relations encompasses distribution, movement, function, and status of water in soils, plants, and the atmosphere (Slatyer 1967; Kramer 1969). Movement of water from soil through plants is a physical process; water is transferred through the plant in the liquid phase, and transfer from sites of evaporation in substomatal cavities to the leaf-atmosphere is by diffusion of vapor (Philip 1966). Water moves from regions of high free energy to regions of low free energy (Cowan 1965); free energy is usually highest in the soil, lowest in the atmosphere, and intermediate in the plant (Brown 1977).

Flux of water through the soil-plant-atmosphere continuum (SPAC) is related to the gradient of free energy and resistance to flow (Jarvis 1975). Van den Honert

(1948) proposed water flux (q) is a function of water potential (ψ) and resistance (R) as:

$$q = \frac{\Delta\psi \text{ soil-root}}{R \text{ soil-root}} = \frac{\Delta\psi \text{ root-leaf}}{R \text{ root-leaf}} = \frac{\Delta\psi \text{ leaf-air}}{R \text{ leaf-air}}$$

However, Richter (1973) concluded this model does not accommodate the following: 1) the ability of various parts of the plant to act as sources or sinks for water (capacitance); 2) the assumption of steady-state, non-elastic flow, may not be valid; 3) stomatal gas and liquid phase resistances are not analogous, and phase changes at the leaf complicate R leaf-air; and 4) the total waterflow through all roots, the stem, branches, and the leaves is probably unequal. Running (1980b) also felt the model should include terms to accommodate variable flow resistances throughout the plant, and non-steady state flow in the plant resulting from dynamic water exchange within the plant. He suggested the following model to account for the various components affecting water flux:

$$q = \frac{\Delta\psi \text{ soil-root}}{R \text{ soil-root}} + \frac{\Delta\psi \text{ root-xylem}}{R \text{ root-xylem}} + \frac{\Delta\psi \text{ xylem-leaf}}{R \text{ xylem-leaf}} + \frac{\Delta\psi \text{ leaf-air}}{R \text{ leaf-air}}$$

Using this model, water flux and resistance can be estimated for each component.

Root Resistance

Resistance in roots may be the most significant component of the total plant-liquid phase resistance (Boyer 1974; Passioura 1982). Tanton and Crowdy (1972) concluded the main area of water absorption by roots is between the zone of elongation and the zone of suberization. However, suberized roots are not necessarily nonfunctional in water uptake (Newman 1976). Kramer and Bullock (1966) concluded suberized roots are permeable to water, and permeability of suberized roots increased with increasing root diameter. Brouwer (1953) found at low fluxes, permeability of roots was highest near the root tips; at higher flux rates, the highest permeability was several centimeters from the tip.

Caldwell (1976) posed the following hypotheses regarding root permeability: 1) although water uptake is not restricted to young, unsuberized root tips, absorption per unit length is much greater than in suberized portions; 2) permeability of suberized roots is contingent on suberin deposition; 3) environmental factors that affect metabolism influence permeability; and, 4) the root resistance term for any root segment is not constant;

it may vary with flux rate, and it may also exhibit self-induction behavior and diurnal periodicity. Resistance to water flux in roots may also be affected by salt accumulation, mycorrhiza, pathogens, temperature, and aeration (Newmán 1976; Tinker 1976).

Weatherly (1982) concluded the cortex, endodermis, and stele impose a resistance to flux about five orders of magnitude greater than the root xylem, and they constitute the major resistance to water flow through plants. There are at least three possible pathways for water movement through the cortex, endodermis, and stele. Water may move from 1) vacuole to vacuole; 2) from cell to cell via plasmadesmata (symplastic); and 3) from cell wall to cell wall - water movement in response to a gradient of hydrostatic pressure (apoplastic movement) (Newman 1976). Water probably moves along all pathways, but symplastic movement seems most important (Weatherly 1982).

Xylem Resistance

The mechanics of xylem resistance are poorly understood and the current understanding is largely based on theoretical considerations. Xylem resistance is thought to be low compared to root resistance and gas flow resistance (Jarvis 1975; Newman 1976).

In general, resistance is usually highest at low flux rates, but as flux increases, resistance decreases, and then stabilizes and remains nearly constant (Stoker and Weatherly 1972; Elfving et al. 1972; Boyer 1974; Roy and Mooney 1982). The asymptotic response indicates resistance declines proportionally with increasing water flux to a point, and then becomes constant (Stoker and Weatherly 1974). Variable resistance may also be related to internal capacitance (Richter 1973; Meyer and Ritchie 1980). Presumably resistance to flow of extensible water is less than the main flow resistance (Waring and Running 1976).

Partitioning of plant resistance is estimated as 50 percent in the roots, 20 percent in the stem and petiole, and 30 percent in the leaf (Neumann et al. 1974; Black 1979). Other estimates for relative resistance of roots, stems, and leaves are 2:1:1 for sunflower, 2:1:1.5 for bean, and 10:1:2.5 for soybean (Boyer 1969). Running (1980b) estimated root resistance and stem resistance in lodgepole pine were 52 and 33 percent at high flux and 74 and 12 percent at low flux.

Partitioning of resistance has not been reported for species from the shrub steppe. De Puit and Caldwell (1975) did, however, postulate high root and stem resistance to water flux may be an important factor in the gas exchange of *Artemisia tridentata* subsp. *tridentata*.

Declining water conductance and water absorption capacity of roots may also influence the seasonal decline of transpiration in Eurotia lanata and Atriplex confertifolia (Moore et al. 1972a). In a study of Heliotropium curassuvicum ecotypes from coastal and desert locations, Roy and Mooney (1982) found the desert ecotype maintained higher transpiration rates than coastal ecotypes. On a diurnal basis, they also found resistance decreased as transpiration rates increased, and the desert ecotype maintained lower resistance. They concluded lower resistance in the desert ecotype was reflected in high transpiration rates without a large reduction in leaf water potential.

Leaf Control of Water Loss

Stomatal control of water vapor exchange from the leaf to air is one of the most extensively studied aspects of plant water relations. Within a plant, the major resistance to water flux lies in the gaseous phase where stomata control flow through the system (Weatherly 1976). Stomatal opening and closing seems the only resistance a plant can actively and rapidly control (Slatyer 1967). More than 90 percent of short term changes in total resistance can be attributed to stomata (Hinckley et al. 1978). Minimum resistance to water vapor flux is mainly determined by the density and geometric properties of open stomata and the boundary layer; maximum resistance is determined by cuticular resistance and the extent of stomatal closure (Schulze and Hall 1982).

Total resistance to diffusion of water vapor from a leaf to air (R_{1a}), or its reciprocal, leaf conductance (g_s), are used to describe gas exchange in plants. Total resistance is the sum of boundary layer resistance (R_b) and leaf resistance (R_1) and is described as:

$$R_{1a} = R_b + R_1$$

Furthermore, R_1 is composed of stomatal (R_s), mesophyll (R_m), and cuticular (R_c) resistances (Hinckley et al. 1978). Thus,

$$R_{1a} = R_b + \frac{(Rs + Rm)\ Rc}{Rs + Rm + Rc}$$

Mesophyll resistance is generally considered relatively small (Cowan and Milthorpe 1968) and R_b is negligible at wind speeds greater than approximately 0.9 m sec^{-1} (Gates 1968). Cuticular resistance is high and most water vapor diffuses through stomata (Cowan 1977). Therefore, R_{1a} or g_s are close estimates of potential water vapor diffusion through stomata (Burrows and Milthorpe 1976).

The rate water is lost through transpiration (J) is determined by a driving force and resistance in the pathway (Gates 1968). The driving force is the difference in vapor pressure between the leaf (VP_l) and air (VP_a) and the resistance to flow between the leaf and air is R_{la} (Moore 1977). Therefore:

$$J = \frac{VP_l - VP_a}{R_{la}}$$

Transpiration is a process of energy exchange between plants and the environment. Energy reaching a plant is converted to heat within the plant, or energy is consumed through photochemical or thermochemical reactions of metabolic or physiological processes (Gates 1968). Energy is dissipated by: 1) reradiation or 2) convection of heat; and, 3) energy is used for vaporization of water which is subsequently transpired (Fitter and Hay 1981). Transpiration is dependent on an energy supply to satisfy the latent heat demand, a water vapor gradient to drive the flow of water vapor, and resistance to vapor flow (Moore 1977; Hinckley et al. 1978). Transpiration is an effective process for short-term control of heat dissipation, and factors such as leaf size, shape, orientation, and wind speed also affect the amount of energy absorbed (Gates 1968).

Moore and associates (1972) found transpiration rates of _Atriplex confertifolia_ and _Eurotia lanata_ declined as leaf or soil water potentials decreased and phenology advanced; it increased as temperatures and vapor pressure deficits rose. They postulated the reduction in transpiration, with increasing phenology, was related to reduced absorption of water by roots, increased xylem resistance, and changes in leaf anatomy. Stark (1967) found younger leaves of *Sarcobatus vermiculatus* transpired more than older leaves. She concluded transpiration rates were related to temperature, humidity, leaf color, and physiological condition of leaves. Stark (1967) also concluded *Artemisia tridentata* and *Chrysothamnus nauseosus* subsp. *albicaulis* controlled water loss more efficiently, and transpiration was less dependent on temperature and humidity during seed development.

Balyan (1972) and Khasanov et al. (1983) reported *Kochia prostrata* reduced transpiration during summer drought. Variable transpiration rates may be related to changes in leaf morphology and anatomy (Balyan 1972). Balyan (1972) also reported transpiration rates of pubescent strains of *K. prostrata* were 12 to 22 percent lower than less pubescent forms.

At least 5 daily patterns of transpiration can be distinguished: 1) dome-shaped curves; 2) single-peaked curves; 3) single-peaked curves with a shoulder; 4) two-peaked curves; and 5) more than two peaks (Lange and Losch 1979). The particular response reflects environmental conditions or genetic integrity (Lange and Losch 1979) and the stress history of the plant (Stewart and Dwyer 1983). A particular plant probably exhibits all patterns depending on environmental conditions, preconditioning, and stage of development.

Stomatal Responses to Leaf Water Status and Atmospheric Water Status

The classical description of stomatal reactions to changes in the water content of leaves is called the feedback theory. The feedback theory implies stomata remain open until leaf water potential declines to a critical point and then stomata close (Ludlow 1980). Upon closing, transpiration is reduced, leaf water potential may rise, and stomata may reopen (Ludlow 1980). Short-term responses to changes in water status may be modified by the long-term water stress history (Hsiao et al. 1976).

Ritchie and Hinckley (1975) proposed three responses of stomata to bulk leaf water status. Stomates may respond linearly to leaf water potential, stomatal opening and leaf water potential may be curvilinearly related, or stomata may close at some threshold water potential. Threshold responses seem more common than linear or curvilinear responses (Ritchie and Hinckley 1975).

There are no reports of threshold water potentials for stomatal closure in species of the shrub steppe. Critical water potentials for stomatal closure have, however, been reported for species of other habitats. Running (1976) found abrupt stomatal closure in <u>Pseudotsuga menzeisii</u> and <u>Pinus contorta</u> at -2.0 and -1.8 MPa, respectively. Nilsen et al. (1981) found stomata of <u>Prosopis glandulosa</u> closed when leaf water potential dropped below -4.8 MPa. Stomata of <u>Simmondsia chinensis</u> close steadily with decreasing leaf water potential, but they close abruptly at approximately -4.0 MPa (Adams et al. 1978). Poole and Miller (1975) reported leaf water potentials at which stomata of chapparal species closed. They estimated stomata of three species closed at -2.0 MPa, one each at -3.5 and -5.0 MPa, and two at -5.5 MPa. From their study they classified plant responses into three groups: 1) plants with low leaf water potentials and stomata that are insensitive to water potentials; 2) plants with high water potentials and stomatal response is tightly coupled to leaf water potential; and 3) plants with intermediate leaf water potentials and stomatal sensitivity. Shallow-rooted species and deep-rooted species were characterized by patterns one and three, respectively.

Schulze and Hall (1982) concluded evidence for threshold responses under natural conditions is not strong and the feedback response may not operate. They concluded leaf water potential, temperature, and humidity change simultaneously, and it is difficult to separate their effects on stomata.

Recently, there has been considerable interest in stomatal response to humidity. Stomatal responses to changing humidity were first reported for desert plants by Lange and associates (1971); subsequent studies have shown stomata of most plants respond to changes in ambient humidity. Decreasing humidity causes closure of stomata in arctic and alpine plants (Johnson and Caldwell 1975), temperate species (Kaufmann 1976; Jarvis 1980; Running 1980a), and tropical plants (Mooney et al. 1983). Lange and Medina (1979) also reported stomata of plants possessing crassulacean acid metabolism (CAM) respond to nocturnal changes in humidity.

Stomatal responses to humidity may reflect a mechanism which prevents high rates of plant water loss and development of extreme plant water deficits when plants are subjected to high evaporative demand (Schulze and Hall 1982). Schulze et al. (1972) felt stomatal response to humidity was the result of cuticular transpiration, but Sheriff and Meidner (1975) concluded stomatal closure may result from evaporation from the inner walls of guard cells and subsidiary cells. Tanton and Crowdy (1972) showed the rate of evaporation from guard cells was greater per unit area of wall exposed to the atmosphere than from other tissue.

The theory for the response of stomata to changes in humidity was formalized by Cowan (1977), and Cowan and Farquhar (1977). Their feedforward theory was developed to explain why transpiration can decline even though evaporative demand increases. Cowan (1977) felt localized depletion of water may cause stomatal closure. Thus, water status of the epidermis or guard cells may be more important than the bulk water status of leaves. Feedforward response enables stomata to open under conditions allowing high photosynthesis and close when evaporative demand is high (Farquhar 1978). This response may minimize water loss and maximize carbon gain (Cowan 1977).

A review of the literature disclosed no studies on stomatal responses to changes in humidity for species of the shrub steppe. Caldwell (Martyn Caldwell, 1984 pers. comm.) felt stomatal closure in <u>Artemisia tridentata</u> and <u>Gutierrezia sarothrae</u> (DePuit and Caldwell 1973, 1975) at temperatures above approximately 20C may reflect stomatal sensitivity to humidity. In a study of <u>Diplacus</u>

aurantiacus, a subshrub of the chaparral, Mooney and Chu (1983) found stomata closed as vapor pressure deficit increased. Stomata of plants from a high humidity environment were not as sensitive to changes in humidity as plants from a low humidity habitat when both were grown at high humidity. However, when grown at low humidity, differences in stomatal response were not profound. Roy and Mooney (1982) studied stomatal behavior of coastal and desert ecotypes of *Heliotropium curvassavicum*. At 30 percent relative humidity, stomatal conductance was about 75 percent lower than at 90 percent relative humidity for both populations. Nilsen et al. (1983) found stomata of *Prosopis glandulosa* opened as humidity decreased during the winter, but closed during summer drought as humidity decreased. The winter response may, however, reflect response to temperature.

Stomatal Response to Light, Temperature, and Wind

The photon flux required for maximum stomatal opening varies between species, leaf age, and preconditioning (Schulze and Hall 1982). Leaf conductance usually exhibits a hyperbolic response to photon flux (Burrows and Milthorpe 1976). Normally under low light, a linear relationship exists between light intensity and stomatal aperture if the leaf water potential is sufficient to allow opening of stomata (Lange and Losch 1979). Plants with the CAM photosynthetic pathway do not, however, require light for stomata opening. Most C_3 species are light saturated at intensities of about one-fourth full sunlight whereas C_4 species may not be light saturated at full sunlight (Moore 1977).

Benecke et al. (1981) found stomata of older leaves were less sensitive to reductions in photon flux than younger leaves. In a study of Tamarix chinensis, Anderson (1982) found stomatal conductance remained high at photon flux densities above one-third of full sunlight, but it decreased linearly with decreasing photon flux below that level. Mooney et al. (1983) reported six species were light saturated at approximately one-fourth full sunlight. Detailed light-stomatal response curves are not available for species of the shrub steppe. The results of DePuit and Caldwell (1973, 1975) shows carbon assimilation in Artemisia tridentata subsp. tridentata and Gutierrezia sarothrae increased as irradiation increased when water was not limiting. If temperatures increased above the optimum for photosynthesis, assimilation decreased.

Stomatal response to temperature is similar to the response to light. Stomatal conductance usually increases with temperature at temperatures above the optimum for photosynthesis (Hall et al. 1976). At temperatures above

30 to 35C, however, stomata tend to close (Schulze et al. 1975). The temperature response of plants closely reflects the thermal environment to which they are adapted (Moore 1977).

Pretreatment at different temperatures may also result in changes in stomatal conductance (Schulze and Hall 1982). Drake and Salisbury (1972) found pretreatment of _Xanthium stramonium_ with low temperatures inhibited stomatal opening, but high temperatures had no effect. Research on conifers has shown that temperatures at or near freezing prevents stomatal opening (Kaufmann 1976; Running 1976; Fahey 1979). Hinckley et al. (1978) hypothesized the duration of inhibiting effect of low temperatures is probably related to the length and severity of the cold treatment. The stage of leaf development may also be important. Because temperatures can be near freezing during the growing season, stomatal responses to low temperatures should be considered when selecting species for revegetation efforts in the shrub steppe.

Mooney and West (1964) and West and Mooney (1972) found various preconditioning temperatures altered the optimum temperature for photosynthesis in _Artemisia tridentata_, _Artemisia nova_ and _Artemisia arbuscula_. Plants acclimated at cool temperatures had lower threshold temperatures than plants acclimated at warm temperatures. Cool acclimation and warm acclimation resulted in threshold temperatures of 15 and 20C, respectively, for *A. tridentata* and *A. arbuscula*; the threshold for *A. nova* remained constant at 20C. DePuit and Caldwell (1973, 1975) found optimal temperatures for photosynthesis in *A. tridentata* subsp. *tridentata* increased as the season progressed. In May, the optimal temperature was 15C, and in June and the remainder of the year, it was 20C. *Gutierrezia sarothrae* showed little shift in optimum temperatures (DePuit and Caldwell 1975).

Wind affects stomatal conductance through its affect on boundary layer resistance and leaf temperature. Gates (1968) showed boundary layer resistance is inversely related to the square root of wind speed. Wind speeds less than approximately 0.5 $m.sec^{-1}$ have the greatest influence on transpiration and leaf temperature (Gates 1968).

High wind speed can promote stomata closure (Moore 1977). Davies et al. (1978) found stomata of *Cytisus scoparius* responded differently to wind depending on the ambient humidity. A subspecies of *C. scoparius*, from a sheltered area, regulated stomata poorly under windy conditions, but a subspecies from windswept habitats showed a pronounced decrease in stomatal conductance with increasing wind. Caldwell (1970) reported stomates of Rhododendron ferrugineum closed quickly with increasing wind speed. Diurnal water loss from arctic and alpine shrubs was directly related to windspeeds below 3 $m.sec^{-1}$ and inversely related to windspeeds between 3 and 4 $m.sec^{-1}$ (Bliss 1960).

The effects of wind on stomata has not been reported for species of the shrub steppe. However, it is logical to assume plants have developed mechanisms to respond to changes in wind speed.

Study Site Descriptions

Studies were conducted on four study sites in Harney Basin, Oregon. Sites are located on the basin floor 30 to 40 km south of Burns. Harney Basin is internally drained and covers approximately 15,000 km^2. Elevation within the basin ranges from 1100 to 1300 m; elevation of all study sites is approximately 1255 m. Precipitation ranges from 200 to 300 mm annually with about 60 percent received from October through March. Although 40 percent of the precipitation is received in spring and summer, it is usually localized or ineffective in promoting growth of most plants. Summer drought is a distinctive feature of the study area. The mean annual temperature is 7C with average daily maximums of 30C in July, and minimum daily temperatures of -9C in January. Freezing temperatures can occur at any time.

Existing vegetation and soils were criteria used for selecting study sites. On all sites, greasewood (*Sarcobatus vermiculatus*) is the most common shrub and *Sitanion hystrix* is the most common perennial grass (Appendix A). Soils of the study sites are aridisols. Soils of two sites were formed on sedimentary deposits and two were formed on alluvial deposits.

The North Harney site is located approximately 2 km north of Mud Lake. Legal description of the site is the SW 1/4, Sec. 21, T26S, R30E. Greasewood is uniformly distributed and provides nearly 19 percent canopy cover (Appendix A). Wyoming big sagebrush (*Artemisia tridentata* subsp. *wyomingensis*) is the second most abundant shrub, and it contributes about 7 percent canopy cover. Perennial grasses are poorly represented, with *Agropyron smithii* the most frequent species. *Bromus tectorum* and *Lepidium perfoliatum* are common throughout the area. Soils are underlain by coarse gravel at a depth of about 1.5 m, and they are fine-loamy, mixed, mesic, Xerollic Haplargids (Appendix B). Depth to the water table is approximately 5 m.

The South Harney site is located approximately 3 km southeast of Harney Lake. Legal description of the site is the SW 1/4, Sec. 16, T27S, R30E. Greasewood is present as a nearly pure stand, and it provides more than 26 percent canopy cover (Appendix A). *S. hystrix* was the only perennial grass identified during vegetation sampling (Appendix A). The annuals, *B. tectorum* and *L. perfoliatum*, are common. Soils are fine-loamy, mixed mesic Xerollic Camborthids, (Appendix B) and coarse gravel is approximately 2 m deep. The depth to a water table is approximately 15 m.

The Coyote Buttes site is located approximately 2 km northwest of the Malheur Environmental Field Station. Legal description of the site is the SE 1/4, Sec. 12, T28S, R30E. Greasewood, *Chrysothamnus nauseosus* subsp. *consimilis*, and Wyoming big sagebrush are the most common shrubs; respective canopy covers are approximately 16, 13, and 8 percent (Appendix A). *S. hystrix* and *Elymus cinereus* are the most common perennial grasses (Appendix A). *B. tectorum* and *L. perfoliatum* are common annuals throughout the study site. Soils were formed from sedimentary deposits, and they are fine, montmorillonitic, mesic Xerollic Haplargids (Appendix B). A water table is present at approximately 3.5 m.

The Saddle Butte site is located about 1 km northwest of Saddle Butte. Legal description of the site is the SW 1/4, Sec. 12, T28S, R30E. Greaswood and *Grayia spinosa* are the most common shrubs, and they provide approximately 17 and 9 percent canopy cover, respectively (Appendix A). *S. hystrix* and *Poa nevadensis* are the most common perennial grasses; *B. tectorum* and *L. perfoliatum* are the most common annuals (Appendix A). Sedimentary deposits are parent materials for the soils, which are coarse-loamy, mixed, mesic Xerollic Haplargids (Appendix B). A water table is present at approximately 3.5 m deep.

Chapter I

EFFECTS OF CHEMICAL PROPERTIES OF SOILS ON GERMINATION OF PROSTRATE KOCHIA (*KOCHIA PROSTRATA*) AND GREASEWOOD (*SARCOBATUS VERMICULATUS*)

Effects of Chemical Properties of Soils on Germination of Prostrate Kochia (Kochia prostrata) and Greasewood (Sarcobatus vermiculatus)

Abstract

Chemical properties of saline soils limits germination of seeds of many species. Germinating seeds in salt affected soils appears to be a technique that can be used for screening salt tolerant species. This screening technique was used for evaluating germination of prostrate kochia (Kochia prostrata L. Schrad.) and greasewood (Sarcobatus vermiculatus (Hook.) Torr.) on soils collected from sites dominated by greasewood. Soils were collected before and after seedbed preparation from 4 sites occupied by greasewood. Seeds were incubated on saturated soils at 10 and 20C, and germination percentage was correlated with concentrations of sodium, calcium, magnesium, potassium, nitrate, and sulfate in saturation extracts. Germination of prostrate kochia and greasewood was significantly higher at 20C than at 10C. Germination of prostrate kochia was significantly correlated (r=0.37) with nitrate concentration at 10C. No other correlations were significant for either greasewood or prostrate kochia at 10 and 20C. Under conditions of no water stress,

prostrate kochia and greasewood can tolerate a wide range of ion concentrations.

Introduction

Defining effects of biotic and abiotic factors on germination is essential for understanding the germination ecology of all species. When selecting species for revegetating saline sites, or studying the population biology of species indigenous to saline sites, the effects of soil chemistry on germination should be considered. Determining the effects of chemical properties of soils on germination can be complicated under uncontrolled conditions because soil chemistry modifies the physical properties of soils. Development of *in vitro* techniques for evaluating the influence of chemical properties of soils on germination, without the confounding effects of physical properties, is needed for defining factors that may limit germination. We examined the possibility of using salt affected soils to evaluate the effects of chemical properties on germination of prostrate kochia (*Kochia prostrata* (L.) Schrad.) and greasewood (*Sarcobatus vermiculatus* (Hook.) Torr.).

The seedbed, the upper few centimeters of the solum, can harbor the greatest concentrations of ions in the profile. Salt content of surface horizons may be enriched by upward transport of salts through evaporation, or it may be enriched by plants. Many plants accumulate ions in their leaves, and through leaf drop and decay, they increase ion concentrations in the soil surface. Accumulation of ions in the seedbed presents a harsh environment for germinating seeds through their effect on reduced water availability, ion toxicity, and alteration of physical properties of soils (Kinsinger and Eckert 1961; Rollins et al. 1968; Eckert et al. 1973).

On sites dominated by greasewood, pH and salt content of soils are usually highest in surface horizions, decreasing with depth (Roberts 1950; Fireman and Hayward 1952; Rickard and Cline 1967). Furthermore, they found pH and salt content of soils increased progressively from shrub interspaces to beneath greasewood canopies. Fireman and Hayward (1952) showed similar changes in soil chemistry were associated with Atriplex confertifolia. Rickard (1965b) found pH, electrical conductivity, and potassium were elevated in surface horizons under Grayia spinosa. Eckert and Kinsinger (1960) discovered Halogeton glomeratus increased soil pH, electrical conductivity, exchangeable sodium, and soluble sodium more in the surface 7.5 cm than at a depth of 10 cm. Although these changes reportedly reduce germination and establishment of seedlings (Kinsinger and Eckert 1961; Rollins et al. 1968; Eckert et al. 1978), it is difficult to separate the effects of chemical and physical properties under field conditions.

We hypothesized the effects of soil chemistry on germination can be isolated by germinating seeds on salt affected soils. By conducting in vitro experiments, we felt we could eliminate the effects of physical properties on germination. We tested our hypothesis by germinating seeds of prostrate kochia, PI 314929, and three collections of greasewood on soils collected from four greasewood communities before and after seedbed preparation.

Methods

Soils were collected before and after seedbed preparation at the North Harney, South Harney, Coyote Buttes, and Saddle Butte study sites. The top 5 cm of the solum was collected in late August, 1982 before and after seedbed preparation. Seedbed preparation consisted of elimination of vegetation with a rotary brush beater and then each site was disked to a depth of 10 to 15 cm. Before disking (pre-disk), five 100m transects were established at each site, soil was collected at 10 random points along each transect, and samples were composited. The same procedure was used for soil collection after disking (post-disk). The soils were sieved through a 1.9 mm mesh before use.

Saturation percentage was determined for each soil using the procedure outlined by Richards (1954). The percent moisture required to saturate soils was used to moisten soils for germination tests. Soil-water extracts were prepared from a composite sample of soil from each site following the procedure of Richards (1954). Extracts were analyzed for pH, sodium, potassium, calcium, magnesium, sulfate, and nitrate by Oregon State University Soil Testing Laboratory.

Seeds (utricles) of greasewood were collected from several plants at the North Harney, South Harney, and Coyote Buttes study sites in October, 1982. Seeds were dried at room temperature, and bracts were removed from seeds with a flail. Seedlots were sorted with air to remove empty seeds and provide uniform seed weight; the heavier one-half of each collection was used in germination tests.

Seeds (utricles) of prostrate kochia, PI 314929, were collected from plants near Ephriam, Utah in October, 1982. The seeds were transported to Eastern Oregon Agricultural Research Center near Burns, Oregon and they were stored in a laboratory. Prior to germination, utricles were hand-rubbed to remove the perianth, and seeds were sorted by air to reduce variation in size; the heavier one-half of the seed lot was studied.

Germination tests were initiated approximately 3 months after seeds were harvested. Seeds were incubated in petri dishes. Twenty-five g of soil were placed in petri dishes, and the appropriate amount of distilled water was added to bring the soil to the predetermined saturation percentage. A #4 Whatman filter paper disk was placed on the soil, lids were placed on dishes, and the dishes were enclosed and sealed in plastic bags. After the soils had equilibrated 24 hours, 50 seeds of prostrate kochia, and each greasewood collection, were placed on the filter disks, and the lids were replaced. Dishes were randomly arranged on trays, and the trays were enclosed and sealed in plastic bags. Seeds were incubated in darkness at 10 and 20C. Germinated seeds were counted at 2-day intervals through 14 days.

A randomized, complete block design was used with 4 replications per soil type, seed source, and temperature. Time was used as blocks because tests were initiated at 2-week intervals.

Analysis of variance was used to test the effect of soil on germination percentage. Relationships between chemical properties and germination percentage were examined with correlation analysis (Snedecor and Cochran 1980). All tests were made with p=0.05.

Results

Soil Properties

Ion concentrations ranged from 441 to 1026 ppm for potassium, 110 to 220 ppm for calcium, 288 to 780 ppm for magnesium, and 621 to 1725 ppm for sodium (Table I.1). Sulfate and nitrate concentratons ranged from 3.8 to 26.9 ppm and 4 to 9.7 ppm, respectively. Soil reactions were pH 8.2 for 7 extracts and pH 8.0 for 1 extract.

Saturation moisture percentages were significantly reduced by disking on all soils except those from the South Harney site (Table I.2). Obliteration of coppice dunes, and mixing with interspace soils, may have altered the textural characteristics, and thus reduced the water holding capacity of soils.

Germination

Prostrate kochia

Germination percentage was similar between soils, but it was reduced by decreasing temperatures. Germination averaged 39.6 percent at 20C, and 21.9 percent at 10C (Table I.3). The only significant correlation between chemical properties and percent germination was the positive correlation with nitrate concentration at 10C (Table I.4).

Table I.1. Ionic concentrations determined from water saturation extracts of the top 5 cm of the solum collected before and after seedbed preparation at the North Harney, South Harney, Coyote Buttes, and Saddle Butte study sites. (Data are based on one composite sample per site.)

Site	Treatment	Ion Concentration (ppm)							
		K	Ca	Mg	Na	B	SO_4	NO_3	pH
North Harney	Pre-disk	881	220	780	621	0.23	7.4	4.0	8.2
North Harney	Post-disk	495	120	360	897	0.82	4.2	6.0	8.2
South Harney	Pre-disk	745	110	312	1725	0.64	6.9	4.8	8.0
South Harney	Post-disk	928	120	288	1702	3.86	26.9	7.9	8.2
Coyote Buttes	Pre-disk	823	110	456	1104	3.06	4.8	6.4	8.2
Coyote Buttes	Post-disk	1026	110	420	1334	--	7.0	9.7	8.2
Saddle Butte	Pre-disk	741	190	468	805	2.12	3.8	3.8	8.2
Saddle Butte	Post-disk	441	120	408	1265	0.86	4.0	6.7	8.2

Table I.2. Percent soil moisture at saturation for soils collected at the North Harney, South Harney, Coyote Buttes, and Saddle Butte study sites. Values in parentheses are standard errors for the mean (n=4).

	Percent Soil Moisture	
Study Site	Pre-disk	Post-disk
North Harney	48.6 (1.2)	38.5 (1.4)
South Harney	48.1 (0.6)	47.1 (0.9)
Coyote Buttes	45.2 (0.8)	39.9 (1.1)
Saddle Butte	37.4 (0.9)	31.1 (0.4)

Table I.3. Percent germination, averaged over soils, for prostrate kochia, and collections of greasewood from the North Harney, South Harney, and Coyote Buttes study sites. Values in parentheses are standard errors for the mean (n=32)

	Temperature (C)	
Species or Collection	10	20
Prostrate kochia	21.9 (0.7)	39.6 (0.9)
Greasewood		
North Harney	23.8 (1.6)	43.6 (1.2)
South Harney	48.1 (2.3)	64.1 (1.3)
Coyote Buttes	26.3 (1.6)	50.3 (1.5)

Table I.4. Correlation coefficients for relationships between percent germination of prostrate kochia and greasewood and chemical characteristics of soils collected at the North Harney, South Harney, Coyote Buttes, and Saddle Butte study sites. * Indicates significant at $p = 0.05$.

Species or Collection	Temperature (C)	Correlation coefficient					
		K	Ca	Mg	Na	SO_4	NO_3
Prostrate kochia	10	0.09	-0.24	-0.24	0.11	0.02	0.37*
	20	-0.18	-0.02	0.04	-0.11	-0.18	-0.08
Greasewood North Harney	10	0.18	0.33	0.30	-0.20	0.19	-0.29
	20	-0.14	-0.22	-0.15	0.31	0.22	0.05
South Harney	10	0.16	0.01	0.12	-0.03	0.12	0.07
	20	0.11	0.05	-0.03	0.18	0.27	-0.24
Coyote Buttes	10	0.23	0.14	0.24	-0.16	0.07	0.01
	20	0.10	-0.01	0.07	0.14	0.32	-0.04

Greasewood

Germination of all greasewood collections was similar on all soils; all collections germinated significantly higher at 20C than at 10C (Table I.3). The South Harney and North Harney collections germinated best and poorest, respectively. Percent germination of all collections was not significantly correlated with any chemical properties (Table I.4).

Discussion

Results of this study indicate prostrate kochia and greasewood can germinate well on saturated soils over a wide range of ion concentrations. Under conditions of free water, low temperature was the primary stress limiting germination.

In the shrub steppe, soil salts were most diluted in early spring (Roundy 1983). During the period when salts are diluted or leached, water potentials may range from -0.5 to -0.8 MPa (Roundy 1983), and soil temperatures are usually low. Therefore, germination may be limited by low soil temperatures and low water potentials during the period of maximum soil moisture. As temperatures rise, soil water potentials decrease rapidly in saline soils (Roundy 1983). Declining soil water potentials are the product of increasing salt concentrations and decreasing soil moisture. Thus, during the period when temperatures are conducive to germination, high salt concentrations and low water potentials may limit germination.

Germination and growth over a broad range of soil conditions are important for establishment of species in the spatially and temporally heterogeneous soils of the shrub steppe (Bleak et al. 1965; Rollins et al. 1968; Wein and West 1971). Since low soil water potentials are a common feature of saline soils, additional research should focus on evaluating the effects of specific ions on germination under conditions of water stress. Potassium and sodium ions were selected for further study because their concentrations were highest and most variable. The effects of these ions and water stress on germination of prostrate kochia and greasewood are presented in Chapters II and III.

CHAPTER II

KOCHIA PROSTRATA GERMINATION RESPONSE TO TEMPERATURE, WATER STRESS, AND SPECIFIC IONS

Kochia prostrata Germination Response to Temperature, Water Stress, and Specific Ions

Abstract

Prostrate kochia (*Kochia prostrata* (L.) Schrad.) is reported to be a useful species for revegetating salt affected soils; however, the effects of water stress and specific ions on germination have not been quantified. Understanding germination requirements will be useful for selecting superior genotypes, isolating suitable sites, and developing cultural practices for establishment from seed. To determine the effects of temperature, water stress, and specific ions on the germination of prostrate kochia, PI 314929, fruits and seeds were germinated at 10, 20 and 30C in solutions of polyethylene glycol (PEG) with water potentials ranging from -0.52 to -2.32 MPa. Seeds were also germinated at 20C in PEG solutions, containing 0 to 4000 ppm potassium chloride (KCl) and sodium chloride (NaCl) with water potentials ranging from -0.3 to -2.2 MPa. The water potential X temperature interaction was significant with total germination highest at 20C and lower at 10 and 30C. As temperature increased, the coefficient of determination between water potential and germination percentage decreased from $R^2 = 0.79$ at 10C, to $R^2 = 0.74$ at 20C, and $r^2 = 0.27$ at 30C. More seeds

germinated abnormally than fruits. These seedlings lacked hypocotyl elongation. Seeds germinated at all water potentials and concentrations of KCl and NaCl tested. Germination percentage was significantly different between KCl and NaCl, but the rate of germination similar in both salts. Percent germination was not affected by increasing NaCl concentrations, was reduced by increasing KCl concentrations. Abnormal germination percentage was not significantly different between salts and their concentrations, but it increased as water potential decreased.

Introduction

Water stress is a primary factor limiting germination, growth, establishment, and reproduction of plants in arid environments. Chemical and physical properties of soils in combination with low precipitation and high evaporative demand, are the major causes of low moisture availability. Knowledge of the effects of water stress on germination can be useful for selecting adapted species for revegetating rangelands.

Prostrate kochia (*Kochia prostrata* (L.) Schrad.), a half-shrub of the *Chenopodiaceae*, may be useful for revegetating western rangelands. In the Great Basin, prostrate kochia appears adapted to areas presently supporting saltgrass (*Distichlis spicata* (L.) Greene), big sagebrush (*Artemisia tridentata* Nutt.), shadscale (*Atriplex confertifolia* (Torr. & Frem.) Wats.), and greasewood (*Sarcobatus vermiculatus* (Hook.) Torr.) (McArthur et al. 1974).

Prostrate kochia may be useful for revegetating greasewood communities because it is salt tolerant and drought resistant (Blauer et al. 1976) and it also produces high quality forage (Davis 1979). Greasewood communities are generally difficult to revegetate because of poor physical properties of soils and high salinity (Rollins et al. 1968). Soils of greasewood communities usually have high concentrations of sodium, and potassium concentrations may also be high (Shantz and Piemeisel 1940; Gates et al. 1956; Rickard 1965a; Wallace et al. 1973). Salinity may affect germination and growth through reduced osmotic potential of the soil solution; ions may be toxic; or nutrients may not be balanced and available (Hayward and Bernstein 1958; Ungar 1982). The effect of ions on germination varies with species or cultivars, environmental conditions, and osmotic potential (Dewey 1960; Ayers 1962; Redmann 1974; Ungar 1978). Depending on the specific ion, germination may be stimulated, depressed, or unaffected (Choudhuri 1968; Hyder and Yasmin 1972; Ungar 1978).

To maximize establishment of prostrate kochia from direct seeding on salt affected soils, germination requirements must be understood. Prostrate kochia establishes well from container grown transplants (Van Epps and McKell 1983), but reports on establishment from direct seeding show inconsistent success. Keller and Bleak (1974), Blauer et al. (1976), and Stevens (Richard Stevens, 1984 pers. comm.) reported unpredictable establishment from seeding. Balyan (1972) attributed variable success of seeding to genotypic variation, chemical and physical properties of soils, and moisture availability during germination.

The purpose of this research was to quantify the effects of temperature, water stress, sodium chloride, and potassium chloride on the germination of prostrate kochia, PI 314929. This accession has been cooperatively released as 'Immigrant' by the Utah State Division of Wildlife Resources, the U.S.D.A. Forest Service, and the U.S.D.A. Soil Conservation Service Plant Materials Center, Aberdeen, Idaho. When prostrate kochia is used for revegetating extensive tracts of rangeland, direct seeding will probably be necessary due to the high costs of propagating and planting container grown transplants. Information from this research will augment our understanding of potential limitations in establishing prostrate kochia from seed.

Materials and Methods

In 1981 and 1982 fruits (utricles) of prostrate kochia, PI 314929, were obtained from plants grown near Ephriam, Utah. After collection, fruits were sent to Eastern Oregon Agricultural Research Center near Burns, Oregon, and they were stored in a laboratory. Prior to germination studies, conducted approximately 6 months after each harvest, fruits were sorted by air to reduce variation in size; the heavier one-half of each seed lot was studied.

The influence of seed appendages on germination at various temperatures and water potentials was studied with the 1981 seedlot. Two classes of seeds were used: fruits with seeds fully enclosed by bracts, and naked seeds whose bracts had been removed by gentle hand rubbing were studied.

Osmotic solutions were prepared by adding polyethylene glycol (PEG) (M.W. 6,000) to distilled water as described by Michel and Kaufmann (1973). Six water potentials were prepared for each temperature. Water potentials were determined the sixth and twelfth day of the germination experiment with a Wescor HR-33T microvoltmeter and a Wescor C-52 sample chamber psychrometer after calibration with standard NaCl solutions. Water potentials ranged from -0.56 to -2.32 MPa at 10C, -0.52 to -2.10 MPa at 20C, and -0.56 to -2.10 MPa at 30C.

Twenty-five fruits or seeds were incubated on a #4 Whatman filter paper disk underlain by germination blotter, and moistened with 25 ml of osmotica in each petri dish. Dishes were covered and sealed in "Ziplock" plastic bags to prevent desication, and arranged in incubators in a randomized, complete block design with 4 replications per seed class and water potential. Seeds were incubated at 10, 20 and 30C without light for 14 days. Germination was recorded daily for the first 10 days and at 2-day intervals through 14 days. Seeds were considered germinated when the embryo completely uncoiled and the hypocotyl arch was raised (Young et al. 1981). Seeds that initiated germination, but failed to meet this criteria were recorded as abnormal germination. The number of days to 50 percent of final germination was used to quantify germination rate.

Water stress in combination with various concentrations of sodium chloride (NaCl) and potassium chloride (KCl) on germination was examined with the 1982 seedlot. Five osmotic solutions of -0.3, -0.7, -1.2, -1.6, and -2.2 MPa were prepared by adding PEG (M.W. 20,000) to distilled water. Solutions were buffered to pH 8.0 with "Tris" (Tris-[Hydroxylmethyl] Amino-Methane) buffer. Each solution was divided into 9 aliquots and 2M NaCl or KCl was added to bring solutions to 0, 500, 1000, 2000, and 4000 ppm for each salt. Salt concentrations were selected to bracket K^+ and Na^+ concentrations determined in soils from the field (Table I.1). Water potential in each petri dish was determined the fourth and eighth day of incubation.

Before commencing germination trials, lots of 50 seeds were counted and stored in paper envelopes. Envelopes were randomly selected and 50 seeds were placed in each petri dish. Twenty-five ml of osmotica were added to dishes, lids were placed on dishes, and dishes were enclosed in "Ziplock" bags. Seeds were incubated in darkness at 20C for 14 days. Germination was recorded at 2-day intervals. Treatments were applied factorially in a randomized, complete block design with 2 replications in each of 3 blocks. Time was used as blocks because trials were started at approximately 2-week intervals.

Within experiments, water potentials were not significantly different between dates of determination; values were averaged and used for statistical analyses. Data from both experiments were initially analyzed with a factorial analysis of variance (Snedecor and Cochran 1980). Polynomial response curves were developed for the seed appendage study, and multiple linear regression was used to develop response surfaces for the water potential and specific ion experiment. Counts were transformed with arcsin $\sqrt{p}$ (Snedecor and Cochran 1980) for analysis of variance; untransformed data were used in regression analyses. All statistical tests were made with $p = 0.05$.

Results

Effects of Seed Appendages on Germination

Total percent germination was similar for fruits and seeds, but the water potential X temperature interaction was significant. Thus, data were pooled within temperatures for regression analyses. Total percent germination was lowest at 10C, and higher at 20 and 30C (Figure II.1). As temperature increased, the coefficient of determination between water potential and germination percentage decreased (Figure II.1).

Seeds and fruits incubated at 10C, germinated at water potentials higher than -2.0 MPa (Figure II.1). At 20C, germination occurred at water potentials above -2.1 MPa (Figure II.1). Germination was observed at all water potentials tested at 30C (Figure II.1); however, variation in observed germination was high.

At all temperatures, water potential and the number of days to 50 percent of final germination were linearly related (Figure II.2). Germination was fastest at 30C and slowest at 10C. At 20C seeds germinated faster than fruits, but at 10 and 30C fruits and seeds germinated at similar rates.

Although germination percentage was similar for fruits and seeds, abnormal germination was greatest

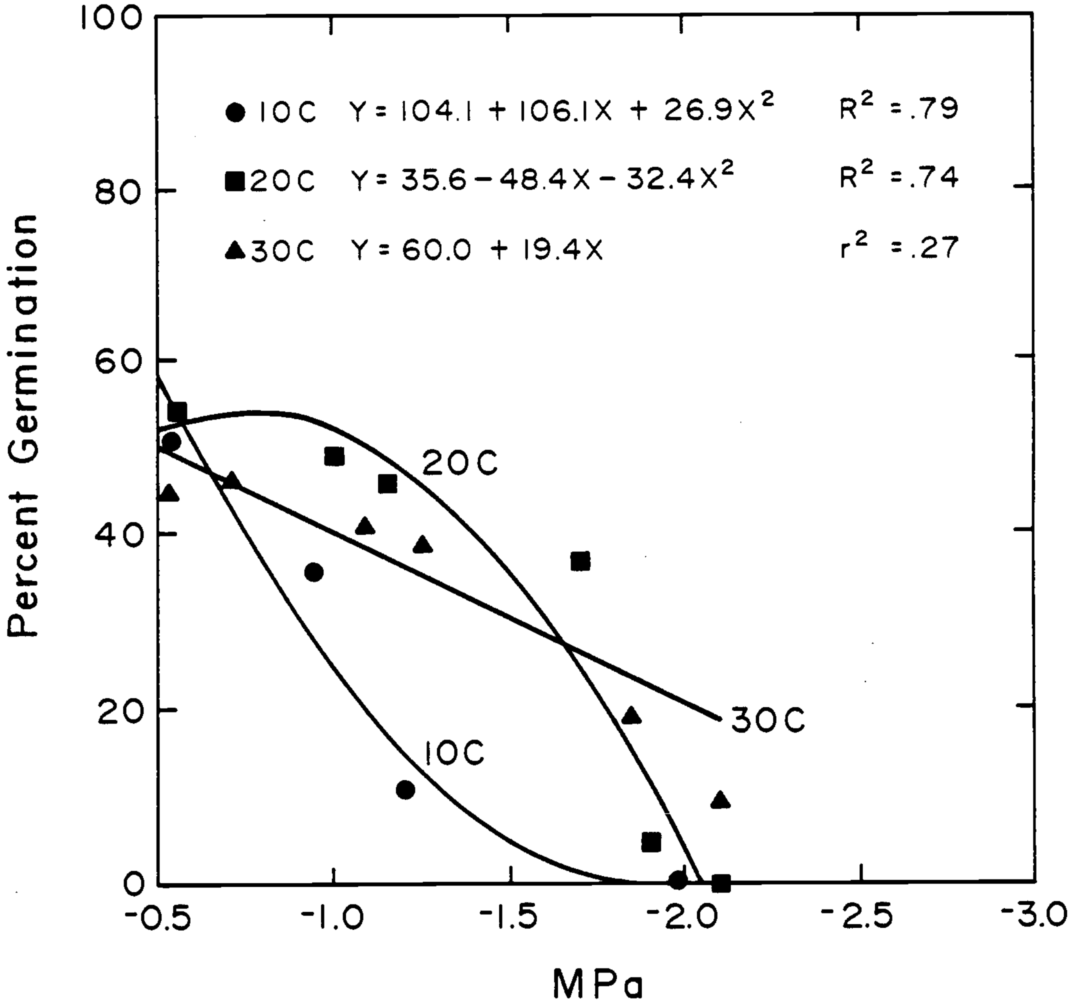

Figure II.1. Total percent germination of prostrate kochia fruits and seeds as affected by water potential at constant temperatures of 10, 20, and 30C. Each symbol represents the mean of 8 replications.

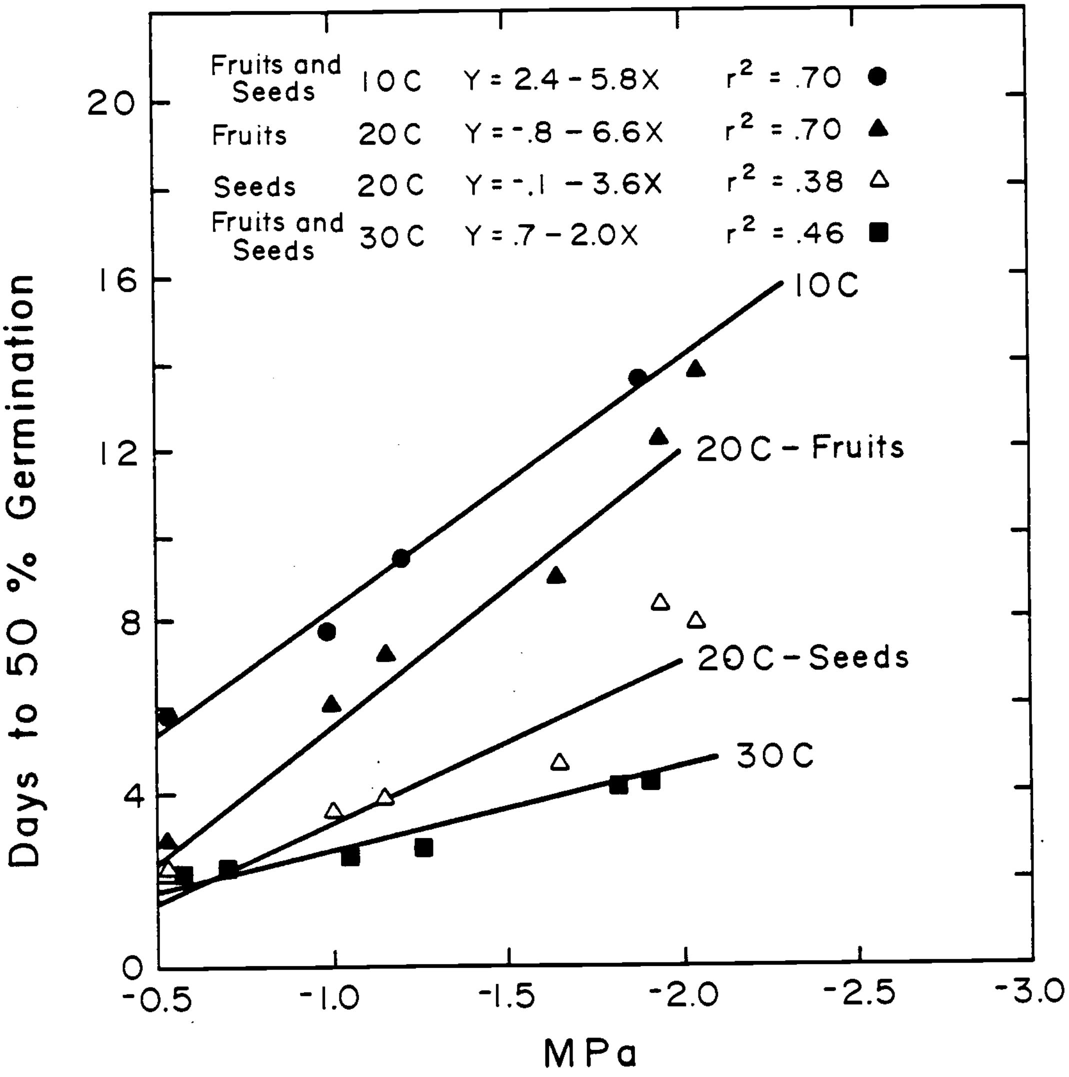

Figure II.2. Days to 50 percent of final germination of prostrate kochia fruits and seeds as affected by water potential at constant temperatures of 10, 20, and 30C. Each symbol represents the mean of 8 replications at 10 and 30C. At 20C, each symbol represents the mean of 4 replications.

in seeds (Table II.1). Significantly more seeds germinated abnormally at 10 and 20C, but not at 30C.

Effects of Water Potential, Potassium Chloride, and Sodium Chloride

Seeds germinated at all water potentials and salt concentrations tested. Germination of seeds in NaCl-PEG solutions was related only to water potential (Figure II.3). However, in KCl-PEG solutions, germination percentage was reduced by the interaction of decreasing water potential and increasing KCl concentration (Figure II.4).

The mean number of days to 50 percent of final germination was similar in NaCl and KCl. Seeds germinated slower as water potential decreased and salt concentration increased (Figure II.5).

Abnormal germination percentage was not influenced by KCl, NaCl, or their concentrations. However, the percentage of seeds germinating abnormally increased as water potentials decreased (Table II.2). Abnormal germination was similar at -0.3 and -0.7 MPa, but the percent of seeds germinating abnormally was significantly higher at lower water potentials (Table II.2). Although fewer seeds germinated normally as water potential

Table II. 1. Mean percent abnormal germination of prostrate kochia averaged over water potentials within temperatures. Values in parentheses are 95 percent confidence limits.

Incubation Temperature (C)	Seeds	Fruits
10	16.8 (7.9)	3.0 (1.6)
20	17.2 (7.5)	6.7 (2.8)
30	8.3 (3.9)	4.0 (2.0)

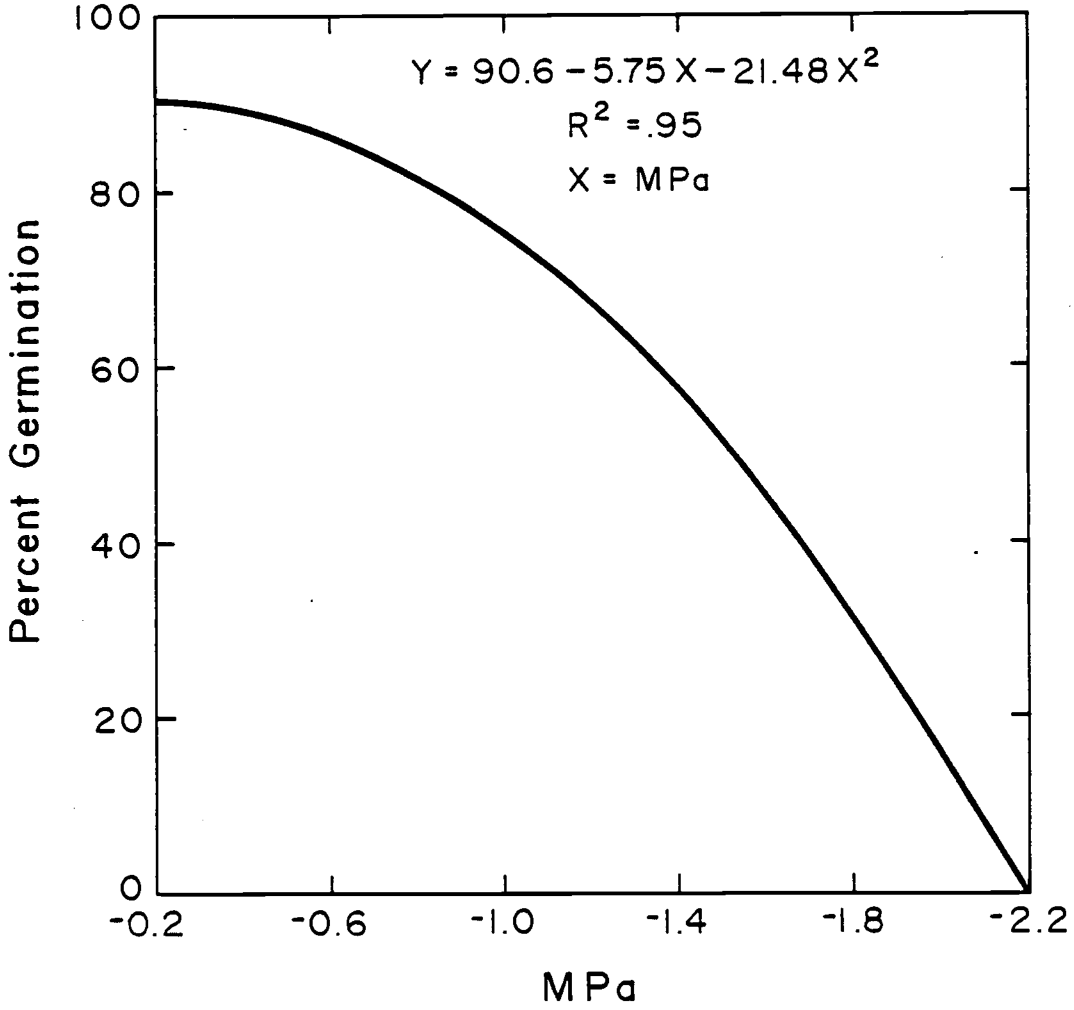

Figure II.3. Response curve and regression equation for total percent germination of prostrate kochia seeds incubated in PEG solutions containing NaCl. Each symbol is percent germination averaged over NaCl concentrations.

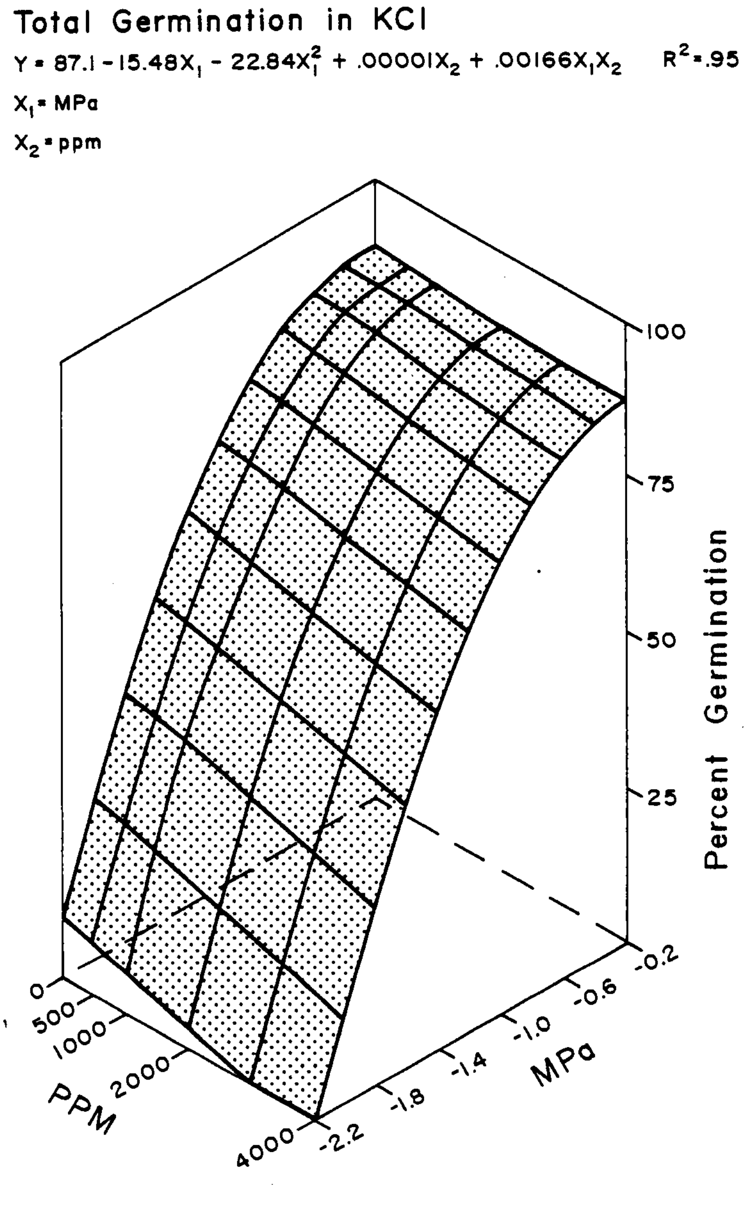

Figure II.4. Response surface and regression equation for total percent germination of prostrate kochia incubated in PEG solutions containing KCl.

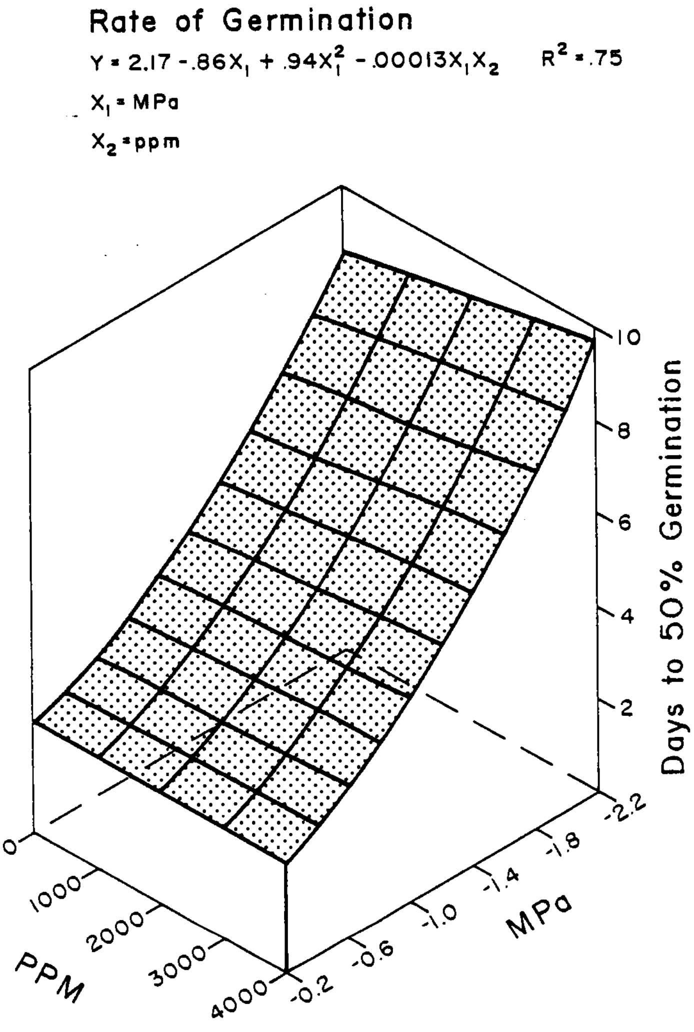

Figure II.5. Response surface and regression equation for days to 50 percent of final germination for prostrate kochia seeds incubated in PEG solutions containing NaCl and KCl.

Table II. 2. Abnormal germination percentage of prostrate kochia seeds averaged over salts and salt concentration. Tukey's Honestly Significant Difference (HSD) is 1.8. p = 0.05.

Water Potential (MPa)	-0.3	-0.7	-1.2	-1.6	-2.2
Percent Abnormal Germination	6.9	7.5	16.0	43.0	35.5

decreased, the proportion of the seed population that germinated abnormally increased disproportionately.

Discussion

Fruits should be planted instead of seeds. Total germination of fruits and seeds was not significantly different, but more seeds germinated abnormally than fruits at all temperatures and water potentials tested. Sowing seeds during periods of high soil moisture may aid rapid establishment, but attrition of the seed population may be high under transient moisture conditions.

Prostrate Kochia seeds and fruits germinate over a broad range of tempertures and water potentials. Germination is closely related to water potential at 10 and 20C. At 30C, seed and seedling vigor appeared low, and the relationship between water potential and germination was weak. These data agree with the findings of Young et al. (1981) that seed vigor of prostrate kochia is low when incubated at 30C and higher. Since water potential effects on germination were more predictable at 10 and 20C, and seed vigor appeared high, seeding should occur earlier or coincide with temperatures in this range. Seedbed temperatures of 10 to 20C, in combination with high soil water potentials, should yield high germination.

In the Intermountain Region, this combination of conditions usually exists in fall or spring.

Francois (1976) concluded prostrate kochia plants are salt tolerant. Results of this study confirm prostrate kochia is also tolerant of high NaCl and KCl concentrations during germination. Germination was primarily reduced by declining water potentials, but a portion of the population was sensitive to KCl. The neutral effect of NaCl on germination is particularly important because Na^+ is often abundant in soils on western rangelands (Shantz and Piemeisel 1940; Gates et al. 1956; Hayward and Bernstein 1958). Since water potential reduced germination more that NaCl or KCl, seedbed treatments should be selected to maintain high soil moisture. Cultural practices that extend the period of high soil water potentials should be applied to maximize establishment of prostrate kochia from direct seeding.

CHAPTER III

EFFECTS OF OSMOTIC POTENTIAL, POTASSIUM CHLORIDE, AND SODIUM CHLORIDE ON GERMINATION OF GREASEWOOD (*SARCOBATUS VERMICULATUS*)

Effects of Osmotic Potential, Potassium Chloride, and Sodium Chloride on Germination of Greasewood (*Sarcobatus vermiculatus*)

Abstract

Greasewood (*Sarcobatus* *vermiculatus* (Hook.) Torr.) is a widespread shrub of the *Chenopodiaceae*. Because greasewood typically grows on salt affected soils, its germination requirements may reflect characteristics necessary for establishment in saline environments. The objective of this study was to determine the effect of osmotic potential and specific ions on the germination of seeds from three populations of greasewood. Seeds were germinated at 20C in solutions of polyethylene glycol with water potentials ranging from -0.3 to -2.2 MPa that contained 0 to 4000 ppm sodium chloride (NaCl) or potassium chloride (KCl). No germination occured at osmotic potentials lower than -1.6 MPa. Inter- and intrapopulation differences in response to osmotic potential and salt concentrations were found. Percent germination, percent abnormal germination, and germination rate were similar in NaCl and KCl. Germination of two populations was reduced by increasing salt concentrations; germination of one population was reduced only by declining osmotic potential. Comparison of results in

this study, with results from other studies, suggest geographic ecotypic development in response to osmotic potential and NaCl and KCl concentrations during germination.

Introduction

Greasewood (*Sarcobatus vermiculatus* (Hook.) Torr.) grows in all states west of the 100th meridian, northern Mexico, and southern Alberta and Saskatchewan (Branson et al. 1967). Throughout its range, greasewood usually grows on fine textured soils that are saline or alkaline, but occasionally it grows on nonsaline and coarse textured soils (Shantz and Piemeisel 1940; Fireman and Hayward 1952; Gates et al. 1956; Rickard and Keough 1968). Because greasewood grows on a variety of soils, we hypothesized populations from different sites respond differentially to osmotic potential and specific ions during germination.

Seed germination and seedling establishment may be the most critical stages in life cycles of plants in saline environments. Germination is a critical phase of plant establishment because it determines the soil conditions to which seedlings will be exposed (Ungar 1982), and it is a major source of attrition in the seedbank (Harper 1977). Salinity may affect germination and growth through reduced osmotic potential, increased availability of a toxic ion, or reduction in absorption of nutrients because of ion imbalance (Richards 1954; Hayward and Bernstein 1958). Generally germination is delayed and reduced when salt stress exceeds a critical level; the level of salinity at which germination is reduced varies with species, genotype, environmental conditions, osmotic potential, and specific ions (Ungar 1978).

Chapman (1974) concluded a reduction in soil salinity is requisite for germination in saline environments. Reduction of soil salinity increases the osmotic potential and reduces ion concentrations (Richards 1954). Germination of some species is reduced more by osmotic potential than specific ions (Choudhuri 1968; Ungar and Capilupo 1969; Ungar and Hogan 1970; Macke and Ungar 1971; Cluff et al. 1983); however, in other species ions depress germination more than osmotic potential (Choudhuri 1968; Hyder and Yasmin 1972; Redmann 1974; Wood et al. 1976; Young and Evans 1981). The effects of osmotic potential and ions also vary within species (Dewey 1960; Springfield 1966; Workman and West 1967; Clarke and West 1969; Clark and West 1972) and differences may be related to genetics or environmental conditions.

The objective of this research was to ascertain the effects of osmotic potential and ions on the germination of greasewood. Seeds from three greasewood populations were incubated in a gradient of osmotic potentials and concentrations of KCl and NaCl.

Materials and Methods

Three sources of greasewood seeds were collected from sites located approximately 30 km south of Burns, Oregon. Elevation of all sites is approximately 1255 m, and the climatic conditions are similar. Soils of the North Harney and South Harney sites were formed from alluvial materials, and they are moderately well drained, fine-loamy, mixed, mesic Xerollic Haplargids and fine loamy, mixed, mesic Xerollic Camborthids, respectively. The soils at the Coyote Buttes site are moderately well drained, fine montmorillonitic, mesic Xerollic Haplargids, formed from alluvial materials. Profile descriptions for each site are presented in Appendix B.

Seeds (utricles) were collected from several plants at each site in October, 1982. After collection seeds were dried at room temperature and stored in paper envelopes. Bracts were removed with a flail, and seeds were sorted with air to reduce variation in size; the heavier half of each seedlot was used for germination trials. Seeds were approximately 8 months old when tested.

Five osmotic solutions were prepared by adding polyethylene glycol (M.W. 20,000) to distilled water. Solutions were buffered to pH 8.0 with "Tris" (Tris-(Hydroxylmethyl) Amino-Methane) buffer. Each solution was divided into 9 aliquots, and 2 M sodium chloride (NaCl) or potassium chloride (KCl) was added to bring solutions to 0, 500, 1000, 2000, and 4000 ppm for each salt. Salt concentrations were selected to bracket K^+ and Na^+ concentrations determined from the top 5 cm of the solum at seed collection sites (Table I.1).

Osmotic potentials of germination solutions, determined on the fourth and eighth day of incubation, were -0.3, -0.7, -1.2, -1.6, and -2.2 MPa. Osmotic potentials were determined from filter paper disks, 5 mm in diameter, placed in petri dishes when incubation was initiated. Osmotic potentials of these discs were determined with a Wescor HR-33T microvoltometer, and a Wescor C-52 sample chamber psychrometer after calibration with standard NaCl solutions.

Before commencing germination tests, lots of 50 seeds were counted and stored in paper envelopes. Ten envelopes of each collection were randomly selected and used for determining seed weights. Another set of envelopes was randomly selected and seeds were placed in petri dishes on a #4 Whatman filter paper disk that was underlain by germination blotter. Twenty-five ml of osmotica were added to each dish, and the dishes were covered and sealed in "Ziplock" plastic bags to prevent desication. Seeds were incubated in darkness at 20C for 14 days, and exposed to light only briefly when germination was recorded at 2-day intervals. Seeds were considered germinated when the embryo had uncoiled and cotyledons were reflexed. Seeds that initiated germination, but failed to meet the germination criteria, were recorded as abnormal germination. At the end of the incubation period, ungerminated seeds were dissected to determine seed fill. The number of days to 50 percent of final germination was used as a measure of germination rate.

Treatments were applied factorially in a randomized, complete block design with 4 replications. Factors were salts, salt concentrations, and osmotic potential. Time was used as blocks because replications were started at approximately 2-week intervals.

Data were initially analyzed within seed sources with a factorial analysis of variance after transforming counts with arc sin $\sqrt{p}$ (Snedecor and Cochran 1980). Polynomial response curves or multiple linear regression response surfaces were then developed using untransformed data (Neter and Wasserman 1974). Tukey's W-procedure was used for testing differences between means (Snedecor and Cochran 1980). All statistical tests were made with $p = 0.05$.

Results

Percent seed fill was similar between collections (Table III.1). Weights of sorted seeds were, however, different between collections, with the South Harney collection significantly heavier than the North Harney and Coyote Buttes collections.

For all seed sources; percent germination, the number of days to 50 percent of final germination (D-50%), and percent abnormal germination were similar in NaCl and KCl. Therefore, data from germination tests in both salts were pooled within collections for analyses. Osmotic potential was the only factor significantly affecting D-50% and percent abnormal germination. As osmotic potential decreased, D-50% increased and percent abnormal germination declined (Table III.2). Relationships between percent germination and osmotic potential and salt concentration varied between collections.

Percent germinatiion of the North Harney collection was related to osmotic potential (Figure III.1), but salt concentration did not affect percent germination. Seeds germinated at all osmotic potentials tested except -2.2 MPa. Days to 50 percent of final germination were significantly different between all osmotic potentials tested (Table III.2). Some abnormal germination occurred at all osmotic potentials, with significantly less

Table III. 1. Seed weights and seed fill for three seed collections of greasewood from southeastern Oregon.

	Collection Source		
	North Harney	South Harney	Coyote Buttes
Mean Weight (mg/50 seeds)	79.6[1]	97.5[1]	81.3[1]
Mean Percent Seed fill	96.4[2]	96.6[2]	96.0[2]

[1] HSD = 12.6

[2] $S_{\bar{x}} = .70$

Table III. 2. The mean number of days to 50 percent of final germination (D-50%) and the mean percent of abnormal germination for greasewood. Tukey's HSD is in parenthesis. p = 0.05.

Seed Source	Osmotic Potential (MPa)	D-50%	Abnormal Germination (Percent)
North Harney	-0.3	4.7	4.2
	-0.7	6.1	3.7
	-1.2	7.0	3.5
	-1.6	12.5	3.7
	-2.2	- [1]	1.8
		(HSD=0.5)	(HSD=0.8)
South Harney	-0.3	5.2	3.0
	-0.7	7.2	2.3
	-1.2	8.5	2.1
	-1.6	- [1]	1.2
	-2.2	- [1]	0.4
		(HSD=0.4)	(HSD=0.6)
Coyote Buttes	-0.3	5.1	4.9
	-0.7	7.4	4.3
	-1.2	9.1	2.9
	-1.6	13.5	1.4
	-2.2	- [1]	0.8
		(HSD=0.5)	(HSD=0.8)

[1] No seeds germinated normally at these osmotic potentials.

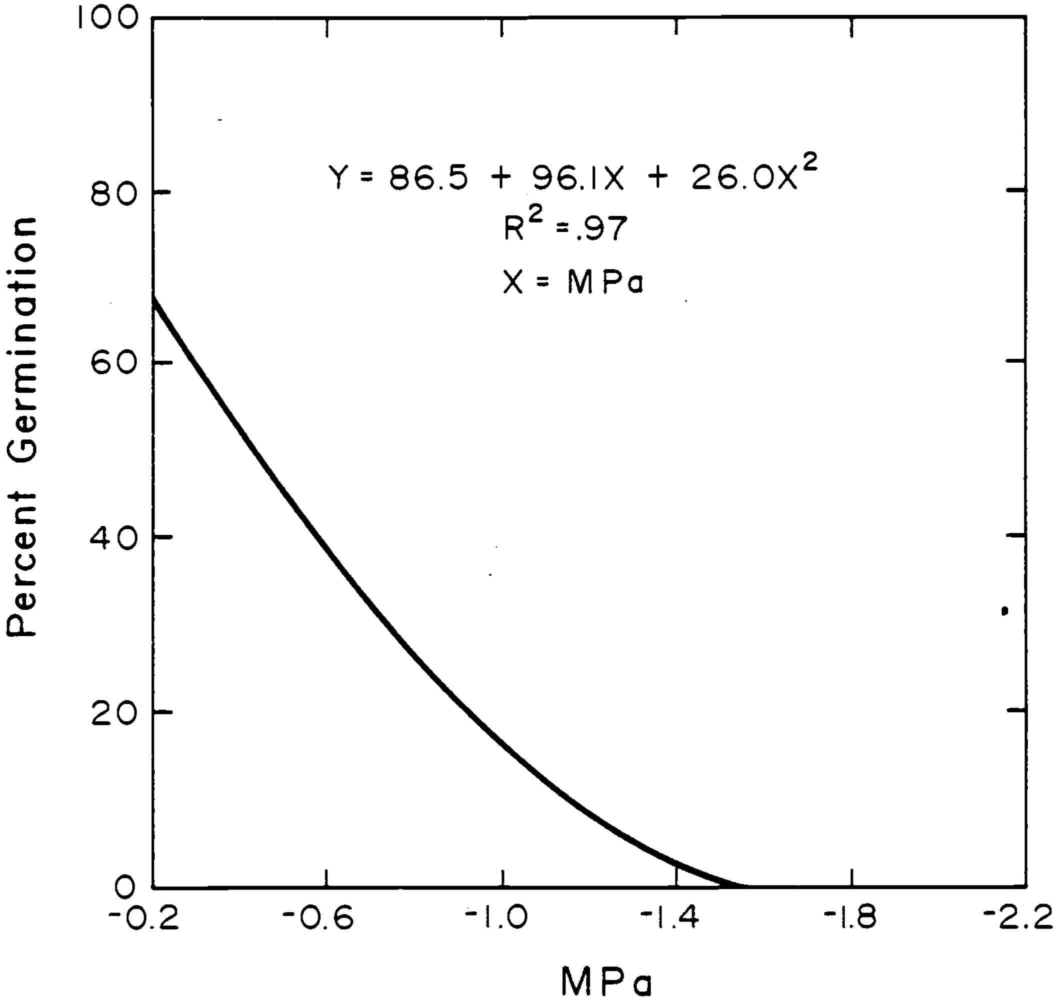

Figure III.1. Regression equation and response curve for percent germination of the North Harney collection of greasewood.

abnormal germination occurring at -2.2 MPa than at higher osmotic potentials (Table III.2)

Germination of the South Harney collection was reduced by declining osmotic potential and increasing salt concentration (Figure III.2). Germination was primarily reduced by declining osmotic potential; each 1000 ppm increment in salt concentration reduced germination about 1.4 percent. Seeds did not germinate at -1.6 and -2.2 MPa, but germination was observed in all salt concentrations at the higher osmotic potentials tested. As osmotic potential decreased, D-50% increased significantly (Table III.2). Over the range of osmotic potentials tested, 3.0 percent or less of the population germinated abnormally (Table III.2).

Germination of the Coyote Buttes collection was significantly affected by the interaction of osmotic potential and salt concentration (Figure III.3). The greatest reduction of germination was caused by declining osmotic potential. As osmotic potential declined, D-50% increased significantly (Table III.2). Abnormal germination was less than 5 percent in all osmotic potentials tested (Table III.2).

$Y = 94.8 + 104.8X_1 + 28.6X_1^2 - 0.001X_2$

$R^2 = .87$

X_1 = MPa

X_2 = ppm

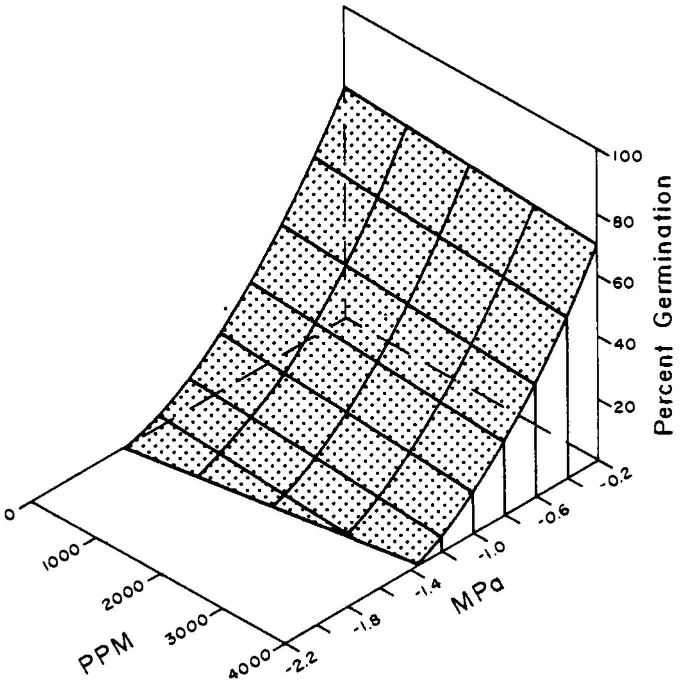

Figure III.2. Regression equation and response surface for percent germination of the South Harney collection of greasewood.

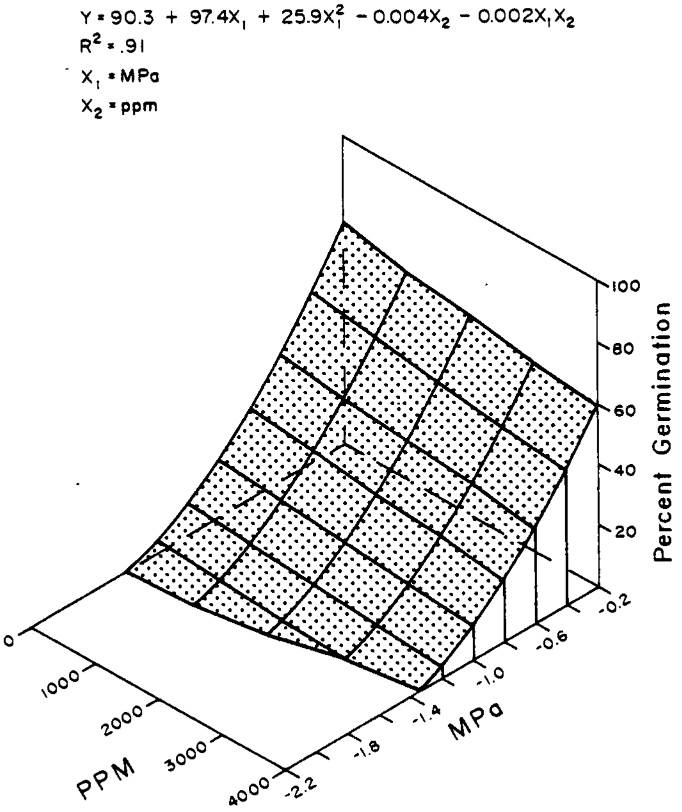

Figure III.3. Regression equation and response surface for percent germination of the Coyote Buttes collection of greasewood.

Discussion

The differences in germination observed in this study may be attributed to genetics of the populations, environmental conditions, or both. Unfortunately, it was not possible to separate their effects in this study. Regardless of which factor influenced germination, there were inter- and intrapopulation differences in response to osmotic potential and salt concentrations.

Germination of all populations was primarily reduced by osmotic potential, but a portion of the South Harney and Coyote Buttes collections were sensitive to salt concentration. Sensitivity to osmotic potential, rather than specific ions, may be important for survival since seeds are exposed to myriad combinations of ions under field conditions (Ungar 1982). Sensitivity to osmotic potential may be a mechanism that limits most germination to periods when salts are diluted or leached, and conditions are favorable for seedling growth. In the Great Basin, soil water potentials are highest and salinity is lowest in the spring because salts are diluted or leached by winter precipitation (Roundy 1983). On sites where seeds were collected for this germination study, greasewood seedlings were observed only during spring. It is likely greasewood has developed a strategy for germinating under moist conditions in southeastern Oregon.

Comparison of results in this study, with previously published studies on greasewood germination, suggested the possiblilty of geographical ecotypic differentiation. Sabo et al. (1979) reported a New Mexico collection of greasewood germinated 80 percent or more at osmotic potentials ranging from 0 to -1.6 MPa. Seeds collected in eastern Montana germinated at osmotic potentials as low as -3.6 MPa (Romo and Eddleman 1985). Furthermore, Romo and Eddleman (1985) reported Na_2SO_4 and NaCl stimulated germination rate and total germination in greasewood. These southeastern Oregon collections germinated only at osmotic potentials higher than -2.2 MPa, and germination was less than 30 percent at osmotic potentials lower than -0.3 MPa. Failure to germinate at low osmotic potentials and high salt concentrations may act to preserve a portion of the seed population and condition them for germination over a wider range of ensuing environmental conditions (Hegarty 1978; Ungar 1978).

Response to osmotic potential and specific ions is only one factor to consider when characterizing the germination ecology of greasewood. This study showed germination of these southeastern Oregon collections of greasewood is limited by availability of water.

Germination and establishment under field conditions may, however, be quite different due to the interaction of environmental factors.

CHAPTER IV

SEASONAL AND DIURNAL WATER RELATIONS OF PROSTRATE KOCHIA (*KOCHIA PROSTRATA*(L.) SCHRAD.)

Seasonal and Diurnal Water Relations of Prostrate Kochia (*Kochia prostrata* (L.) Schrad.)

Abstract

Prostrate kochia (*Kochia prostrata* (L.) Schrad) may be useful for forage seedings and for stabilizing soils in semiarid and arid areas. To fully utilize its potential, physiological responses to water stress must be understood. The objective of this study was to quantify seasonal and diurnal water relations of prostrate kochia in the field. Predawn leaf water potential (B ψ_1) and midday leaf water potential (ψ_{1m}) were determined during 2 growing seasons. Stomatal conductance (g_s), transpiration rates (J), and leaf water potential (ψ_1) were determined during diurnal measurements. B ψ_1 was significantly correlated with soil moisture to depths of 90 cm. J and g_s were highest from spring through mid-summer and lowest in late summer. The decline of g_s appeared related to the water stress history of plants and leaf aging. J declined in late summer from the combined effects of declining g_s and increasing resistance to water conductance in the soil-plant-atmosphere continuum. Spring and early summer are critical periods for growth of prostrate kochia, and management systems should be tailored to favor growth during this period.

Introduction

Knowledge of seasonal and diurnal water relations of plants is essential when attempting to extend the range of a plant species. Success of a species is controlled by the incidence of favorable growing conditions and the ability to exploit them (Westoby 1980). Species introduced to areas beyond their native range should possess rhythmns of physiological activity that favor growth during periods of high soil moisture availability and survival during periods of low soil moisture. Growth and survival of plants are manifest in their ability to balance absorption of water from soil and loss of water through transpiration (Larcher 1980). In arid areas, water deficit is common in most species (Hsiao et al. 1976), and availability of soil moisture is one of the most important factors determining plant success or failure (Daubenmire 1972). In areas with limited soil moisture, early phenological development is consequential for growth and survival (Harris 1967).

Few introduced species are adapted to the climate and soils of the sagebrush steppe in eastern Oregon. Introduced species that initiate and complete growth early in the season are most persistent and productive. The climate of this region is characterized by low precipitation and a short growing season (Carnahan et al.

1967). Annual precipitation ranges from 180 to 300 mm with approximately 60 percent received from October through March. Although nearly 40 percent of annual precipitation is received from April through September, it is often localized and ineffective in promoting vegetative growth. Summer drought is a distinctive characteristic of the region. Consequently, growth of plants is largely dependent on soil moisture that is recharged during winter and early spring when most plants are dormant or growing slowly.

Spring and early summer are periods of peak physiological activity in most species of the sagebrush steppe. Generally, leaf water potential, stomatal conductance, transpiration, and carbon gain are highest in the spring, and they decline as summer drought intensifies (Moore et al. 1972a; DePuit and Caldwell 1975; Campbell and Harris 1977; Barker and McKell 1983). Reduced physiological activity may be related to changes in leaf morphology (Moore et al. 1972a), and leaf aging and water stress (DePuit and Caldwell 1973; 1975).

Prostrate kochia (Kochia prostrata (L.) Schrad.), a half-shrub introduced to the United States from the steppe of Russia, appears adapted to the climate and soils of the Intermountain Region (Keller and Bleak 1974). In Russia, prostrate kochia is one of the most promising forage species for improving deteriorated rangelands (Balyan 1972). Because it is adapted to saline, alkaline, or neutral soils it may be useful for revegetating western rangelands (McArthur et al. 1974) and stabilizing soil (Young et al. 1981b).

Prostrate kochia is drought resistant, salt tolerant, and tolerant of temperature extremes (Balyan 1972). Yet, in spite of its high drought resistance and the ability to thrive in areas with as little as 160 mm annual precipitation, early season moisture is essential for growth (Balyan 1972). Prostrate kochia grows rapidly in the spring and growth is reduced during warm periods (Tukhtaev 1983). Concomitant with reduction of growth, is a reduction in transpiration (Khasanov et al. 1982) and an increase in heat tolerance (Tukhtaev 1983).

Prostrate kochia is highly polymorphic and many geographical races and ecotypes exist (Shishkin 1936). Thus, only generalizations can be posited regarding physiological characteristics and requirements. Prostrate kochia, PI 314929, has been released by the Soil Conservation Service Plant Materials Center at Aberdeen, Idaho as 'Immigrant'. This accession is salt tolerant (Francois 1976) and produces high quality forage (Davis 1979). The purpose of this study was to quantify seasonal and diurnal water relations of this accession under field conditions. Elucidating characteristics of water relations may be useful for breeding programs, identifying suitability for various areas, and developing management systems.

Materials and Methods

This study was conducted in a nursery at Squaw Butte Experiment Range, located 65 km west of Burns, Oregon. Elevation of the site is 1360 m and, approximately 300 mm of precipitation are received annually. Soils of the nursery are coarse-loamy, mixed, frigid Orthidic Durixerolls (Appendix C). The nursery was previously occupied by Wyoming big sagebrush (*Artemisia tridentata* Nutt. subsp. *wyomingensis*) and bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. and Smith).

Seeds of prostrate kochia (PI 314929), harvested from plants grown near Ephraim, Utah, were planted in late April, 1982. The study plot was irrigated after planting to insure germination. Irrigation was terminated in late May as acceptable numbers of seedlings had emerged.

Beginning in early July, 1982 and continuing until early October, leaf water potential (ψ_1) was determined biweekly for 8 plants using a pressure chamber (Scholander et al. 1965). Leaf water potential was determined before dawn (B ψ_1) and between 1200 and 1300 hours (ψ_{1m}). In

1983, assessment of ψ_1 was expanded to include diurnal measurements; $B\psi_1$ was determined biweekly from early May through early October and ψ_{1m} was determined from diurnal ψ_1 determinations. Eight plants were used for ψ_1 determinations in 1983. Vegetative branches were used for all ψ_1 determinations.

Diurnal changes of ψ_1, stomatal conductance (g_s), and transpiration (J) were determined on 23 May, 6 July, 30 July, 29 August, and 4 October 1983. The terminal 5 cm of vegetative branches, bearing several fasicles of leaves, were used for measurement. Measurements were begun before sunrise, and they were usually made at 2 hour intervals during the day. A LI-COR LI-1600 steady state porometer, equipped with a cylindrical cuvette, was used for estimating g_s, temperature (T), and relative humidity (RH). Photosynthetically active radiation (PAR) was measured with a LI-COR LI-1905 quantum sensor. T and RH were used for calculating vapor pressure deficit (VPD) and J was estimated by: $J = g_s \times VPD$. At the end of each set of diurnal measurements, branches were collected, leaves were removed, and leaf area was determined with a LI-COR LI-3100 area meter.

Resistance to water conductance in the soil-plant-atmosphere continuum (R_{SPAC}) was estimated for each plant on each day at the point of ψ_{1m} (Running 1980a). R_{SPAC} is computed by:

$$R_{SPAC} = \frac{\psi_s - \psi_{1m}}{J}$$

Where ψ_s is the soil water potential estimated by $B\psi_1$.

Plant phenology was recorded on each sample date using the following scoring system:

Score	Phenophase
1	Dormant, no visible growth (early April to early May)
2	Vegetative growth initiated (mid-May to early June)
3	Rapid vegetative growth (late June to early August)
4	Slow vegetative growth, inflorescences developing (mid-August to mid-September)
5	Anthesis, stems and leaves beginning to turn red (mid-September to late September)
6	Green seed, stems and leaves red (early October to late October)

On days $B\psi_1$ was determined 4 or 5 soil samples were collected from 0-30, 31-60, and 61-90 cm depths. Gravimetric soil moisture was determined after drying soil samples for at least 48 hours at 105C. Precipitation, daily minimum temperature, and daily maximum temperature were recorded at a weather station approximately 300 m from the nursery.

Seasonal changes of $B\psi_1$ were analyzed by constucting 95 percent confidence limits for means (Snedecor and Cochran 1980). Regression analysis was used to examine relationships of g_s and J with ψ_1, T, VPD, PAR, and phenology (Neter and Wasserman 1974). All statistical analyses were made with $p = 0.05$.

Results and Discussion

Seasonal Leaf Water Potential

Mean weekly maximum temperature, mean weekly minimum temperature, and precipitation during the study are shown in Figure IV.1. The mean annual temperature was approximately 3C below normal in 1982 and 1983. Annual precipitation was approximately 7 cm and 20 cm above normal in 1982 and 1983, respectively.

Generally, $B\psi_1$ declined through the growing season, but it increased or stabilized when soil moisture increased (Figure IV.2). Correlations of $B\psi_1$ and soil moisture were significant for all soil depths (Table IV.1). Higher correlations between $B\psi_1$ and deeper soil moisture highlight the importance of deep soil moisture in seasonal water relations of prostrate kochia. Balyan (1972) concluded the well developed root system of

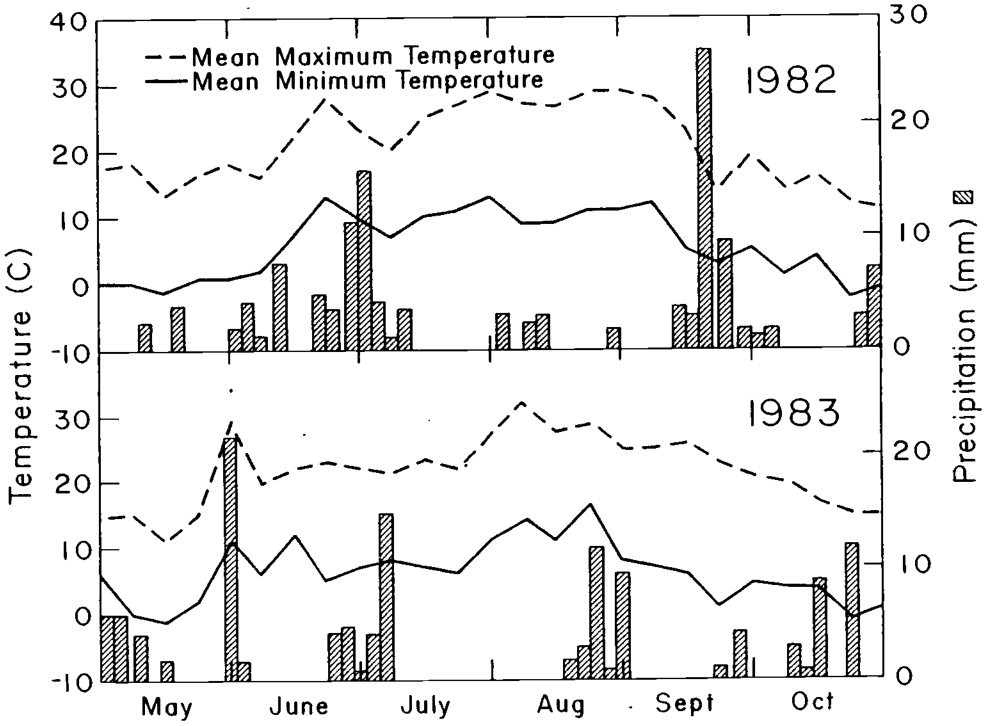

Figure IV.1. Mean maximum weekly temperature, mean minimum weekly temperature, and precipitation at Squaw Butte Experiment Range during the study in 1982 and 1983.

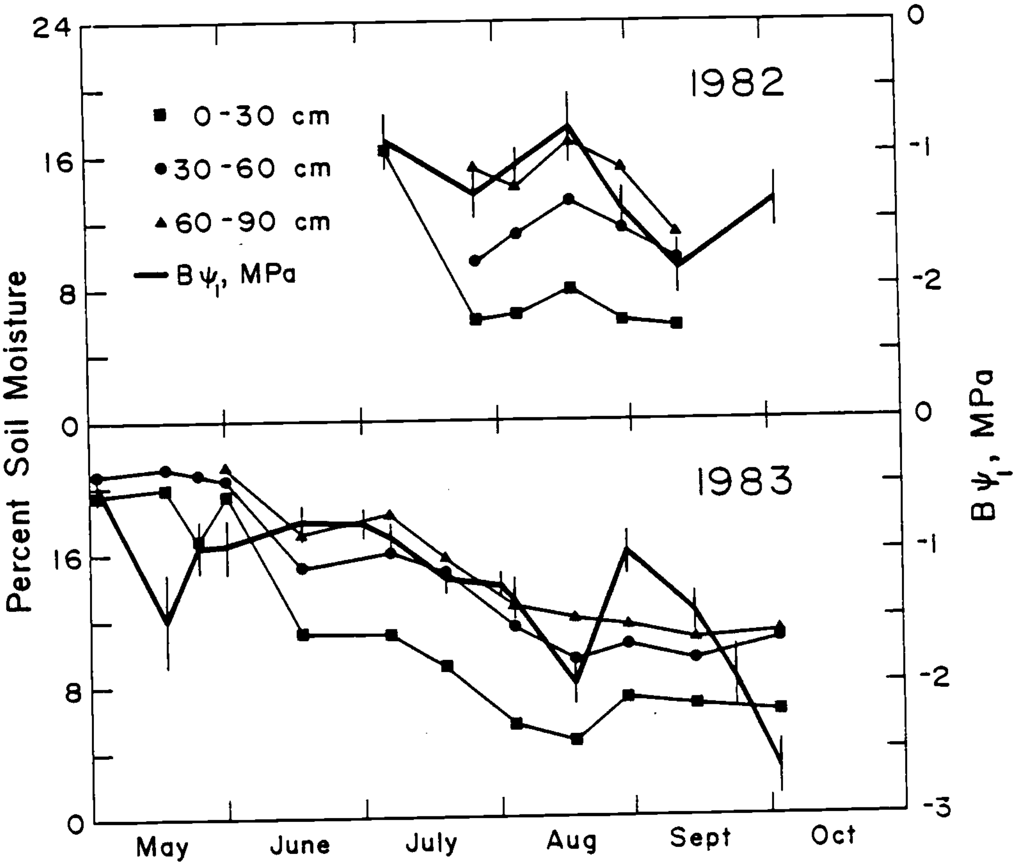

Figure IV.2. Gravimetric soil moisture and predawn leaf water potential ($B\psi_1$) of prostrate kochia in 1982 and 1983. Vertical bars are 95 percent confidence limits.

prostrate kochia is important for its drought resistance. It develops a deep taproot in its first year of growth, but later the taproot senesces, and is replaced by extensively branched lateral roots that can penetrate to 5 m deep (Balyan 1972). An extensive root system may enable efficient use of the soil profile for extracting moisture (Fernandez and Caldwell 1975).

Table IV. 1. Correlations between predawn leaf water potential of prostrate kochia and soil moisture during 1982 and 1983. All correlations are significant at $p = 0.05$.

Year	Soil Depth (cm)	Correlation Coefficient
1982	0 - 30	.58
	31 - 60	.73
	61 - 90	.83
1983	0 - 30	.42
	31 - 60	.43
	61 - 90	.64

In 1982, $B\psi_1$ decreased from -0.9 MPa in early July to -1.8 MPa in early September and then increased to -1.3 MPa in October (Figure IV.2). Increase of $B\psi_1$ from mid-July to mid-August corresponds with increasing soil moisture at 31-90 cm, however, only 5 mm of precipitation was received during this period. Soil moisture may have increased from percolation of precipitation received in late June and early July or from lateral movement of water from nearby nursery plots that were irrigated.

In 1983, $B\psi_1$ decreased from -0.5 MPa in early May to a low of -2.6 MPa in early October (Figure IV.2). Despite high soil moisture on May 17, $B\psi_1$ was -2.0 MPa, but increased to -0.9 MPa on May 23. Exact cause cannot be ascribed to the temporary but sharp decline of $B\psi_1$ in mid-May, but low soil temperature (Kaufmann 1981) coupled with initiation of vegetative growth and high VPD may have been important. On nearby study sites soil temperatures at 30 and 60 cm increased from 9 to 14C and 9 to 13C, respectively, between 16 May and 26 May.

Midday leaf water potential (ψ_{1m}) declined through the growing season. In 1982 ψ_{1m} declined from -1.0 MPa in early July to a low of -2.6 MPa in mid-September. It decreased from -2.3 MPa on 17 May 1983 to -4.3 MPa on 4 October 1983.

Seasonal and Diurnal Changes in Stomatal Conductance and Transpiration

Plant phenology, T, VPD, and PAR accounted for 57 percent of the variation observed in g_s. Mean daily g_s decreased from a high of 0.91 $cm.sec^{-1}$ on 23 May to a low of 0.25 $cm.sec^{-1}$ on 4 October (Figure IV.3). Mean daily g_s dropped sharply from 0.72 $cm.sec^{-1}$ on 30 July to 0.28 $cm.sec^{-1}$ on 29 August.

Seventy percent of the variation observed in diurnal J was explained by g_s, T, PAR, and phenology. Mean daily J declined from a high of 21.4 $\mu g.cm^{-2}.sec^{-1}$ on 30 July to a low of 3.6 $\mu g.cm^{-2}.sec^{-1}$ on 4 October (Figure IV.3). These results agree with those reported by Khasanov et al. (1982) who also found prostrate kochia reduced J through the summer.

Transient midday stomatal closure is indicated by bimodal peaks in g_s on 23 May and 6 July (Figure IV.3). Although g_s increased in the afternoon, it remained below morning values. Schulze and Hall (1982) concluded bimodal peaks of g_s may be related to T, VPD, or ψ_1. In this study it is not clear whether stomates responded to ψ_1 or environmental conditions. Concomitant with the midday reduction in g_s on 23 May, J increased, but ψ_1 stabilized. Stabilization of ψ_1 indicates equilibrium between transpirational water loss and replenishment of leaf water

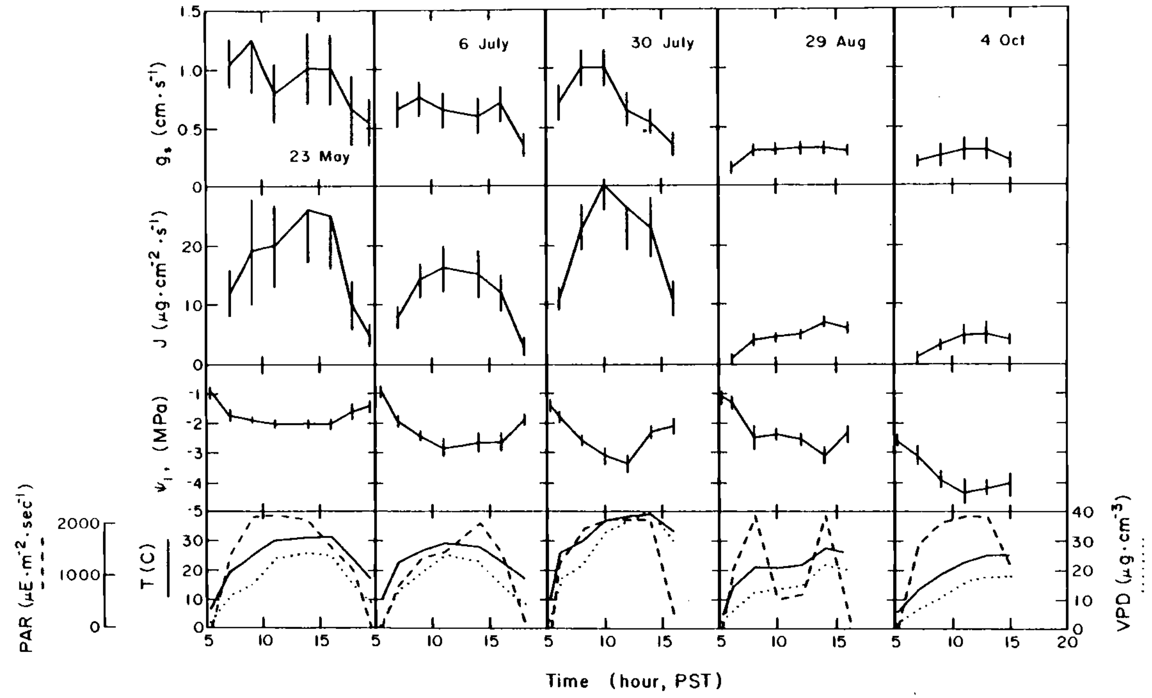

Figure IV.3. Stomatal conductance (g_s), transpiration (J), leaf water potential (ψ_l), photosynthetically active radiation (PAR), temperature (T), and vapor pressure deficit (VPD) during diurnal measurements of prostrate kochia in 1983. Vertical bars are 95 percent confidence limits.

(Ritchie and Hinckley 1975). In late afternoon ψ_1 increased as g_s and J decreased. After J reached a midmorning maximum of 16.5 $\mu g.cm^{-2}.sec^{-1}$ on 6 July, it declined the remainder of the day. Decline of J coincided with decreasing T and VPD.

On 30 July, g_s and J were highest in midmorning (1.02 $cm.sec^{-1}$ and 29.8 $\mu g.cm^{-2}.sec^{-1}$, respectively) and they declined through the day. Effective stomatal control of water loss is reflected in the decrease of J and increase of ψ_1 even though T and VPD remained high.

Compared to earlier dates, g_s and J were low on 29 August and 4 October. Stomates apparently remained closed since there were no distinct peaks in g_s. On both days maximum J was coincidental with maximum T and VPD. Despite low g_s and J, ψ_1 declined sharply from $B\psi_1$ levels. The sharp decline of ψ_1, despite low J, indicates resistance to water conductance in the soil-plant-atmosphere continuum (R_{SPAC}) was high (Kaufmann 1981; Schulze and Hall 1982).

R_{SPAC} is significantly related ($R^2 = 0.55$) to $B\psi_1$ (Figure IV.4). Decreasing soil water potential, as estimated by $B\psi_1$, was a major source of resistance to water flux in prostrate kochia (Figure IV.4). Increasing R_{SPAC} may also be related to the inability of the plant to fully recharge its internal water storage as soil moisture

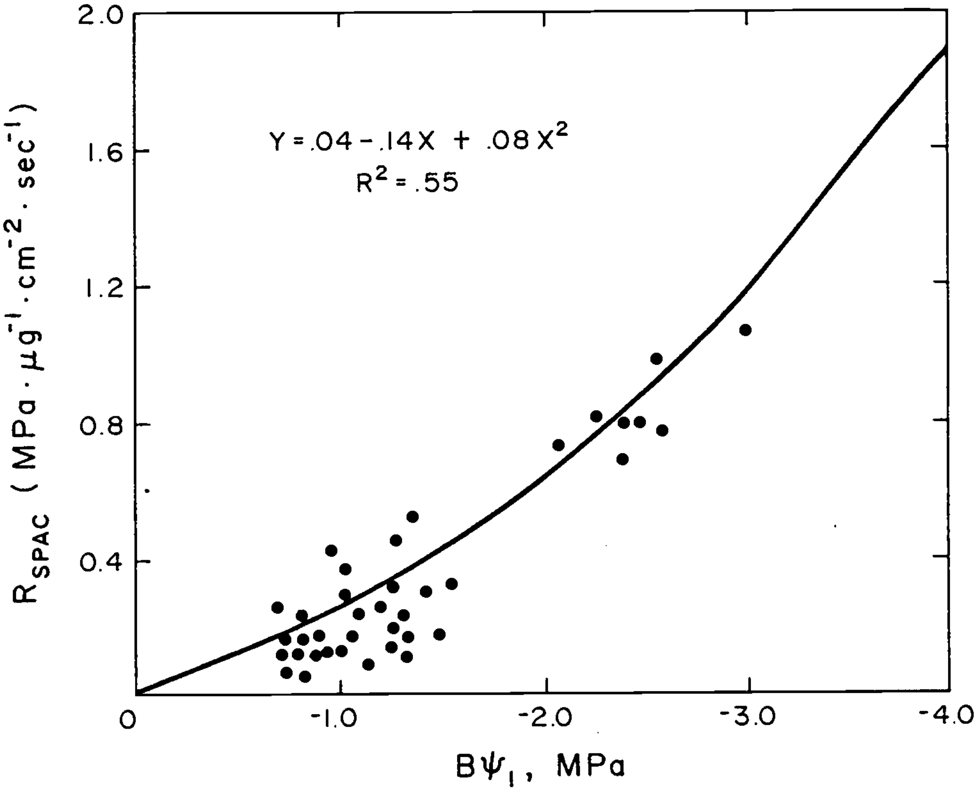

Figure IV.4. The influence of predawn leaf water potential ($B\psi_1$) of prostrate kochia on the seasonal increase of resistance (R_{SPAC}) to water conductance in the soil-plant-atmosphere continuum. Each point represents observed values.

declines (Running 1980a). The reduced capacity of the roots to absorb water may be related to suberization and aging of roots (Caldwell 1976).

Running (1976, 1980a) reported $B\psi_1$ and maximum g_s were closely related in conifers. His analysis demonstrated maximum g_s decreased linearly or curvilinearly with a progressive decline of $B\psi_1$. Our analysis of this relationship revealed a nonsignificant correlation, thus indicating $B\psi_1$ had minimal influence on the behavior of stomates. We conclude the water stress history of plants (Cline and Campbell 1976; Hsiao et al. 1976), aging of leaves (DePuit and Caldwell 1973; Roberts et al. 1981; Field and Mooney 1983), acted in concert to effect lower stomatal conductance through the summer. This conclusion is supported when g_s values on 6 July, 30 July, and 29 August are compared (Figure IV.3). Although ψ_1 and environmental conditions were similar on these dates, g_s was substantially lower on 29 August than on earlier dates.

Conclusions

Characteristics of seasonal water relations of prostrate kochia indicate a high degree of adaptability to the climate of eastern Oregon. Prostrate kochia's adaptation is exemplified by a pattern of growth and physiological activity similar to native plants of the sagebrush steppe. Rapid growth and high gas exchange rates during spring through mid-summer coincide with periods of highest soil moisture and environmental conditions conducive to growth. Reduced transpiration during late summer appears the product of more effective stomatal control of water loss brought about by advancing phenology, and increased resistance to water conductance in the soil-plant-atmosphere continuum.

Since spring through mid-summer are periods of highest gas exchange rates in prostrate kochia, grazing systems should be developed to favor growth during this period. Late summer, fall or winter grazing of prostrate kochia may provide utilization of high quality forage (Davis 1979) and have minimal influence on plant vigor. Defoliation studies should be developed to test this hypothesis.

Chapter V

SEASONAL AND DIURNAL WATER RELATIONS OF GREASEWOOD (*SARCOBATUS VERMICULATUS*) AND WYOMING BIG SAGEBRUSH (*ARTEMISIA TRIDENTATA* SUBSP. *WYOMINGENSIS*)

Seasonal and Diurnal Water Relations of Greasewood (*Sarcobatus vermiculatus* (Hook.) Torr.) and Wyoming Big Sagebrush (*Artemisia tridentata* Nutt. subsp. *wyomingensis*)

Abstract

Greasewood (*Sarcobatus vermiculatus* (Hook.) Torr.) and Wyoming big sagebrush (*Artemisia tridentata* Nutt. subsp. *wyomingensis*) are common species in the cool shrub steppe; however, they differ in morphology, phenology, and ecology. This research quantified and compared seasonal and diurnal water relations of greasewood and Wyoming big sagebrush and related these responses to environmental conditions. Leaf water potential (ψ_1), stomatal conductance (g_s), transpiration rates (J), and resistance to water conductance in the soil-plant-atmosphere continuum (R_{SPAC}) were studied in the field during the summers of 1982 and 1983. Predawn ψ_1 and midday ψ_1 declined in both species as the season progressed. Depression of midday ψ_1 from predawn ψ_1 increased for sagebrush as summer drought intensifed, but remained nearly constant for greasewood. In early summer, ψ_1, g_s, J, and R_{SPAC} were similar for both species. Stomata of both species closed when the atmospheric vapor pressure deficit exceeded approximately 10 $\mu g.cm^{-3}$. As summer drought intensified, g_s and J declined for sagebrush, but

they remained high for greasewood. Maximum g_s and predawn ψ_1 were closely related for sagebrush but not for greasewood. As $B\psi_1$ decreased, R_{SPAC} increased in both species and the increase was most pronounced in sagebrush. The seasonal reduction of J in sagebrush was related to a declining g_s and an increasing R_{SPAC}. J and g_s for greasewood were modulated by environmental conditions. Nighttime temperatures near freezing delayed stomata opening in greasewood. Maximum stomata opening was related to nocturnal temperatures and daytime vapor pressure deficit.

Introduction

Although shrubs are the dominant lifeform of the cool shrub steppe of North America, few detailed studies have been focused on their water relations. Furthermore, past studies were limited in scope, thus only generalizations can be made. Detailed studies of water relations provide information that is crucial for comprehension of the structure and function of arid ecosystems.

Greasewood (Sarcobatus vermiculatus (Hook.) Torr.) and Wyoming big sagebrush (Artemisia tridentata Nutt. subsp. wyomingensis) are important components of the cool shrub steppe, but they differ in morphology, phenology, and ecology. Sagebrush maintains considerable leaf area throughout the year whereas greasewood is deciduous and displays foliage from late spring to early fall. Greasewood is a phreatophyte (Robinson 1958) and sagebrush is a mesophyte. Because greasewood is a phreatophyte and maintains leaves for a shorter time than sagebrush, we hypothesized that seasonal and diurnal water relations would be the product of differential response to environmental conditions.

Diurnal and seasonal water deficits are common in plants in arid environments (Hsaio et al. 1976). Plants have, however, developed a suite of strategies that allow growth and survival despite diurnal and seasonal water deficits. Structural and functional adaptations, that enable plants to exploit soil moisture in space and time, while simultaneously minimizing water loss and maximizing growth, are manifest in competitive ability and distribution. Success of a species is determined by the incidence of favorable growing conditions and the ability to exploit them (Westoby 1980).

Seasonal trends of water stress in several shrubs of the cold desert are reported (DePuit and Caldwell 1973, 1975; Love and West 1972; Dina and Klikoff 1973; Campbell and Harris 1977; Everett et al. 1977; Barker and McKell 1983). In general, these studies have shown leaf water potential is highest in the spring, declining as summer drought intensifies. These studies also show differences in leaf water potential between species and subspecies. However, differences in leaf water potential may be due to differences in morphology, physiology, water holding capacity, root distribution, and resistance to water conductance in the soil-plant-atmosphere continuum (Moore et al. 1972a; DePuit and Caldwell 1973, 1975; Everett et al. 1977; Roy and Mooney 1982).

Studies on root characteristics of some shrubs have been reported. Sturges (1977) found sagebrush possessed a taproot with shallow and well developed laterals. Fernandez and Caldwell (1975) studied root growth of

Wyoming big sagebrush, shadscale (Atriplex confertifolia (Torr. and Frem.) S. Wats.), and winterfat (Ceratoides lanata Nevski.). They observed most roots in the upper 1 m of soil, where soil moisture recharge was highest. Furthermore, root growth of all three species progressed from upper layers of the profile to greater depths through the season. Shantz and Piemeisel (1940) found greasewood had a taproot down to 6 m, and abundant laterals were present at 3 to 4 m. Greasewood can root to depths of nearly 17 m (Robinson 1958).

Studies of gas exchange characteristics have demonstrated seasonal and species differences; highest gas exchange rates usually occur in spring, and they decline through the summer. Generally stomatal conductance (g_s) and transpiration rates (J) decline as phenology advances and leaf water potential (ψ_1) declines. Moore et al. (1972a) found J was higher for winterfat than shadscale in early summer, but J was higher for shadscale in the latter part of the summer. They concluded anatomical and morphological changes in leaves, and xylem resistance, may have been important for reduced J late in the season. Peak physiological activity of sagebrush corresponds with favorable growing conditions in the spring (DePuit and Caldwell 1973). During summer drought, sagebrush reduces water loss by reducing g_s (Campbell and Harris 1977;

Barker and McKell 1983) and shedding leaves (Diettert 1938). DePuit and Caldwell (1973) concluded ψ_1 and leaf age of sagebrush may contribute to variable g_s during the summer. Stark (1967) also reported variability in J between different aged leaves in greasewood; however, seasonal trends of g_s and J were not studied. In the above studies, changes in resistance to water conductance in the roots and stems were not determined.

The purpose of this research was to quantify seasonal and diurnal water relations of Wyoming big sagebrush and greasewood. To test our hypothesis that greasewood and sagebrush respond differently to environmental conditions, we quantified changes ψ_1, g_s, J, and resistance to water conductance in the soil-plant-atmosphere continuum (R_{SPAC}) and related the changes to environmental variables and plant phenology.

Materials and Methods

Research was conducted during the growing seasons of 1982 and 1983 and consisted of 3 experiments. Experiment I was designed to quantify seasonal changes of predawn leaf water potential ($B\psi_1$) of sagebrush and greasewood on 2 sites with different soil properties. In Experiment II, seasonal trends of $B\psi_1$ of greasewood were studied on 4 sites in 1983. Experiment III was designed to quantify seasonal and diurnal changes in Ψ_1, g_s, J, and R_{SPAC} for sagebrush and greasewood during the 1983 growing season.

Study Sites

Research was conducted in Harney Basin in southeastern Oregon. Harney Basin covers approximately 15,000 km^2, and is located on the northern edge of the Great Basin Desert. Piper et al. (1939) and Walker and Swanson (1968) provide the geologic history of Harney Basin. Annual precipitation in Harney Basin ranges from 200 to 300 mm with approximately 60 percent received from October through March; summer drought is a distinctive characteristic of the region. The mean annual temperature is 7C with an average daily maximum of 30C in July and an average daily minimum of -9C in January.

Study sites were located 30 to 40 km south of Burns, Oregon. The study sites differ in soils and vegetative composition. Elevation of all study sites is approximately 1255 m. North Harney and South Harney study sites were formed from alluvial materials and soils are fine-loamy, mixed, mesic Xerollic Haplargids, and fine-loamy, mixed, mesic Xerollic Camborthids, respectively. The water table is approximately 5 m deep at North Harney and 15 m deep at South Harney. The Coyote Buttes and Saddle Butte study sites were formed from sedimentary materials. Soils are fine montmorillonitic, mesic Xerollic Haplargids and coarse-loamy, mixed, mesic Xerollic Haplargids at Coyote Buttes and Saddle Butte, respectively. At both sites, the water table is approximately 3.5 m deep. Soil profile descriptions for each site are provided in Appendix B.

Greasewood is the most abundant species on all study sites. However, the amount of sagebrush, shadscale, rabbitbrush (Chrysothamnus sp.), spiny hopsage (Grayia spinosa (Hook.) Moq.) and basin wildrye (Elymus cinereus Scribn. and Merr.) varies between sites. Line intercept was used to determine canopy cover and composition of shrubs at each site. Herbaceous vegetative compostion was determined from frequency in 500 0.1 m^2 quadrats. Vegetative characteristics of each site are presented in Appendix A.

Experiment I

In 1982, an 800 m transect, with five stations 200 m apart, was established at Coyote Buttes and North Harney sites. Two average size greasewood and sagebrush plants were marked at each station giving a total of ten plants per species at each site. $B\psi_1$ was determined for these plants approximately biweekly from mid-July to early October, 1982, and May through September, 1983. A pressure chamber (Scholander et al. 1965) was used for $B\psi_1$ determinations. $B\psi_1$ of vegetative branches was determined about 1 hour before sunrise. Soil samples were collected at each station the days of $B\psi_1$ determinations and used for soil moisture determination. Samples were collected from 0-30, 31-60, and 61-90 cm depths and soil moisture was determined gravimetrically, after drying samples at 105C for at least 48 hours. Rain gauges were established at both study sites, and precipitation was recorded at least weekly from July through September, 1982, and May through October, 1983.

Phenology of marked plants was recorded approximately biweekly. In 1982, general phenological observations were made, but in 1983 a phenology index and growth measurements were used. The phenological index for sagebrush was developed by DePuit and Caldwell (1973), and it is presented in Table V.1. We developed a similar index for greasewood (Table V.1). Lengths of two vegetative branches on each plant were recorded to determine growth rates.

Experiment II

Seasonal changes in $B\psi_1$ of greasewood were compared for all study sites in 1983. Transects were established at the Saddle Butte and South Harney sites as described

Table V. 1. Phenology scoring criteria for Wyoming big sagebrush and greasewood.

Phenophase	Sagebrush	Greasewood
0	Winter Dormancy	-
1	Post dormant quiescence	Winter dormancy
2	Leaf buds swelling	Vegetative bud burst
3	New leaves developing	Branch emergence and new leaves developing
4	Rapid stem growth (>1mm/day), inflorescences developing	Rapid stem growth (>1mm/day), leaves developing
5	Slow stem and leaf growth (<1mm/day), ephemeral leaves shedding; inflorescences developing	Rapid vegetative growth (>1mm/day), leaves developing, anthesis
6	Slow stem and leaf growth (<1mm/day), inflorescences full-size	Slow vegetative growth (<1mm/day), seeds developing
7	Flower buds fully developed	Basal leaves senescing, seeds developing
8	Anthesis	Leaves senescing, seeds fully developed, green
9	Seeds developing	Leaves senescing, seeds ripe and shattering
10	Seeds ripe and shedding	Dormant, seeds shattering

above. At each station two greasewood plants were marked and $B\psi_1$ was determined biweekly.

Experiment III

In 1983 diurnal measurements of environmental conditions, ψ_1, g_s, and J were made in June, July, August, and September at Coyote Buttes and North Harney. At each site, a transect with eight stations, approximately 10 m apart, was established. One sagebrush and one greasewood plant of close proximity were marked at each station and used for ψ_1, g_s, and J determinations through the experiment. A LI-COR LI-1600 steady state porometer, equipped with a cylindrical cuvette, was used to measure g_s, temperature (T), and relative humidity (RH). Photosynthetically active radiation (PAR) was measured with a LI-COR LI-1905 quantum sensor. Wind speed at 80 cm above ground level was recorded with a Bellfort anemometer.

Stomatal conductance and ψ_1 determinations were made on vegetative branches near the top of plants. The terminal 4 to 5 cm of branches, each bearing several leaves, were used. A typical day of measurements began by determining $B\psi_1$ about 1/2 hour before sunrise. Stomatal conductance and ψ_1 determinations were usually begun within 1 hour after sunrise and they were made at 2 hour intervals through the day. On some mornings, g_s determinations were delayed because of dew on leaves. At the end of each day, branches were collected, leaves were removed, and leaf area was determined with a LI-COR LI-3100 area meter. T and RH were used to determine vapor pressure deficit (VPD) and J was estimated by: J=VPD x g_s.

The daily course of R_{SPAC} was calculated from: $R_{SPAC} = \frac{B\psi_1 - \psi_1}{J}$ where ψ_1 and J are values determined through the day. The influence of soil water potential (ψ_s) on R_{SPAC} was determined for individuals of each species on each date at the point of minimum leaf water potential (ψ_{1m}) (Running 1980a). R_{SPAC} is estimated by: $\frac{\psi_s - \psi_{1m}}{J}$ with ψ_s estimated by $B\psi_1$.

Data Analysis

Data were analyzed with boundary line analysis (Webb 1972; Watts et al. 1976), regression analysis (Neter and Wasserman 1974) and by constructing confidence limits for means. All statistical analyses were made at $p = 0.05$.

Results

Phenology

Within species, phenology was similar at Coyote Buttes and North Harney sites (Figures V.1 and V.2). The most notable difference was the rapid growth phenophase of sagebrush and greasewood terminated approximately 2 weeks earlier at the Coyote Buttes site.

Sagebrush initiated growth in late April and grew rapidly from mid-May to late June; ephemeral leaves were shed in July (Figure V.1). Inflorescences were fully developed by late August and flowers bloomed in mid-September. Seeds were ripe and dehiscing in early October.

Greasewood initiated growth in mid-April and some new leaves had developed by mid-May (Figure V.2). Leaders elongated more than 1 mm per day from late May until mid-July. In response to precipitation in late August, growth exceeded 1 mm per day in early September. Anthesis occurred in late June and early July; seeds matured during the summer and shattered in late September. Leaf abcission occurred in late September and October.

Seasonal Changes in Predawn Leaf Water Potential

In 1982, $B\Psi_1$ of sagebrush and greasewood declined from mid-July until mid-September and increased in early

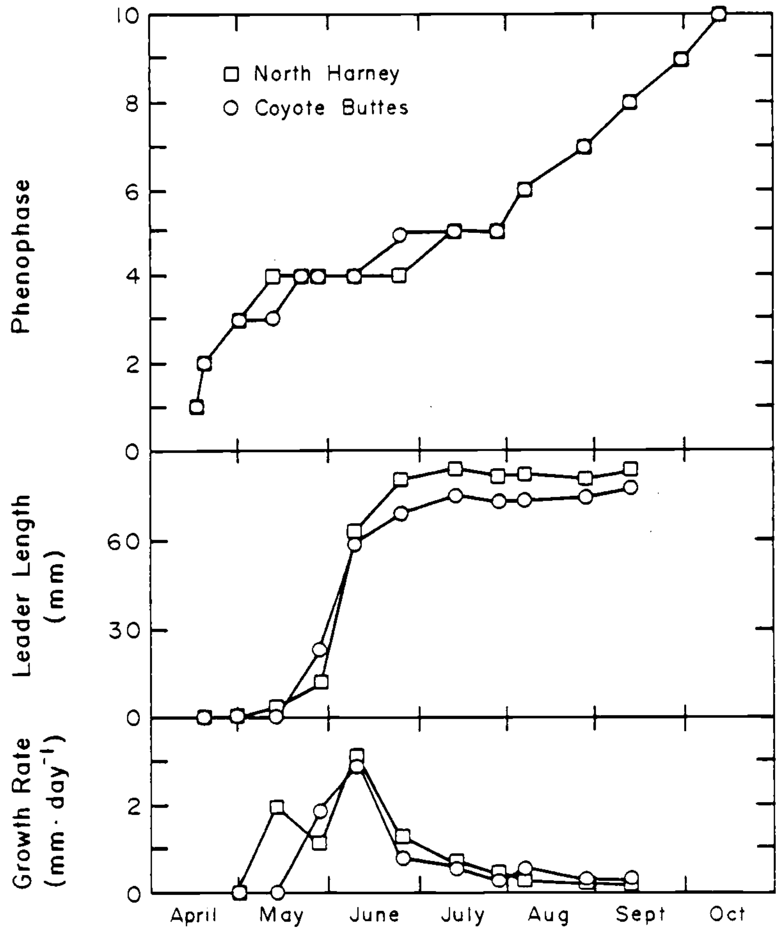

Figure V.1. Phenology of sagebrush at the North Harney and Coyote Buttes study sites in 1983. See Table V.1 for phenophase descriptions.

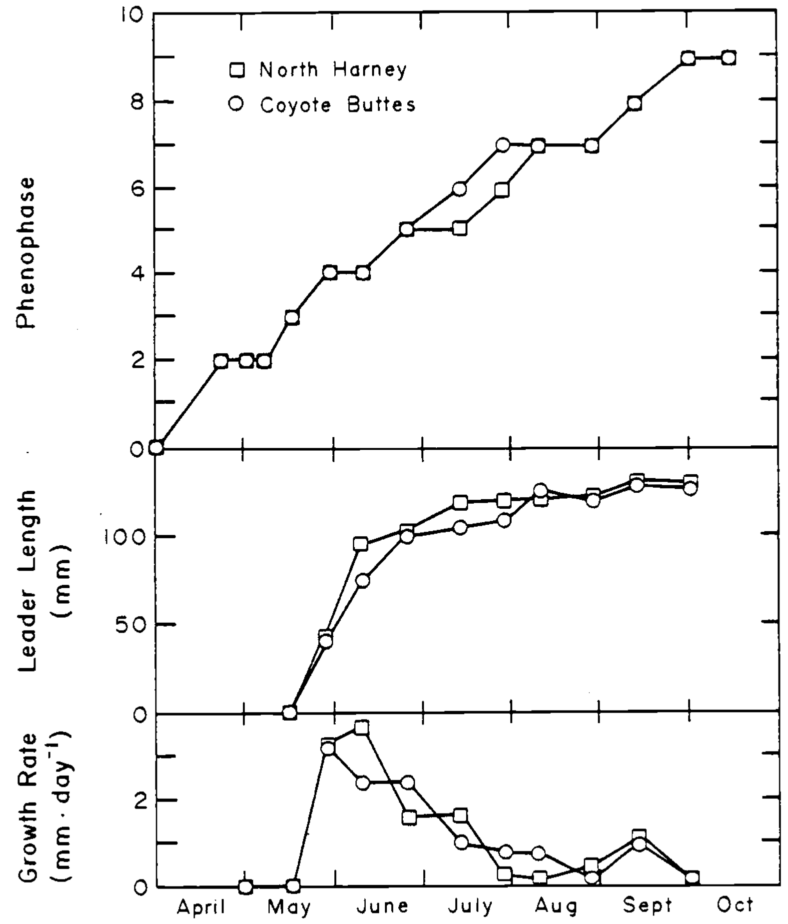

Figure V.2. Phenology of greasewood at the North Harney and Coyote Buttes study sites in 1983. See Table V.1 for phenophase descriptions.

October after fall rains were received (Figures V.3 and V.4). From mid-July until to mid-August, $B\psi_1$ of sagebrush averaged 1.2 MPa higher at North Harney than at Coyote Buttes; however, on later dates $B\psi_1$ was not significantly different between sites. $B\psi_1$ of greasewood was not significantly different between the Coyote Buttes and North Harney sites. At Coyote Buttes $B\psi_1$ of greasewood was significantly higher than sagebrush on all dates, but at the North Harney site $B\psi_1$ of greasewood was significantly higher than sagebrush only in early September.

$B\psi_1$ of sagebrush at Coyote Buttes was correlated with soil moisture at 0-30 cm; at North Harney $B\psi_1$ was correlated with soil moisture at 61-90 cm (Table V.2). Soil moisture and $B\psi_1$ of greasewood were not correlated (Table V.2).

In 1983, $B\psi_1$ of sagebrush was significantly lower at Coyote Buttes than at North Harney from late June until early August (Figure V.3). During this period, $B\psi_1$ averaged 0.8 MPa higher at North Harney. Cessation of the rapid growth phenophase at Coyote Buttes was coincidental with the first date $B\psi_1$ was significantly lower than North Harney. The rapid growth phenophase ended when $B\psi_1$ was between -1.4 and -1.9 MPa at Coyote Buttes and between -1.3 and -1.6 MPa at North Harney.

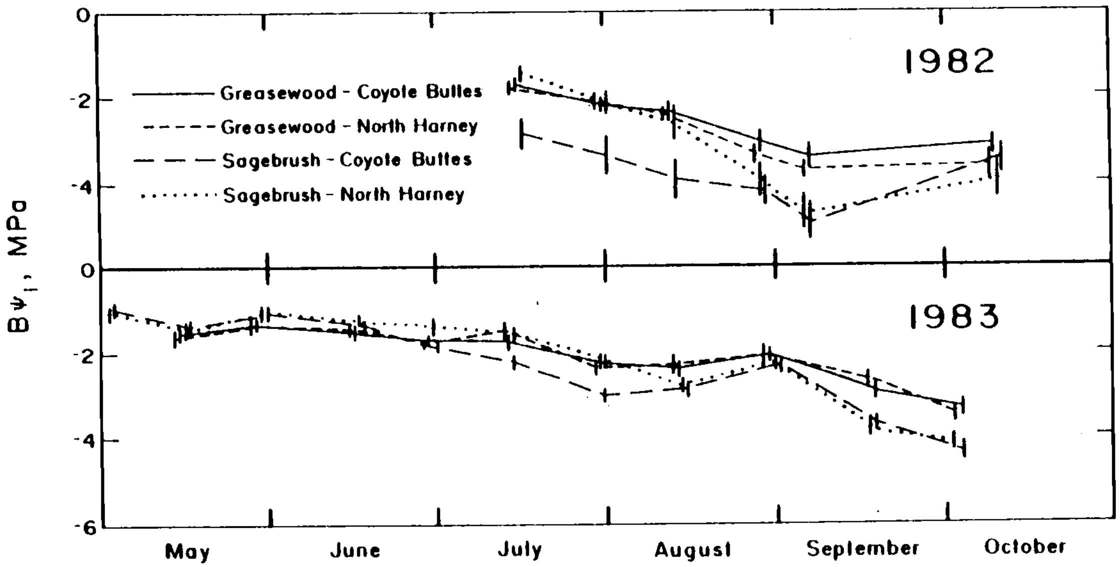

Figure V.3. Predawn leaf water potential ($B\Psi_l$) of greasewood and sagebrush at the North Harney and Coyote Buttes study sites in 1982 and 1983. Vertical bars are 95 percent confidence limits.

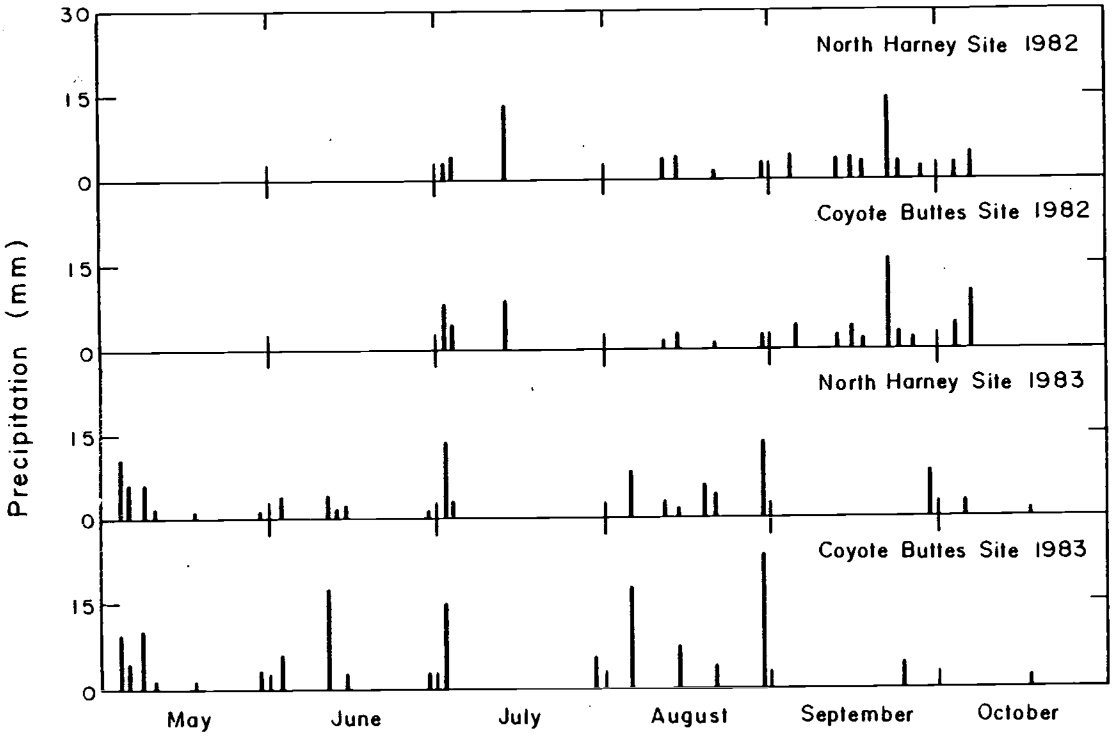

Figure V.4. Precipitation received at the North Harney and Coyote Buttes study sites in 1982 and 1983.

Table V. 2. Correlation coefficients (r) of predawn leaf water potential and gravimetric soil moisture at Coyote Buttes and North Harney in 1982 and 1983. *Indicates significance at p = 0.05.

Year	Sites	Soil Depth (cm)	Wyoming big sagebrush r	Greasewood r
1982	Coyote Buttes	0-30	.66*	.14
		31-60	.18	.33
		61-90	-.33	.07
1982	North Harney	0-30	.41	.43
		31-60	.33	.26
		61-90	.47*	.40
1983	Coyote Buttes	0-30	.38*	.30*
		31-60	.60*	.52*
		61-90	.32*	.29*
1983	North Harney	0-30	.48*	.15
		31-60	.45*	.15
		61-90	.13	-.08

B ψ_1 of greasewood was similar at Coyote Buttes and North Harney in 1983 (Figure V.4). In September, Bψ_1 of greasewood was significantly higher than sagebrush at both sites.

In 1983, B ψ_1 of greasewood and sagebrush were correlated with soil moisture at all depths at Coyote Buttes (Table V.2). At North Harney Bψ_1 of sagebrush was correlated with soil moisture at 0-60 cm, but correlations were not significant for greasewood (Table V.2).

B ψ_1 of greasewood at Coyote Buttes and North Harney are represenative of Bψ_1 at South Harney and Saddle Buttes (Appendix D). When Bψ_1 was compared for all sites, they were not significantly different.

B ψ_1 of sagebrush and greasewood increased within 48 hours of receipt of rain in late August, 1983 (Figures V.3 and V.4). In this study, Bψ_1 increased when more than about 6 mm of rain was received.

Diurnal Cycles

Diurnal measurements of g_s, J, ψ_1, and environmental conditions were similar at North Harney and Coyote Buttes. Therefore, data from both sites were combined for analyses. Six sets of diurnal measurements made at North Harney were selected to graphically represent plant responses and environmental conditions. Diurnal measurements made at Coyote Buttes are presented in Appendix E.

Environmental Conditions

Diurnal measurements of PAR, T, VPD, and wind illustrate characteristics of the aerial environment during the growing season in southeastern Oregon (Figure V.5). Days are typically clear, warm, and have low humidity; nights are usually cool, and relative himidity is often high. Diurnal variation in T and VPD is considerable. Temperatures can be near freezing on any night, and daytime temperatures can reach 40C. Similarly, VPD is usually low at night, and dew often forms, but VPD can increase to 35 $\mu g.cm^{-3}$ during the day. PAR usually reaches a maximum between mid-morning and noon, but it often declines in late afternoon as clouds increase from developing convectional storm systems. Wind often increases in late afternoon as convectional storms develop.

Plant Responses

Leaf Water Potential

Leaf water potential of sagebrush and greasewood declined as the season progressed with sagebrush

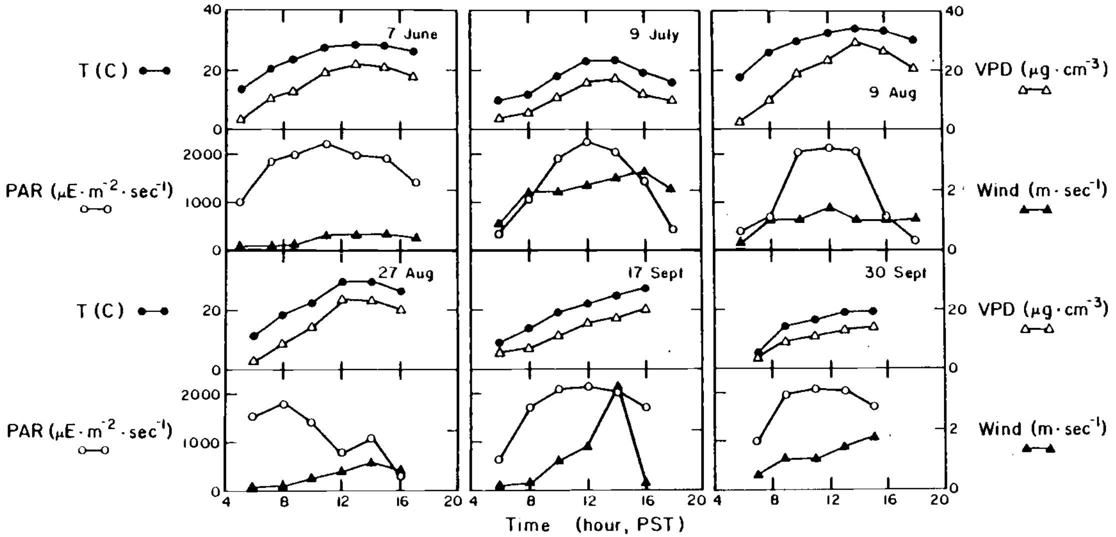

Figure V.5. Diurnal measurements of temperature (T), photosynthetically active radiation (PAR), vapor pressure deficit (VPD), and wind at the North Harney study site in 1983. Each point represents the mean of 8 measurements.

experiencing the greatest reduction (Figure V.6). From June to September, diurnal variation of ψ_1 for sagebrush increased from 1.1 to 2.2 MPa. Diurnal fluctuations of ψ_1 for greasewood increased from 1.6 MPa in June to 2.2 MPa in August, and then declined to 0.8 MPa in late September.

Leaf Conductance

In June and July, g_s was similar for sagebrush and greasewood, but in August and September, g_s was significantly lower for sagebrush (Figure V.6). Low and stable g_s (<0.20 cm.sec^{-1}) for sagebrush in August and September suggests stomata were nearly closed. Stomatal conductance for greasewood showed no consistent trends; maximum g_s and its temporal occurrence were variable (Figure V.6). Stomatal conductance of greasewood was low on the mornings of 9 July, 27 August, 17 September, and 30 September, even though PAR was high and VPD was low (Figure V.5). Stomatal conductance increased during the morning and gradually declined in the afternoon. Gradual reduction of g_s indicates stomates responded to increasing VPD (Lange et al. 1971).

Stomatal closure, triggered by VPD, was detected in sagebrush in early summer, and it was noted in greasewood throughout the season. Stomatal conductance of both

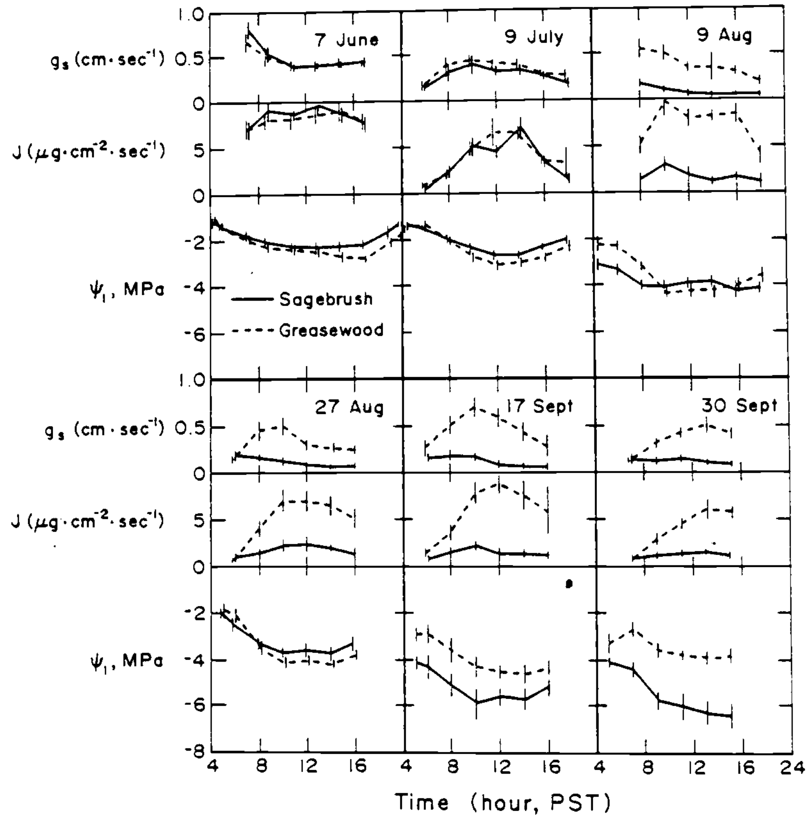

Figure V.6. Diurnal stomatal conductance (g_s), transpiration (J), and leaf water potential (ψ_l) for sagebrush and greasewood at the North Harney site in 1983. Vertical bars are 95 percent confidence limits.

species declined when VPD exceeded approximately 10 $\mu g.cm^{-3}$ (Figure V.7). The preponderance of low g_s for sagebrush at all levels of VPD is an artifact of low ψ_1; low g_s for greasewood at VPD less than 10 $\mu g.cm^{-3}$ may be related to nightime temperatures.

Stomatal conductance and ψ_1 were closely related for sagebrush (Figure V.8), but they were not significantly related for greasewood (Figure V.8). The curvilinear function of ψ_1 and g_s is significant for sagebrush, but the coefficient of determination is low (R^2=.48). A better relationship, R^2=.79, was obtained for Bψ_1 and maximum g_s (Figure V.9). Bψ_1 and maximum g_s were not significantly related for greasewood.

Daytime temperature was not examined as a controlling factor of g_s because T and VPD are inextricably related. Normally stomates open as temperature increases, provided VPD or ψ_1 is not limiting (Schulze and Hall 1982). Exposure to low temperatures can inhibit stomatal opening (Drake and Salisbury 1972; Kaufmann 1976; Fahey 1979), and the duration of this inhibiting effect may be related to the length and severity of the cold period (Hinckley et al. 1978).

The relationship between temperature (BT) at the time Bψ_1 was determined, and maximum g_s, was not significant for either species. However, BT was significantly related

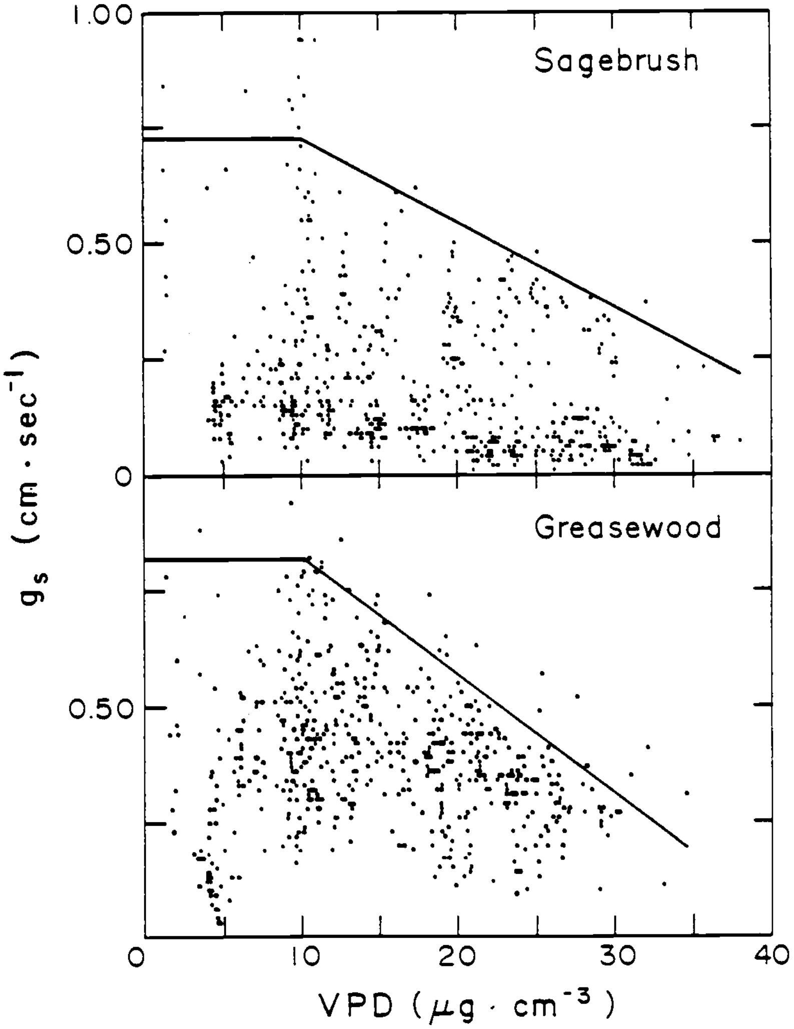

Figure V.7. The relationship between vapor pressure deficit (VPD) and stomata conductance (g_s) for sagebrush and greasewood at the North Harney and Coyote Buttes study sites in 1983. The solid line is the estimated boundary line.

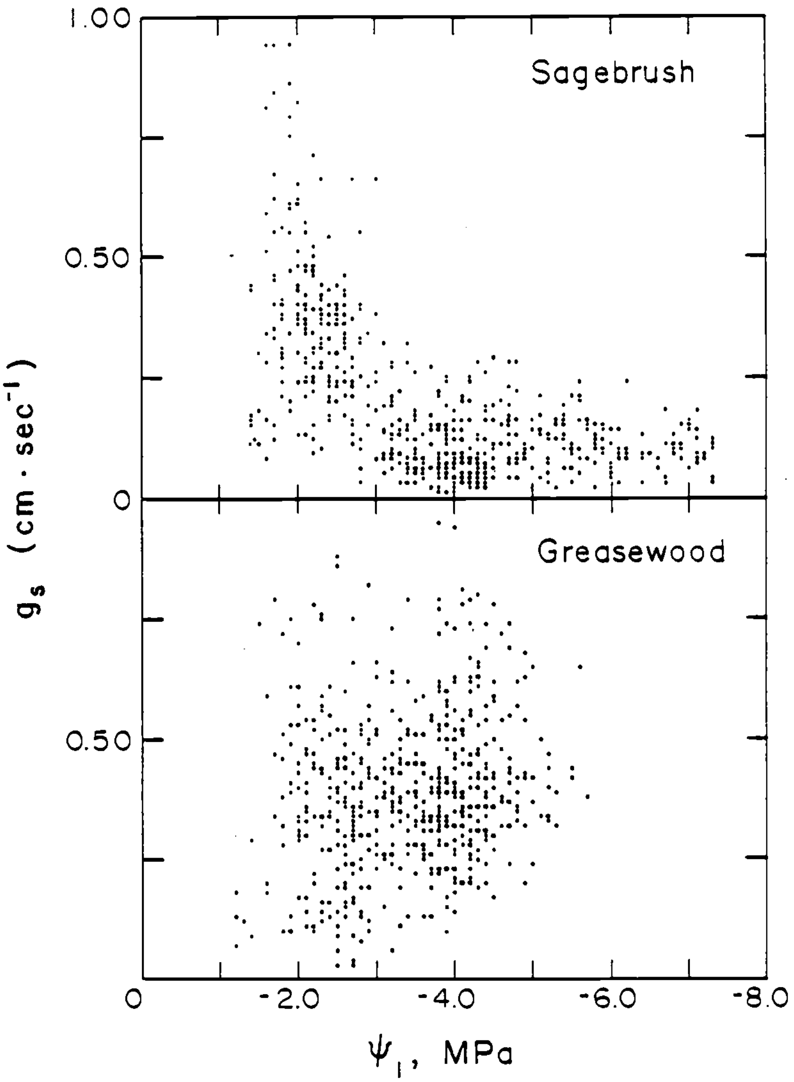

Figure V.8. The relationship between leaf water potential (ψ_1) and stomatal conductance (g_s) for sagebrush and greasewood at the North Harney and Coyote Buttes study sites in 1983.

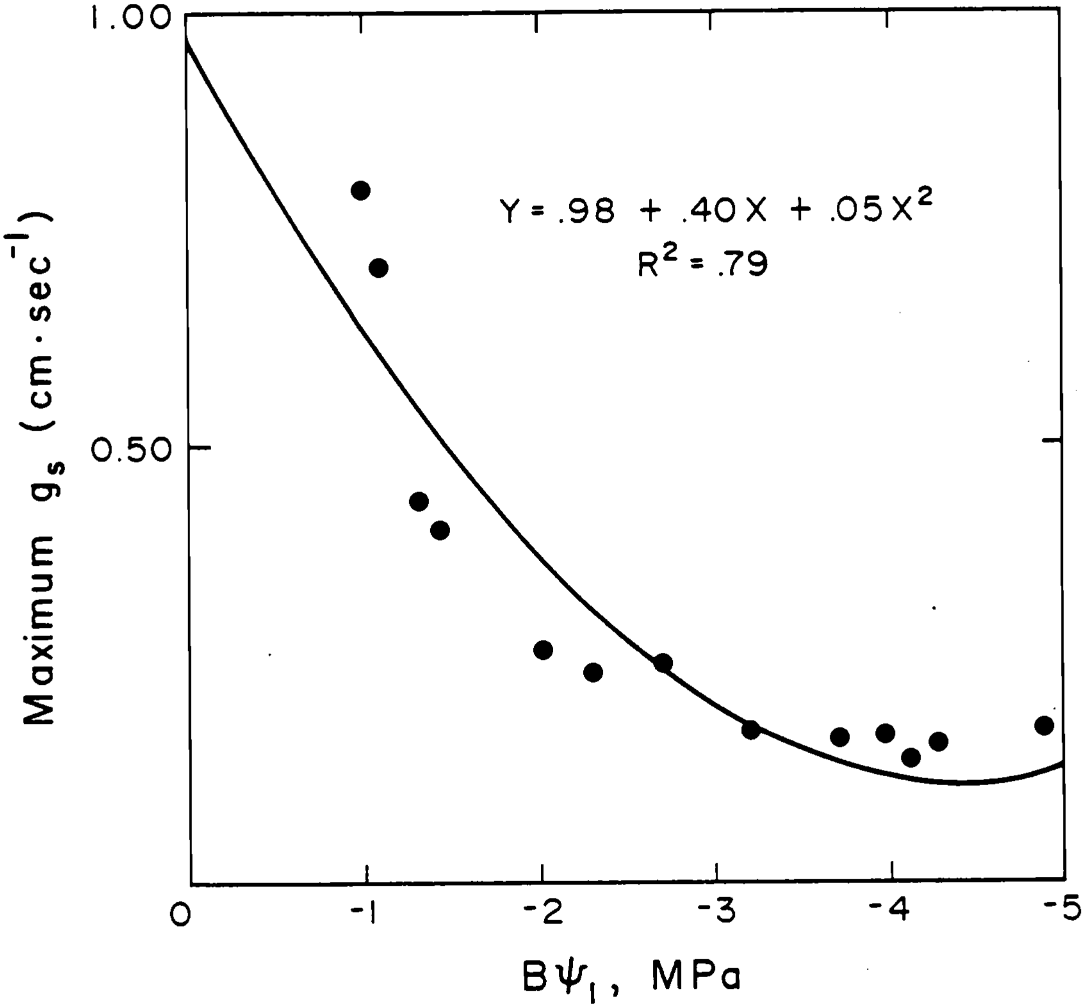

Figure V.9. Maximum stomatal conductance (g_s) as a function of $B\psi_l$ for sagebrush at the North Harney and Coyote Buttes study sites in 1983. Each point represents the mean of measurements on 8 plants.

to the time elapsed from sunrise until the time of day maximum g_s occurred for greasewood. The function in Figure V.10 implies low nighttime temperatures postponed stomatal opening in greasewood. The relationship between BT and the time of day maximum g_s occurred was not significant for sagebrush. This is probably due to the influence of low ψ_1. A more careful analysis, using plants with ψ_1 higher than -2.5 MPa, indicated a significant relationship (Figure V.10). The poor relationship for sagebrush may reflect the lack of measurements early in the season when ψ_1 was not limiting, or it may indicate stomates respond quickly after exposure to low temperatures. Sagebrush can indeed acclimate rapidly to prevailing environmental conditions (Mooney and West 1964; West and Mooney 1972).

Transpiration Flux

Depression of ψ_1 from $B\psi_1$ is a function of the water absorbed by roots, internal water storage, transpiration flux, and resistance to water conductance (Jarvis 1975). We examined the relationship between ψ_1 and J. The relationship between daily J and ψ_1 was not significant for either species. In sagebrush, ψ_1 decreased as J increased, but it remained nearly constant for greasewood. Internal water storage and variable R_{SPAC} are factors that

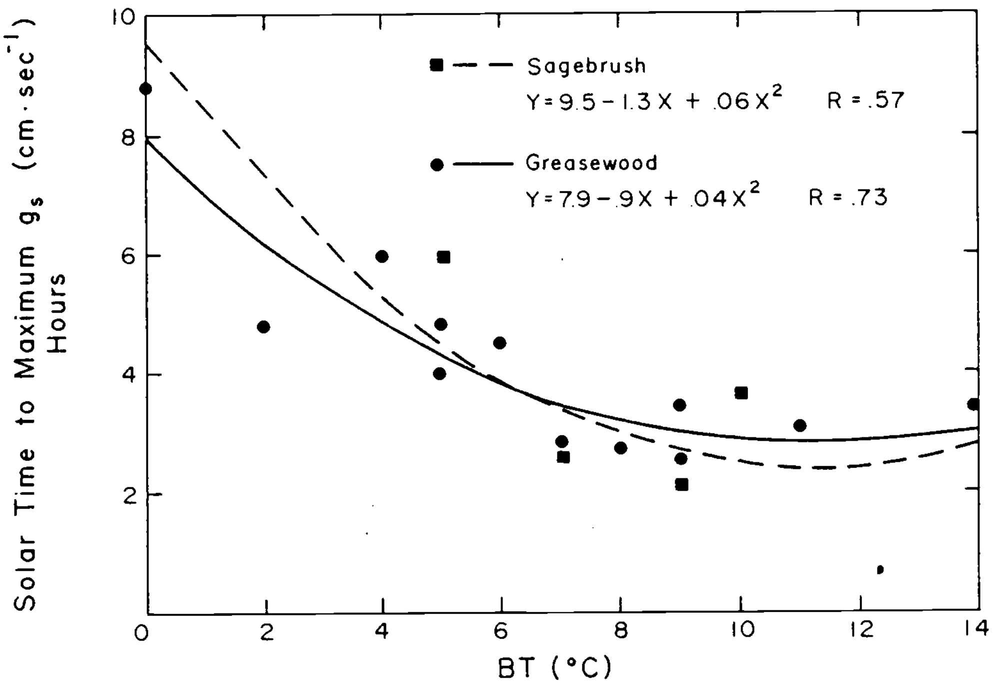

Figure V.10. The influence of temperature (BT) at the time of predawn leaf water potential determinations and solar hours to maximum stomatal conductance (g_s). Each point represents the mean of measurements from 8 plants. Sagebrush plants with predawn leaf water potentials higher than -2.5 MPa were used for analyses.

may contribute to this poor relationship (Jarvis 1975; Running 1980b).

R_{SPAC} was estimated for each plant on each day at the point of ψ_{1m} (Running 1980a). R_{SPAC} and $B\,\psi_1$ were significantly related for both species (Figure V.11). R_{SPAC} increased for both species as $B\,\psi_1$ decreased, however, it increased more rapidly for sagebrush than greasewood. Thus, the decline of soil water potential and soil conductivity, associated with drying soils, was a significant component in increasing resistance to water flux in sagebrush. On the other hand, R_{SPAC} increased slowly in greasewood as soils dried.

Multiple regression models were developed to describe transpiration rates for sagebrush and greasewood. The variables tested in the models were g_s, VPD, and R_{SPAC}.

Transpiration rate of greasewood was a function of VPD and g_s. The partial correlation coefficients for J with VPD and g_s were r = .66. R_{SPAC} was not significant in the model. When VPD and g_s were used in a multiple regression model, they explained 68 percent of the variation observed in J (Table V.3).

The transpiration rate of sagebrush was the product of g_s, VPD, and R_{SPAC}. Respective partial correlation coefficients for g_s, VPD, and R_{SPAC} were r = .64, r = .66,

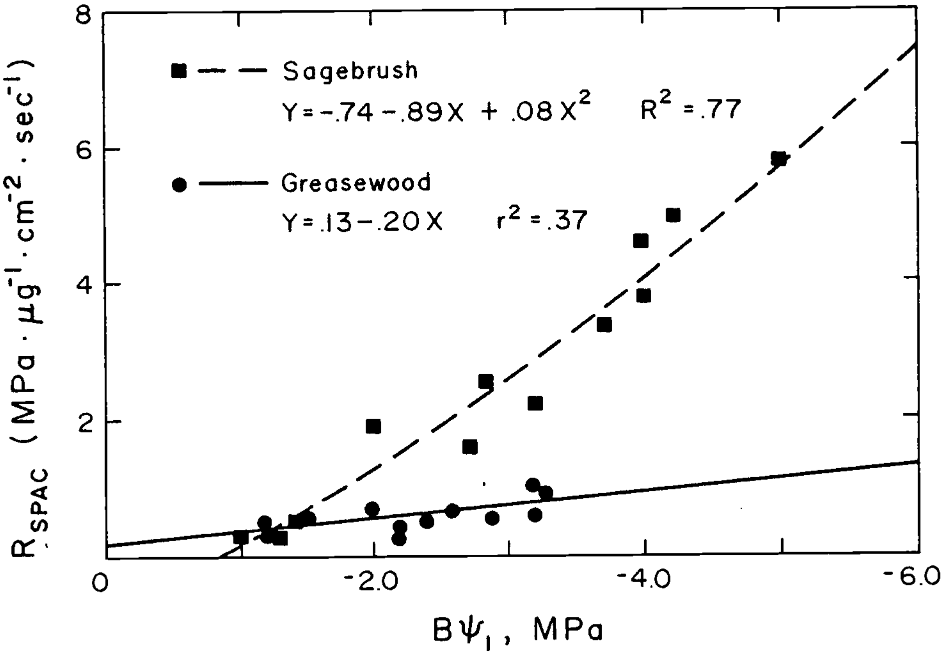

Figure V.11. The seasonal increase of resistance to water conductance in the soil-plant-atmosphere continuum (R_{SPAC}) as related to predawn leaf water potential for sagebrush and greasewood at the North Harney and Coyote Buttes study sites in 1983. Each point represents the mean of measurements from 8 plants.

and $r = .26$. These variables accounted for 69 percent of the variation observed in J (Table V.3).

Table V.3. Multiple regression equations describing observed transpiration in greasewood and Wyoming big sagebrush.

Greasewood

$Y = -1.77 + 5.78X_1 + 0.35X_2$ $R^2 = .68$ s.e. = 1.92

Wyoming big sagebrush

$Y = 1.28 + 8.98X_1 + 0.17X_2 - 0.65X_3$ $R^2 = .69$ s.e. = 1.40

Y = transpiration rate ($\mu g.cm^{-2}.sec^{-1}$)

X_1 = stomata conductance ($cm.sec^{-1}$)

X^2 = vapor pressure deficit ($\mu g.cm^{-3}$)

X_3 = R_{SPAC} ($MPa.\mu g^{-1}.cm^{-2}.sec^{-1}$)

Discussion

The water relations of sagebrush and greasewood are similar in some respects, yet there are striking differences, and they are manifest in time. Early in the season, species differences were not profound; but as the growing season progressed, and summer drought intensified, differences in diurnal water relations were amplified.

In a general sense, seasonal changes in the diurnal water relations of sagebrush were a phased response to atmospheric evaporative demand, resistance to water flux in the soil-plant-atmosphere continuum, and leaf water potential. Diurnal water relations of greasewood were modulated by atmospheric conditions.

The seasonal decline of ψ_1 of sagebrush is consistent with results in other studies (DePuit and Caldwell 1973; Branson and Shown 1975; Campbell and Harris 1977; Barker and McKell 1983), and seasonal trends of ψ_1 for greasewood were similar to the results of Detling and Klikoff (1973). Although greasewood is classified as a phreatophyte, it is interesting that $B\psi_1$ declined steadily through the season. Decline of $B\psi_1$ may be related to high resistance to conductance of water from the soil to leaves at low transpiration rates (Elfving et al. 1972), or it may be related to decreasing hydraulic conductivity of soils commensurate with decreasing soil moisture (Slatyer 1967). Our analysis did indeed indicate resistance to water flux increased as $B\psi_1$ of greasewood decreased through the season. Declining water absorbing capacity of roots may have also contributed to the increase in R_{SPAC} and the decrease in $B\psi_1$.

$B\psi_1$ of sagebrush and greasewood increased rapidly after precipitation was received. In late August, an increase in Bψ_1 was noted within 48 hours after it rained. Love and West (1972) also found ψ_1 of winterfat and shadscale increased rapidly after precipitation. However, DePuit and Caldwell (1973) noted a 1 to 2 week lag between rain and an increase in ψ_1 for sagebrush. Total precipitation and infiltration of moisture may play a role in the rate ψ_1 increases (Love and West 1972). Also, the moisture content of the soil prior to rainfall is probably important, and response should be less if soils are very wet or dry.

Early in the season, when soil moisture was not limiting, J, g_s, ψ_1, and R_{SPAC} were similar for sagebrush and greasewood. Although transpiration rates were high during spring and early summer, stomatal response to ψ_1 was not pronounced. During this period, stomata responded to VPD as described in the feedforward theory (Cowan 1977). Stomata of sagebrush and greasewood gradually closed when VPD exceeded approximately 10μg.cm^{-3}.

It is well established that stomata respond to changes in humidity, and this response has been observed in plants from diverse habitats (Lange et al. 1971; Johnson and Caldwell 1975; Kaufmann 1976; Mooney et al. 1983). Stomatal response to humidity may reflect an adaptation that prevents high rates of water loss when plants experience high evaporative demand (Hall et al.

1976). Sensitivity to VPD enables stomata to close and avoid development of severe leaf water deficits (Schulze et al. 1972), while simultaneously maximizing carbon gain (Cowan 1977). When soil moisture is not limiting, and stomata respond to VPD, leaf water may be replenished by mobilizing internal water reserves, or water may be rapidly absorbed by the roots (Jarvis 1975, 1976; Running 1980a).

As soil moisture declined during the summer, the relationship between gs and VPD diminished in sagebrush, but g_s was related to ψ_1. Despite an increase of $B\psi_1$ in sagebrush in late August, stomatal opening was low. Thus, in addition to changes in leaf morphology and age (DePuit and Caldwell 1973), the cumulative effects of water stress apparently modify stomatal behavior in sagebrush. Our model (Figure V.9) shows, the phase of ψ_1 control of g_s dominates, when $B\psi_1$ is lower than approximately -2.5 to -3.0 MPa. Since g_s remained below 0.20 cm.sec^{-1} in August and September we postulated stomates of sagebrush were nearly closed. If this postulation is valid, the function in Figure V.9 predicts stomata opening will be slight on days when $B\psi_1$ is lower than approximately -2.5 to -3.0 MPa. This closely agrees with results of Dina and Klikoff (1973), who reported net photosynthesis of sagebrush ceased when ψ_1 was about -3.0 MPa. The results of

Campbell and Harris (1977) also show g_s was less than 0.20 $cm.sec^{-1}$ at ψ_1 lower than approximately -2.0 to -3.0 MPa. By using $B\psi_1$ values determined in 1982 and 1983, the model predicts stomata closed approximately 2 weeks earlier at the Coyote Buttes site than at the North Harney site.

The function in Figure V.11 shows R_{SPAC} increases rapidly as $B\psi_1$ declines in sagebrush. The close relationship between $B\psi_1$ and R_{SPAC} indicates declining soil water potential and soil conductivity are major factors involved in the decrease of J and depression of ψ_1 from $B\psi_1$ levels. Therefore, J declined through the season from the combined effects of decreasing g_s and increasing R_{SPAC}. The increase in R_{SPAC} can be explained by at least three possible mechanisms.

First, although root growth of sagebrush shifts from the upper soil profile to greater depths with the progression of the season (Fernandez and Caldwell 1975), the water absorbing capacity of the root system may decline (Caldwell 1976). Second, hydraulic conductivity of soil decreases as soil dries (Slatyer 1967; Weatherly 1982). And third, as a result of low water absorbing capacity of the roots and decreased hydraulic conductivity in the soil, internal plant water storage declined as summer drought intensified and full storage capacity was not reached (Waring and Running 1976). The significance of internal water storage, in seasonal and diurnal water relations, is not understood for sagebrush. However, internal water storage is probably an important component of diurnal water relations, particularly in spring and early summer, when soil moisture is high.

The diurnal pattern of g_s for greasewood was dependent on temporally separated effects of T and VPD. Nighttime temperature and the rate VPD increased during the day, were major determinents in the degree of stomatal opening. This seemingly paradoxical response is, however, apparently offset by maintaining high transpiration rates, open stomata, and low R_{SPAC} over a wide range of conditions. Stomata remained open at temperatures as high as 36C and at VPD near $30 \mu g.cm^{-3}$. Stomata also remained open at leaf water potentials as low as -5.7 MPa. The ability to maintain high g_s, despite low leaf water potentials, may be related to changes in the osmotic potential of leaves (Turner 1979). Decrease in osmotic potential results in maintenance of bulk leaf turgor at low leaf water potentials (Jones and Turner 1978), and stomata may remain open. Greasewood is known to accumulate copius quantities of ions in its leaves, particularly sodium, which may be used for osmoregulation (Rickard 1965b, 1982; Wallace et al. 1973).

Osmoregulation is an aspect of physiology that should be examined in greasewood.

Sagebrush has developed the capacity to exploit soil moisture in time and thus its peak physiological activity is restricted to spring and early summer. The development of internal water deficits, as a result of the inability to exploit soil moisture in space, is a major limitation in its physiological activity. Distribution of sagebrush may be limited by the availability of soil moisture during spring and early summer.

Greasewood's seasonal pattern of stomatal conductance and transpiration is unlike most shrubs of the cool shrub steppe. The ability of greasewood to utilize readily available water or maintain high internal water reserves, is expressed in low R_{SPAC}, and high g_s and J, at low leaf water potentials. Greasewood can apparently exploit soil moisture in space, thereby curbing severe water deficts. The amount of time for optimal physiological activity may be a factor limiting distribution and growth of greasewood. Sensitivity of stomata to low temperatures may limit the period of carbon gain in greasewood. Thus, distribution of greasewood may be related to the intensity and frequency of low temperatures during the growing season.

Chapter VI

Summary

The environment of the sagebrush steppe is stressful to all stages of plant life cycles. Although the environment is defined as the sum of all external forces and substances affecting growth, structure, and reproduction of plants, it is usually feasible to study the effects of only one or a few factors (Billings 1952). This research was designed to evaluate the effects of water stress on germination and plant function.

Germination Studies

Germination of prostrate kochia was limited more by low temperatures than specific ions when seeds were incubated on saturated soils. However, germination was related to temperature and specific ions under conditions of water stress.

Prostrate kochia germinated well over a range of temperatures, water potentials, and salt concentrations. Total germination and rate of germination were highest at 20C and lower at 10 and 30C . Seed vigor appeared low at 30C, but it appeared high at the lower temperatures. Abnormal germination may be a problem during periods of water stress; however, in laboratory tests, this weakness was alleviated by germinating intact utricles. This observation should be examined further under field conditions.

Total germination of prostrate kochia was significantly reduced by declining water potentials, but it was not affected by sodium chloride; germination was stimulated by potassium chloride. Prostrate kochia appears tolerant of high salt concentrations during germination. However, since the period immediately following germination is the most critical time in establishment, studies should be designed to evaluate the effects of temperature, water stress, and specific ions on early seedling growth.

When greasewood was incubated on saturated soils, ions had no significant effect on germination percentage, but low temperatures limited germination. Results of the germination study of greasewood, in the presence of water stress and specific ions, suggest intra- and interpopulation differences in response to water stress and concentrations of sodium chloride and potassium chloride. Germination in sodium chloride and potassium chloride were similar, but germination of a portion of two populations was reduced by increasing salt concentration. Sensitivity of seeds to water potential and specific ions may be important for maintaining seed reserves, and may also function to restrict germination to periods when soil moisture is high and salt concentrations are low. Lowest concentrations of salts occur in the spring and presumably, these conditions are also near optimal for seedling growth.

A more accurate determination of ecotypic differentiation may be attained by including more areas for seed collection. Seeds should also be germinated from collections made in more than one year. Detailed field studies of population dynamics would also help verify laboratory studies.

Studies of Plant Water Relations

Since prostrate kochia has a seasonal pattern of gas exchange similar to indigenous species of the sagebrush steppe, it appears adapted to the climate. Spring and early summer appear as critical periods for growth. More accurate estimates of the adaptability of prostrate kochia can be achieved by determining physiological responses to a variety of conditions. The next phase of evaluating prostrate kochia should include a systematic approach to determine the genetic potential on a variety of sites.

The seasonal decline of transpiration in prostrate kochia appears related to increased resistance to water conductance in the soil-plant-atmosphere continuum and reduced stomatal conductance. Analyses indicated declining soil water potential was an important factor in lower transpiration rates and depression of leaf water potentials. Increasing resistance during the summer may also be related to declining water absorption capacity of roots. The exact cause of declining stomatal conductance was not determined, but aging of leaves and the water stress history of plants may be important.

Results obtained from the study of water relations in greasewood and sagebrush are in general agreement with previously published studies. Results show physiological activity of sagebrush is largely restricted to spring and early summer, and greasewood is active throughout the summer. Stomata of both species closed when vapor pressure deficits increased above approximately 10 $\mu g.cm^{-3}$. The seasonal decline of transpiration rates for sagebrush are related to modification of stomatal behavior by the decline of leaf water potentials, and increasing resistance to conductance of water in the soil-plant-atmosphere continuum. The seasonal decline of leaf water potential is coupled to declining soil moisture and may be related to the inability of roots to absorb adequate amounts of water.

Although greasewood is classified as a phreatophyte, it does not function as a simple conduit for movement of water from soil to the atmosphere. The physiological activity of greasewood is closely related to the aerial environment. Transpiration rates and stomatal conductance do not appear related to the bulk water status of leaves. This suggests there may be considerable osmotic adjustment in the leaves of greasewood. Osmotic adjustment would allow maintenance of turgor and stomatal opening in spite of low leaf water potentials. This aspect should be addressed in future research.

Nighttime temperatures and daytime vapor pressure deficits appear as important factors influencing stomatal behavior in greasewood. The intensity, frequency, and duration of summer nighttime temperatures may be a determinent in the distribution and growth of greasewood. Low nighttime temperatures coupled with warm and dry days may effectively reduce the period of carbon gain and thus reduce growth of greasewood.

Although the study of water relations of prostrate kochia was conducted on a site separate from those of greasewood and sagebrush, it is possible to compare results in a general way. The most outstanding feature in this comparison is the high rates of transpiration measured for prostrate kochia compared to greasewood and sagebrush. Because water may be the primary factor limiting growth and survival of plants in the sagebrush steppe, it may be necessary to select genotypes of prostrate kochia that use water more efficiently. Improving water use efficiency may extend the period of growth, increase production, and enhance survival. Variation associated with the high transpiration rates in prostrate kochia, suggest selection would be possible. Evaluation of photosynthesis-transpiration ratios would be useful for determining water use efficiency.

There is developing interest in mathematical modeling of water use by plants of rangelands. However, without an estimate of water capacitance in plants, and resistance to water flux in the soil-plant-atmosphere continuum, as affected by soil water potential and soil temperature, models will have low accuracy in predicting water use. These aspects should be determined in future studies.

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Appendices

Appendix A

Canopy cover of shrubs and frequency of shrubs, grasses, and forbs at the North Harney, South Harney, Coyote Buttes, and Saddle Butte Study Sites.

Table A 1. Canopy cover of shrubs and frequency of shrubs, grasses, and forbs at the North Harney study site. Canopy cover and frequency of shrubs were determined from line intercept. Frequency of grasses and forbs was determined from 0.10 m^2 quadrats.

	Canopy Cover (%)	Frequency (%)
Shrubs		
Artemisia spinescens	0.1	2.5
Artemisia tridentata subsp. *wyomingensis*	6.8	80.0
Atriplex confertifolia	0.2	7.5
Chrysothamnus viscidiflorus subsp. *viscidiflorus*	0.8	5.0
Grayia spinosa	0.4	12.5
Kochia americana	0.1	2.5
Sarcobatus vermiculatus	18.9	97.5
Grasses		
Agropyron smithii	-	16.0
Bromus tectorum	-	88.0
Elymus cinereus	-	0.1
Oryzopsis hymenoides	-	2.0
Sitanion hystrix	-	86.0
Forbs		
Lepidium perfoliatum	-	100.0

Table A 2. Canopy cover of shrubs and frequency of shrubs, grasses, and forbs at the South Harney study site. Canopy cover and frequency of shrubs were determined from line intercept. Frequency of grasses and forbs was determined from 0.10 m^2 quadrats.

	Canopy Cover(%)	Frequency (%)
Shrubs		
Atriplex confertifolia	0.1	7.5
Grayia spinosa	0.1	5.0
Sarcobatus vermiculatus	26.7	97.5
Suaeda intermedia	0.6	15.0
Grasses		
Bromus tectorum	-	70.0
Sitanion hystrix	-	86.0
Forbs		
Atriplex argentea	-	1.0
Lepidium perfoliatum	-	100.0

Table A 3. Canopy cover of shrubs and frequency of shrubs, grasses, and forbs at the Coyote Buttes study site. Canopy cover and frequency of shrubs were determined from line intercept. Frequency of grasses and forbs was determined from 0.10 m^2 quadrats.

	Canopy Cover(%)	Frequency (%)
Shrubs		
Artemisia tridentata subsp. *wyomingensis*	7.7	85.0
Atriplex confertifolia	0.1	2.5
Chrysothamnus nauseosus subsp. *consimilis*	12.5	92.5
Grayia spinosa	0.1	5.0
Sarcobatus vermiculatus	15.7	85.0
Grasses		
Bromus tectorum	-	81.0
Distichlis stricta	-	8.0
Elymus cinereus	-	13.0
Sitanion hystrix	-	90.0
Forbs		
Lepidium perfoliatum	-	76.0

Table A 4. Canopy cover of shrubs and frequency of shrubs, grasses, and forbs at the Saddle Butte study site. Canopy cover and frequency of shrubs were determined from line intercept. Frequency of grasses and forbs was determined from 0.10 m^2 quadrats.

	Canopy Cover (%)	Frequency (%)
Shrubs		
Artemisia tridentata subsp. *wyomingensis*	0.1	2.5
Artemisia spinescens	0.7	2.8
Artiplex confertifolia	2.9	42.5
Chrysothamnus viscidiflorus subsp. *viscidiflorus*	0.3	2.5
Grayia spinosa	8.6	77.5
Sarcobatus vermiculatus	17.1	97.5
Tetradymia spinosa	0.1	2.5
Grasses		
Bromus tectorum	-	96.0
Oryzopsis hymenoides	-	2.0
Poa nevadensis	-	22.0
Sitanion hystrix	-	60.0
Forbs		
Lepidium perfoliatum	-	58.0

Appendix B. Soil profile descriptions for the North Harney, South Harney, Coyote Buttes, and Saddle Butte study sites.

Table B 1. Soil Profile description for the North Harney Study Site.

Fine-loamy, mixed, mesic Xerollic Haplargid

A1 1 to 13 cm; light brownish gray (10YR 6/2) silty clay loam, very dark gray brown (10YR 3/2) moist; weak coarse platy structure; soft, very friable, slightly sticky and plastic; common very fine and medium roots and many very fine discontinous and vesicular pores; moderately alkaline (pH 8.0); abrupt smooth.

BAtk 13 to 62 cm; light brown (7.5 YR 6/4) silty clay (7.5 YR 5/4) moist; moderate coarse platy structure; very hard, friable, sticky and plastic; many very fine and fine roots and few medium roots and common very fine vesicular and many very fine tubular roots; many very dark grayish brown (10 YR 3/4) moderately thichk clay films on ped faces and pores; secondary lime on about 10 percent of ped faces; strongly effervescent; moderately alkaline (pH 8.2); abrupt wavy boundary.

2Bk 62 to 73 cm; brown (10 YR 5/3) sandy clay loam, dark brown (10 YR 4/3) moist; massive structure; hard, friable, slightly sticky and plastic; common very fine, fine, and medium roots and common very fine pores; pores filled with secondary lime very pale brown (10 YR 7/3) slightly effervescent; moderately alkaline (pH 8.0) abrupt wavy boundary.

2C1k 73 to 108 cm; brown (10 YR 5/3) sandy loam, brown (10 YR 4/3) moist; massive structure; hard, firm, slightly sticky and plastic; few very fine and coarse roots and few very fine pores; moderately alkaline (pH 8.0) abrupt wavy boundary.

3C2 108 to 133 cm; grayish brown (10 YR 5/2) silty clay loam, dark grayish brown (10 YR 4/2) moist; massive structure; soft, friable, slightly sticky and plastic, few very fine pores; moderately alkaline (pH 8.0)

Table B 2. Soil Profile description for the South Harney Study Site.

Fine-loamy, mixed, mesic Xerollic Camborthid

A1 0 to 8 cm; pale brown (10 YR 6/3) loam, dark brown (10 YR 3/3) moist; weak coarse platy structure parting to weak fine platy; soft, friable, slightly sticky and plastic; many very fine and common fine roots and many very fine and few fine vesicular pores; moderately alkaline (pH 8.0); abrupt smooth boundary.

BKt+1 8 to 28 cm; pale brown (10 YR 6/3) loam, dark brown (10 YR 4/3) moist; weak medium subangular blocky structure; soft, friable, slightly sticky and plastic; common fine roots and common very fine vesicular pores; few thin clay films on ped faces; moderately alkaline (pH 8.2); abrupt smooth boundary.

B2 28 to 50 cm; pale brown (10 YR 6/3) loam, darek brown (10 YR 4/3) moist; massive structure; slightly hard, firm, slightly sticky and plastic; few very fine roots; strongly ef-fervescent; moderately alkaline (pH 8.2); abrupt smooth boundary.

2BKt3 50 to 120 cm; pale brown (10 YR 6/3) clay loam, brown (10 YR 5/3) moist; weak medium subangular blocky structure; slightly hard, firm, slightly sticky and plastic; few very fine roots and common very fine tubular and vesicular pores; strongly effervescent; moderately alkaline (pH 8.2); abrupt smooth boundary.

Table B 3. Soil Profile description for the Coyote Buttes Study Site.

Fine montmorillonitic, mesic Xerollic Haplargid

A1 0 to 21 cm; grayish brown (10 YR 5/2) silt loam; dark grayish brown (10 YR 4/2) moist; weak medium platy structure parting to weak fine platy; soft very friable, slightly sticky and plastic, common very fine roots and many very fine vesicular pores; moderately alkaline (pH 8.2) abrupt smooth boundary.

Bt1 21 to 48 cm; light gray (10 YR 7/2) clay, very dark brown (10 YR 2/2) moist; moderate coarse prismatic structure parting to weak medium angular blocky; slightly hard, firm, sticky and plastic; common very fine and few medium roots and common very fine tubular pores; moderately alkaline (pH 8.4); abrupt smooth boundary.

Bt2 48 to 66 cm; dark grayish brown (10 YR 4/2) silty clay, very dark brown (10 YR 2/2) moist; weak medium subangular blocky and plastic; common very fine and few medium roots and common very fine tubular and vesicular pores; moderately alkaline (pH 8.4); abrupt smooth boundary.

Bt3 66 to 74 cm; brown (10 YR 5/3) clay, dark grayish brown (10 YR 4/2) dry; weak medium subangular blocky structure; slightly hard, firm, sticky and plastic; few medium and fine roots; secondary lime on 10 percent of one surface (white(10YR 8/2)); slightly effervescent; moderately alkaline (pH 8.0); abrupt smooth boundary.

BC 74 to 113 cm; pale brown (10 YR 6/3) loam, brown (10 YR 8/2) moist; weak medium subangular blocky structure; slightly hard, firm, sticky and plastic; few very fine and fine roots; strongly effervescent; moderately alkaline (pH 8.4); abrupt smooth boundary.

C 113 to 143 cm; pale brown (10 YR 6/3) loam, brown (10 YR 5/3) moist; massive structure; hard, firm, slightly sticky and plastic; common fine irregular shaped yellow (10 YR 7/6) nodules; strongly effervescent; moderately alkaline (pH 8.4).

Table B 4. Soil profile description for the Saddle Butte Study Site.

Coarse-loamy, mixed, mesic Xerollic Haplargid

A1 0 to 15 cm; light gray (10 YR 7/2) loam; dark grayish brown (10 YR 4/2) moist; weak coarse platy structure parting to weak fine platy; soft, friable, slightly sticky and plastic; few fine roots and common very fine and fine vesicular pores; slightly effervescent; moderately alkaline (pH 8.0) abrupt smooth boundary.

BA 15 to 33 cm; light brownish gray (10 YR 6/2) loam; dark gray brown (10 YR 4/2) moist; weak medium subangular blocky structure; soft, friable, slightly sticky and plastic; common very fine and few fine roots and common very fine and fine vesicular pores; stongly effervescent; moderately alkaline (pH 8.4) abrupt smooth boundary.

BK1 33 to 60 cm; gray brown (10 YR 5/2) loam, dark grayish brown (10 YR 4/2) moist; weak medium angular blocky structure; slightly hard, friable slightly sticky and plastic; common very fine and few fine roots, and common very fine and fine vesicular pores; strongly effervescent; moderately alkaline (pH 8.4); abrupt smooth boundary.

BKt2 60 to 73 cm; light brownish gray (10 YR 6/2) clay loam, very dark grayish brown (10 YR 3/2) moist; weak medium subangular blocky structure; slightly hard, friable, slightly sticky and plastic; few very fine and medium roots and common very fine and fine pores; strongly effervescent; moderately alkaline (pH 8.0); abrupt smooth boundary.

BKt3 73 to 104 cm; light brownish gray (10 YR 6.2) loam, very dary grayish brown (10 YR 3/2) moist; massive structure; slightly hard, friable slightly sticky and plastic; few thin gray brown (10 YR 5/2) clay films on ped faces; strongly effervescent; moderately alkaline (pH 8.4).

Appendix C. Soil profile description of the soils at the Squaw Butte nursery.

Coarse-loamy, mixed, frigid Orthidic Durixeroll

A--0 to 10 cm; grayish brown (10YR 5/2) fine sandy loam, dark brown (10YR) 3/3) moist; moderate thick platy structure; slightly hard, friable, nonsticky, nonplastic; common very fine and fine roots; common very fine and fine vesicular pores; 5 percent pebbles; noneffervescent; neutral (pH 7.2); abrupt smooth boundary.

AB--10 to 20 cm; brown (10YR 5/2) fine sandy loam, dark brown (10YR 3/3) moist; moderate medium subangular blocky structure parting to moderate fine granular structure; slightly hard, very fiable, nonsticky, nonplastic; common very fine and fine roots; common very fine tubular pores; 5 percent pebbles; noneffervescent; neutral (pH 7.2); clear smooth boundary.

Bw--20 to 33 cm; brown (10YR 5/3) loam, dark brown (10 YR 3/3) moist; moderate medium subangular blocky structure; slightly hard, friable, slightly sticky, slightly plastic; common very fine and fine roots; common very fine tubular pores; 5 percent pebbles; noneffervescent; neutral (pH 7.2); clear wavy boundary.

B4--33 to 53 cm; pale brown (10 YR 6/3) loam, dark brown (10 YR 3/3) moist; massive; hard, friable, slightly sticky, slightly plastic; few very fine roots; very few very fine tubular pores; 25 percent weakly silica cemented masses; 10 percent pebbles; noneffervescent; mildly alkaline (pH 7.6); clear wavy boundary.

2BCq--53 to 76 cm; pale brown (10 YR 6/3) gravelly sandy loam, dark brown (10 YR 3/3) moist; massive; soft, very friable, nonsticky, nonplastic; common very fine and fine roots; common very fine tubular and interstitial pores; 20 percent weakly or strongly silica and lime cemented masses; few very fine lime concretions and common thin and moderatley thick lime coatings on the undersides of rock fragments; 25 percent pebbles and 5 percent cobbles; strongly effervescent; moderately alkaline (pH 8.0); abrupt irregular boundary.

3Cgkm--76 to 90 cm; very pale brown (10YR 7/3) strongly cemented boccly duripan, light yellowish brown (10 YR 6/4) moist; massive with continuous 2 to 20 mm indurated laminations forming all upper cap and interlayers within strongly cemented strata; extremely hard, extremely firm; strongly effervescent.

R--68 cm; hard basalt bedrock with a 2 inch weathered and fractured zone forming the upper contact.

Appendix D. Predawn leaf water potentials ($B\psi_1$) of *Sarcobatus vermiculatus* at the North Harney, Coyote Buttes, South Harney, and Saddle Butte study sites in 1983. Each value is the mean of ten measurements.

	Study Site							
Date	North Harney		Coyote Buttes		South Harney		Saddle Butte	
	$B\psi_1$ (-MPa)							
	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
13 May	1.64	0.15	1.54	0.15	1.72	0.15	1.70	0.14
26 May	1.35	0.11	1.35	0.18	1.35	0.20	1.35	0.15
15 June	1.44	0.21	1.47	0.09	1.46	0.13	1.38	0.12
24 June	1.69	0.19	1.63	0.14	1.48	0.24	1.41	0.18
11 July	1.54	0.21	1.74	0.18	1.76	0.45	1.85	0.39
26 July	2.35	0.25	2.27	0.14	2.55	0.48	2.31	0.18
12 August	2.27	0.28	2.32	0.33	2.54	0.53	2.45	0.24
27 August	2.16	0.28	2.13	0.21	2.51	0.41	2.36	0.34
17 September	2.76	0.37	2.92	0.29	2.61	0.54	2.45	0.47
3 October	3.52	0.19	3.38	0.18	3.58	0.79	3.42	0.55

Appendix E

Diurnal course of temperature (T), vapor pressure deficit (VPD), photosynthetically active radiation (PAR), wind, leaf water potential (ψ_l), stomata conductance (g_s), and transpiration (J) of *Artemisia tridentata* subsp. *wyomingensis* and *Sarcobatus vermiculatus* at the Coyote Buttes study site.

Table E 1.

						Artemisia			Sarcobatus		
Date	Time	T	VPD	PAR	Wind	ψ_l	g_s	J	ψ_l	g_s	J
		(C)	($\mu g.cm^{-3}$)	($\mu E.m^{-2}.sec^{-1}$)	($m.sec^{-1}$)	(MPa)	($cm.sec^{-1}$)	($\mu g.cm^{-2}.sec^{-1}$)	(MPa)	($cm.sec^{-1}$)	($\mu g.cm^{-2}.sec^{-1}$)
June 10	0400	8	2.8	0	0.1	-1.1	-	-	-1.5	-	-
	0630	18	9.1	1490	2.4	-1.9	.98	7.1	-2.3	.55	5.6
	0900	19	9.7	360	2.4	-1.9	.50	4.9	-2.0	.39	4.5
	1100	20	9.8	300	4.8	-1.6	.47	4.5	-2.1	.41	3.7
June 17	0400	10	5.4	0	0.5	-1.3	-	-	-1.5	-	-
	0700	19	9.1	190	0.5	-1.7	.36	3.3	-1.9	.47	4.2
	0830	22	11.6	650	3.6	-2.1	.43	4.8	-2.1	.57	7.1
	0900	27	18.6	640	6.0	-2.2	.36	6.8	-2.5	.34	5.7
	1100	31	26.3	1930	6.0	-2.5	.30	8.0	-2.8	.38	10.3
	1300	32	29.4	2110	7.2	-2.5	.30	8.9	-2.9	.33	8.5
	1500	27	21.5	470	8.3	-2.3	.26	5.5	-2.4	.22	6.0
	1700	25	17.9	480	7.2	-2.2	.28	5.0	-2.5	.14	3.0
July 19	0400	9	4.2	0	0.2	-2.7	-	-	-2.2	-	-
	0600	18	11.1	1390	0.2	-3.2	.24	2.6	-3.1	.53	5.6
	0800	24	17.5	2060	0.5	-3.8	.23	4.1	-3.9	.87	18.2
	1000	28	24.2	2070	2.1	-3.9	.12	3.0	-4.1	.46	10.0
	1200	29	26.0	2100	1.4	-3.6	.12	3.1	-3.9	.38	9.2
	1400	31	29.9	370	2.6	-3.7	.08	2.4	-3.5	.37	8.5
	1600	27	22.2	670	1.2	-3.6	.08	1.8	-3.7	.33	10.2
	1800	27	21.2	660	0.7	-3.5	.09	1.9	-3.7	.28	5.0
August 12	0500	5	1.6	0	0.2	-3.7	-	-	-2.6	-	-
	0600	12	5.0	1310	0.2	-3.9	.22	0.5	-2.8	.07	0.4
	0800	20	9.8	2010	0.2	-4.8	.17	1.6	-3.8	.40	4.0
	1000	24	15.8	2080	0.7	-4.8	.14	2.2	-4.4	.53	7.6
August 26	0500	7	0.9	0	0.2	-2.3	-	-	-2.4	-	-
	0600	8	1.3	1030	0.2	-2.4	.25	0.9	-2.5	.45	0.8
	0800	19	8.6	1750	0.7	-3.2	.14	1.2	-3.3	.42	3.1
	1000	23	13.3	2040	1.7	-3.7	.17	2.3	-4.1	.58	7.0
	1200	26	18.3	2110	1.2	-3.7	.13	2.4	-4.6	.41	8.0
	1400	26	19.0	2050	1.4	-3.7	.11	2.1	-4.2	.44	7.9
	1600	27	20.0	1720	1.2	-3.6	.10	1.9	-4.5	.39	7.4

Table E 1. (Continued).

						Artemisia			Sarcobatus		
Date	Time	T (C)	VPD ($\mu g.cm^{-3}$)	PAR ($\mu F.m^{-2}.sec^{-1}$)	Wind ($m.sec^{-1}$)	ψ_1 (MPa)	g_s ($cm.sec^{-1}$)	J ($\mu g.cm^{-2}.sec^{-1}$)	ψ_1 (MPa)	g_s ($cm.sec^{-1}$)	J ($\mu g.cm^{-2}.sec^{-1}$)
September 16	0500	5	3.4	0	0.2	-4.0	-	-	-3.2	-	-
	0600	15	7.0	1190	0.5	-4.3	.20	1.4	-3.3	.43	2.6
	0800	19	11.0	1840	0.7	-5.2	.21	2.3	-4.3	.73	7.2
	1000	23	15.9	2090	1.4	-5.6	.13	2.1	-4.8	.64	9.6
	1200	28	23.6	2140	2.4	-5.3	.08	1.8	-4.8	.46	9.6
	1400	30	28.2	1930	3.6	-5.2	.05	1.4	-4.9	.32	8.3
	1600	29	24.8	1600	3.8	-5.2	.06	1.5	-4.8	.37	8.9
October 2	0500	2	1.1	0	0.2	-4.9	-	-	-3.2	-	-
	0700	9	4.2	1080	1.4	-5.0	.17	0.7	-3.4	.34	1.5
	0900	14	8.0	1750	2.4	-6.0	.16	1.3	-3.9	.43	2.9
	1100	17	10.7	2250	2.4	-6.9	.13	1.4	-3.9	.41	4.2
	1300	19	12.2	2150	3.8	-6.6	.09	1.2	-4.2	.36	4.0
	1500	20	13.5	1950	3.8	-6.5	.11	1.4	-4.0	.34	4.4