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AUTECOLOGY OF *Atriplex canescens* (PURSH) NUTT. IN SOUTHWESTERN UNITED STATES

by
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Bachelor of Science, University of California-Irvine, 1974

A Dissertation
Submitted to the Graduate Faculty
of the
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in partial fulfillment of the requirements
for the degree of
Doctor of Philosophy

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December
1980

This Dissertation submitted by Roger W. Ruess in partial fulfillment of the requirements for the Degree of Doctor of Philosophy from the University of North Dakota is hereby approved by the Faculty Advisory Committee under whom the work has been done.

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This Dissertation meets the standards for appearance and conforms to the style and format requirements of the Graduate School of the University of North Dakota, and is hereby approved.

A. William Johnson
Dean of the Graduate School

Permission

Title: AUTECOLOGY OF *Atriplex canescens* (PURSH) NUTT. IN SOUTHWESTERN UNITED STATES

Department: BIOLOGY

Degree: DOCTOR OF PHILOSOPHY

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Signature Ger Warren Lucas

Date 21 July 1980

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ABSTRACT

Atriplex canescens, a facultatively evergreen dioecious shrub inhabiting cold and warm winter deserts of western United States, was studied at four sites in the Great Basin. The species was commonly a co-dominant in communities throughout its distribution, and was frequently found with other members of the Chenopodiaceae and members of Compositae. It was found to resprout vigorously and experiments indicated that seeds from all sites germinated easily in wetted, well aerated soil. The mean plant size ranged from 0.62±0.48 to 7.05±2.19 m^3. Density and cover ranged from 400 to 1.022 X 10^3 plants ha^{-1}, and from 5.7 to 38.4% of the ground space, respectively.

Atriplex canescens had a significant influence on the chemical and physical properties of the soil. Vegetated soils had significantly higher moisture content, organic matter, electrical conductivity, alkaline earth carbonates, nitrogen, potassium, sodium, calcium, magnesium and manganese than unvegetated soils. Both organic matter and nitrogen of unvegetated soils from the four study sites were typical of semiarid environments, generally below 0.7 and 0.03%, respectively. Fertile islands beneath the shrub canopies provided microclimates favorable to the growth of ephemeral grass species.

Major cations in plant parts were in the order K > Ca > Mg > Na. Concentrations of these cations in plant parts decreased thus: leaves, fruits, twigs, middle and old growth. The mean of major cations in leaf tissue was 317.96±42.78 me 100 g^{-1} dry weight. Major anions in leaf tissue followed the order $Cl > C_2O_4 > N > P$. The mean sum of major anions in leaf tissue was 116.15±15.54 me 100 g^{-1} dry weight. High K/Na ratios were found in plant tissue, in contrast to low K/Na ratios in unvegetated soils. Leaf chloride content of *Atriplex canescens* was negatively correlated with total oxalate but positively correlated with the sum of major cations in the leaf.

Water potential (ψ) measurements of *Atriplex canescens* at Tipton revealed a range of -15.5 to -45.1 bars. Minimum values coincided with the lowest air and soil temperatures, maximum with the greatest atmospheric evaporative demand. Change in ψ exceeded 12 bars hr^{-1} during periods of rapidly moving storm systems. Changes in ψ appeared to be independent of plant size, age, sex and the spatial location of plants. Chemical analyses revealed that expressed sap was up to three times more concentrated at high than at low ψ. The increase in water movement accounted for the dilution of the concentration of sap solutes. Together, K, Ca, Mg and Na contributed 58% of the mean osmolality of the expressed sap; the dominant ions, however, were K and Cl.

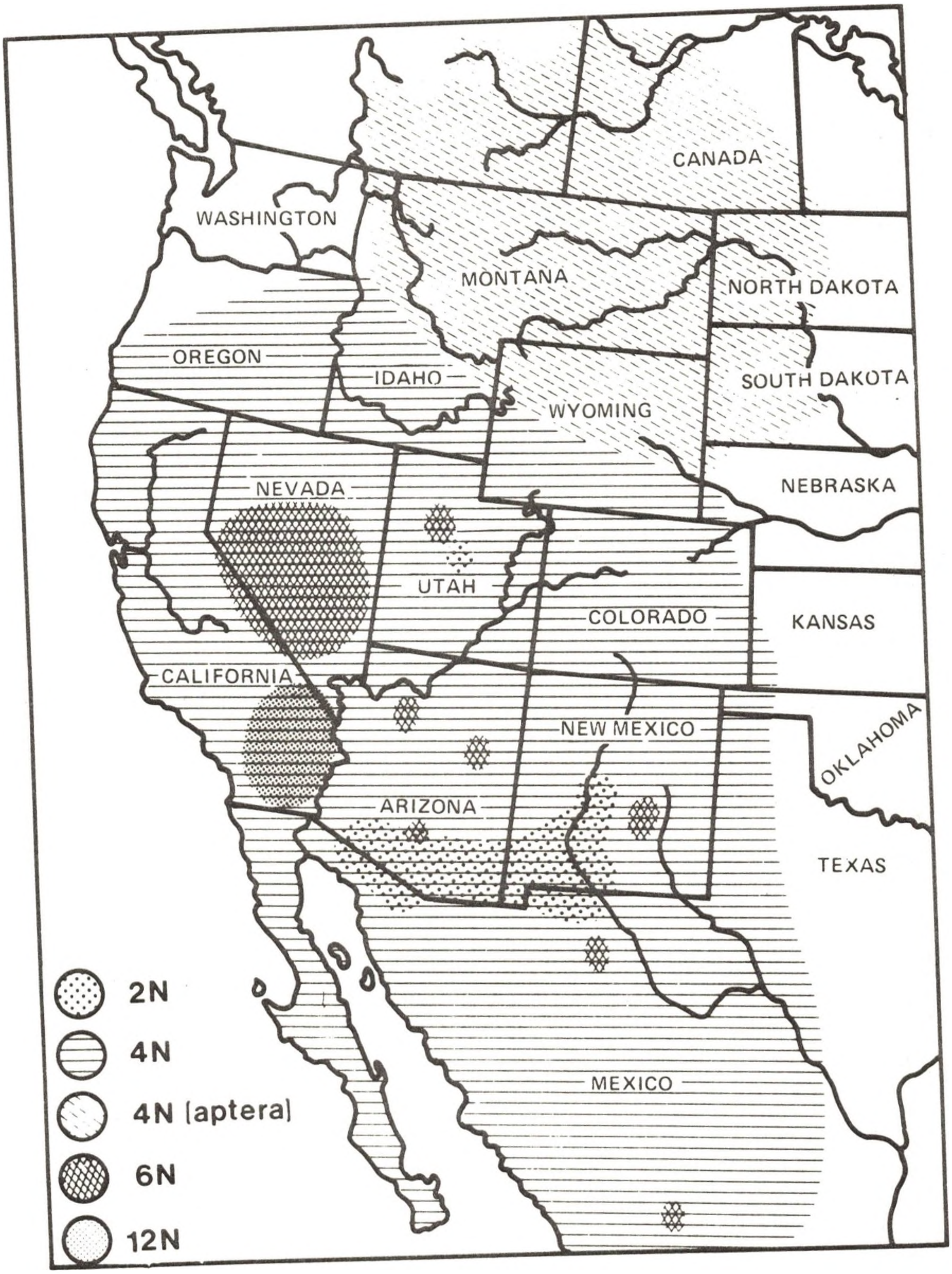
Productivity of *Atriplex canescens* at southern warm-desert sites was significantly greater than that at the cold-desert locations. Net annual productivity estimated from species-specific prediction equations ranged from 0.203 X 10^3 to 2.482 X 10^3 kg ha^{-1} yr^{-1}. Potassium had the highest rate of return of any single element in plant litter. Rates of potassium mobilization from leaf litter at the cold-desert site ranged from 3.94 to 11.12 g K yr^{-1}. Data suggest that K and N, and possibly other elements are redistributed to other plant parts from leaves prior to leaf senescence.

INTRODUCTION

Shrubs are the dominant vegetation over a considerable portion of the arid and semiarid regions of the world. Their success in these regions is attributable to physiological, morphological and reproductive adaptations which have co-evolved with the xeric landscapes. Through mechanisms of both tolerance and avoidance, desert shrubs have been able to circumvent the influences of physical and physiological drought, and invade habitats inhospitable to most other species. The economy of water is achieved by both a deep and extensive root system, which allows them to acquire water from deeper strata, from a larger mass of soil, and from surface layers infrequently wetted. The development of an extensive root system has also resulted in a relatively low shoot/root ratio. A sensitive mechanism for stomatal closure--relying on shrub responses to moisture stress--helps minimize water loss during periods of growth. The cooling benefit accrued from transpiration of water is maximized by other leaf adaptations. The small sclerophyllous, scurfy leaves of many desert shrubs have high surface to volume ratios; are lightly colored to increase heat energy reflection; and are oriented in order to minimize the drying effects of direct radiation.

Atriplex canescens (Pursh) Nutt., fourwing saltbush, is an important component of semiarid and arid environments in western United States (Fig. 1). Although some physical and physiological factors affecting localized populations of the species have been reported (Wallace, Romney and Hale 1973), comparative studies of several populations are few. Due

Fig. 1: Distribution and ploidy levels of *Atriplex canescens* (Pursh) Nutt. in western United States (from Stutz and Sandersen 1979).


CANADA
WASHINGTON
MONTANA
NORTH DAKOTA
OREGON
IDAHO
SOUTH DAKOTA
WYOMING
NEVADA
NEBRASKA
UTAH
COLORADO
KANSAS
CALIFORNIA
NEW MEXICO
OKLAHOMA
ARIZONA
TEXAS
MEXICO
2N
4N
4N (aptera)
6N
12N

to the increasing demand for information regarding the ecology of some of the more important species used in the revegetation of man or naturally disturbed semiarid landscapes, the present investigation was undertaken in an effort to more clearly understand the (1) productivity, (2) plant-soil nutrient interactions, and (3) water relations of *Atriplex canescens*.

Taxonomic Considerations

The genus *Atriplex* is composed of approximately 200 herbaceous and shrubby species, 17 of which are found in the northern deserts of the United States. The genus is the largest member of Chenopodiaceae, a family of cosmopolitan distribution inhabiting xeric and halophytic environments. *Atriplex canescens* (Pursh) Nutt., has by far the most extensive distribution of any of the shrubby species in the genus. It is found from dry plains to hillsides attaining altitudes of 2200 m on sandy and to moderately saline soils throughout the western portion of the United States and northern Mexico. The center of its distribution is in the central Great Basin, although the species extends into the mixed-prairie regions of Nebraska, Kansas, and Oklahoma; the intermountain regions of Montana, Idaho, and eastern Oregon; the Mohave and Sonoran deserts, and south into Baja California, Sinaloa and Zacatecas (Wallace and Romney 1972) (Fig. 1).

The shrubs are woody, to 2.5 m high, in elliptical or cylindrical mounds with stout terete branches. Leaves are evergreen or deciduous, alternate, scurfy, basal with entire margins, linear-spatulate to oblong, 2-8 mm wide, and 1.5-5.0 cm long. Plants are predominantly dioecious, although monoecious plants are common (Stutz et al. 1975). Pistillate flowers are borne in dense panicles or leafy-bracted spikes. Staminate flowers are yellow, in glomerules 2-3 mm wide, in dense nearly leafless terminal spikes and panicles. Such a reduction of floral parts to the bare essentials or nondescript foliage is a relatively advanced character common among other desert flora (Hall and Clements 1923). Flowering begins in May and may continue through July depending on elevation, latitude and the ecotype. The fruit is a utricle, dispersed by wind and gravity from late fall to the following May.

Atriplex canescens freely hybridizes in the northern deserts with several other *Atriplex* species including *A. confertifolia, A. cuneata, A. buxifolia, A. flacata*, and *A. acanthocarpa.* Two of these hybrids are recognized as separate species (Hanson 1962). *Atriplex canescens* exhibits great morphological variation, with a number of variants. Several subspecies have been recognized, the most notable being ssp. *linearis*, distributed widely throughout the Colorado and Sonoran deserts (Jepson 1951, Shreve and Wiggins 1964).

Populations of *Atriplex canescens* are autotetraploids (4N=36) predominantly, however, populations of allo- and autohexaploids as well as twelve-ploids have been identified (Stutz and Sanderson 1979). Diploid populations, including a relic gigas population in central Utah, have been described (Stutz et al. 1975). A putative hybrid, *Atriplex aptera* Nelson, between *A. canescens* and *A. gardneri* (Moq) Dietrich exists in the regions of northern Wyoming, the Dakotas and Montana.

The Great Basin Environment

The Great Basin is the northernmost of the four North American Deserts. It includes the states of Utah and Nevada, and portions of

Wyoming, Oregon, Washington, California, Colorado and Arizona. The physiographic boundaries of the Great Basin include the Sierra Nevada on the west, the Wasatch Mountains on the east, the Snake River Plains on the north and by the arbitrary 35'30" delineation on the south (Tidwell et al. 1972). While some authors have included the rain-shadow deserts in western Wyoming as extensions of the Great Basin (Shreve 1942), others have excluded these regions owing to the absence of characteristic fauna (MacMahon 1979). Aside from its geographical location, the uniqueness of the Great Basin lies in great part in its climate and elevation. The major portion of the Great Basin desert lies above 1200 m. Precipitation ranges from 100 to 270 mm of which 60% falls during the winter months, most in the form of snow. Winters are long and characterized in places by extremely low temperatures restricting plant growth to a short growing season.

The vegetation of the Great Basin is characterized by a low species diversity dominated by a small number of deciduous low shrubs with small sclerophyllous leaves. Members of the families Compositae and Chenopodiaceae comprise bulk of the individuals; the most common genera are *Artemisia, Atriplex, Chrysothamnus,* and *Eurotia.* Plant communities are relatively simple, 90% often dominated by one or two species.

Although the vegetation dynamics of the Great Basin has no doubt closely followed climatic change and has closely paralleled in development the arid floras in the rest of the world, the age and origin of this and other North American deserts has been the subject of considerable debate (Johnson 1968). Axelrod (1950, 1958) proposed the development of three geofloras in southwestern North America by the Tertiary from which could have arisen the ancestors of some of the present cold and warm deserts species. Fossil floras indicate a general trend toward increasingly drier climate at this time (Axelrod 1979). Major plate movements and orogeny resulted in desert conditions during the Miocene and Pliocene, and the advance of important xerophytic plant families (Tidwell et al. 1972). By the end of the Miocene, moisture had decreased in the northern portion of the Great Basin and members of the Chenopodiaceae and Compositae were believed to have increased in dominance dramatically. The desert environment, expanding greatly in this area as a result of climatic changes during the Pleistocene, was comprised of a flora essentially the same as that existing throughout this region today. Although the age and origin of *Atriplex canescens* in North America is unknown, evidence from woodrat middens (food and debris stored by the rodent) indicates that the species has been an important component of the vegetation for at least 18,000 years (Wells and Berger 1967; Van Devender and Spaulding 1979).

Importance of the Species

Historically, fires have never had an important influence on the desert areas of North America (Humphrey 1962). Unlike the chaparral region (Parsons 1976), fire played no role in the evolution of shrub community succession over much of the Great Basin. Because many shrubs are severely damaged by burning and reestablish slowly, fires can have a devasting and long-lasting effect on shrub communities. However, *Atriplex canescens* and some other desert shrub species have the capacity to resprout vigorously after a fire (Dwyer and Pieper 1967). *Atriplex canescens* has been reported to show fire resistant qualities favoring it as one of the readily established species used in reclamation and revegetation of disturbed areas (Nord and Countryman 1972).

Grazing has been an important component in the succession of arid lands in North America for the past 100 years. The species composition of the desert scrub is differentially affected by intensity and timing of grazing pressure. Long term studies have indicated that mismanagement has led to complete loss of some of the most valuable species and increased the dominance of others. However, under careful management practices, the physiognomic qualities of rangeland can be profitably regulated (Holmgren and Hutchings 1972).

Atriplex canescens is considered by many to be high in many important nutritive characteristics and one of the most palatable shrubs in the southwest (Nemati 1977, Pieper et al. 1959, Cook et al. 1959). The leaves, stems, flowers and fruits are consumed by all classes of livestock and many other native mammals and birds (Judd 1962). Fourwing saltbush has low fiber and lignin contents, high protein and phosphorus contents, and is high *in vitro* organic matter digestibility (Cordova 1974). Continuous grazing has reduced production and yield of *Atriplex canescens* (Cook and Goebel 1962, Nord and Stallings 1976, Buwai and Trlica 1977, Trlica and Buwai 1977), and has similarly affected the yield of other *Atriplex* species (Leigh and Mulham 1971, Hodgkinson and Becking 1977). However, fourwing saltbush stands subjected to a controlled rotation grazing system have shown increased yield in comparison to ungrazed plants (Pieper and Donart 1978).

The need for an economical and practical method for increasing available forage on southwestern ranges stimulated early studies on the controlling factors of germination and growth of *Atriplex canescens* (Wilson 1928). Presently, the species is being used successfully for the revegetation of coal spoil banks, new road cuts, mining exploration sites, and overgrazed ranges. From its distribution, it is clear that *Atriplex canescens* is adaptable to a wide range of ecological and physical conditions and there are several establishment qualities of the species which make it attractive for purposes of revegetation. Considerable time and monies have been devoted in order to better understand the species in this latter role. Morphological and physiological characteristics affecting seed germination of the species have been reviewed (Gerard 1965, Springfield 1970, Gamrath 1972, Graves et al. 1975). Propagation techniques to enhance success of planted seedlings of fourwing saltbush have been defined (Wieland et al. 1971, Nord et al. 1971, Aldon and Springfield 1974, Van Epps 1975, Wiesner and Johnson 1977, Richardson et al. 1979). However, a far more economic means of establishment is by areal and hand broadcast seeding; this technique has been found to be a satisfactory means of establishing the species for use on fresh terraced cut and fill slopes along highways in southern California (Nord 1977). In some instances, seedlings must undergo an initial period of protection from rabbits and squirrels, but once established, the species provides ideal browse and habitat for grazing animals, game species, and upland game birds (Robinette 1972). Several nurseries for seed and transplant material have been successfully established (Stroh and Thornburg 1969, Van Epps 1974, McArthur et al. 1978).

The U.S. Forest Service has used fourwing saltbush widely for ground cover and soil stabilization on many arid soils and is now conducting research on the species for reestablishment on mine spoils in the Northern

Great Plains (Bjugstad 1978). Once established on mine tailings, the species has shown strong competitive abilities, especially in eliminating annual weeds such as Russian thistle (Hassell 1977). Laboratory and field studies on coal mine spoils have shown that production of the species is enhanced by the presence of vesicular-arbuscular endomycorrhizae (Williams et al. 1974, Aldon 1975, Williams and Aldon 1976). Other reports have shown that *Atriplex canescens* growing on mine spoil materials in New Mexico is greatly stimulated by the addition of fertilizer (Williams and O'Connor 1973, Aldon et al. 1976). Additional studies and projects have used fourwing saltbush for mine reclamation in the southwest (Grogen et al. 1979, Scholl and Aldon 1979).

Mature plants have deep and spreading root systems, making the species ideal for erosion control and soil stabilization. Characteristics and specifications in establishing fourwing saltbush seedlings for alluvial flood plain management in New Mexico have also been studied (Aldon 1970 a,b,c).

Since *Atriplex canescens* is more cold tolerant than other *Atriplex* species, it appears suitable for use in northwestern United States. However, seeds from plants growing in warm climates have failed to thrive in colder regions, indicating that important ecotypic properties of the species must be considered when acquiring bulk seed (Plummer 1977).

THE STUDY AREAS

Four sites were chosen for study along a NE-SW transect through the Great Basin including both warm- and cold-winter deserts (Fig. 2). Although plants at all sites could have been subjected to grazing at some time in their history, none of the plants at these sites were grazed within the past five to ten years.

Tipton - Site 1

Site 1 was located near Tipton, Wyoming (42°38'N 108°15'W) approximately 30 km northwest of Wamsutter, Wyoming, situated at the base of the Red Desert on the northern boundary of the species distribution. As in most desert ecosystems, rainfall at Tipton is characterized by infrequent and unpredictable drizzles and thunderstorms, total amounts received are small. A significant portion of the precipitation falls as snow during the winter months and is therefore unavailable to plants. The climate at the site is cold-desert (mean growing period of 92 days) with water stress occurring throughout (Figs. 3 and 4, following Walter and Lieth 1960). Dominant soils in the area are Haplargids and *Atriplex canescens-Artemisia tridentata* form the dominant vegetation. The genera *Artemisia, Atriplex* and *Chrysothamnus* formed the dominant vegetation at all sites (Table 1).

Cedar Mountain - Site 2

Site 2 (39°12'N 110°22'W) (Figs. 5 and 6) was located 30 km northwest of Green River, Utah on Joe Hole Wash at an elevation of 1,488 m,

Fig. 2: Location of the study sites.

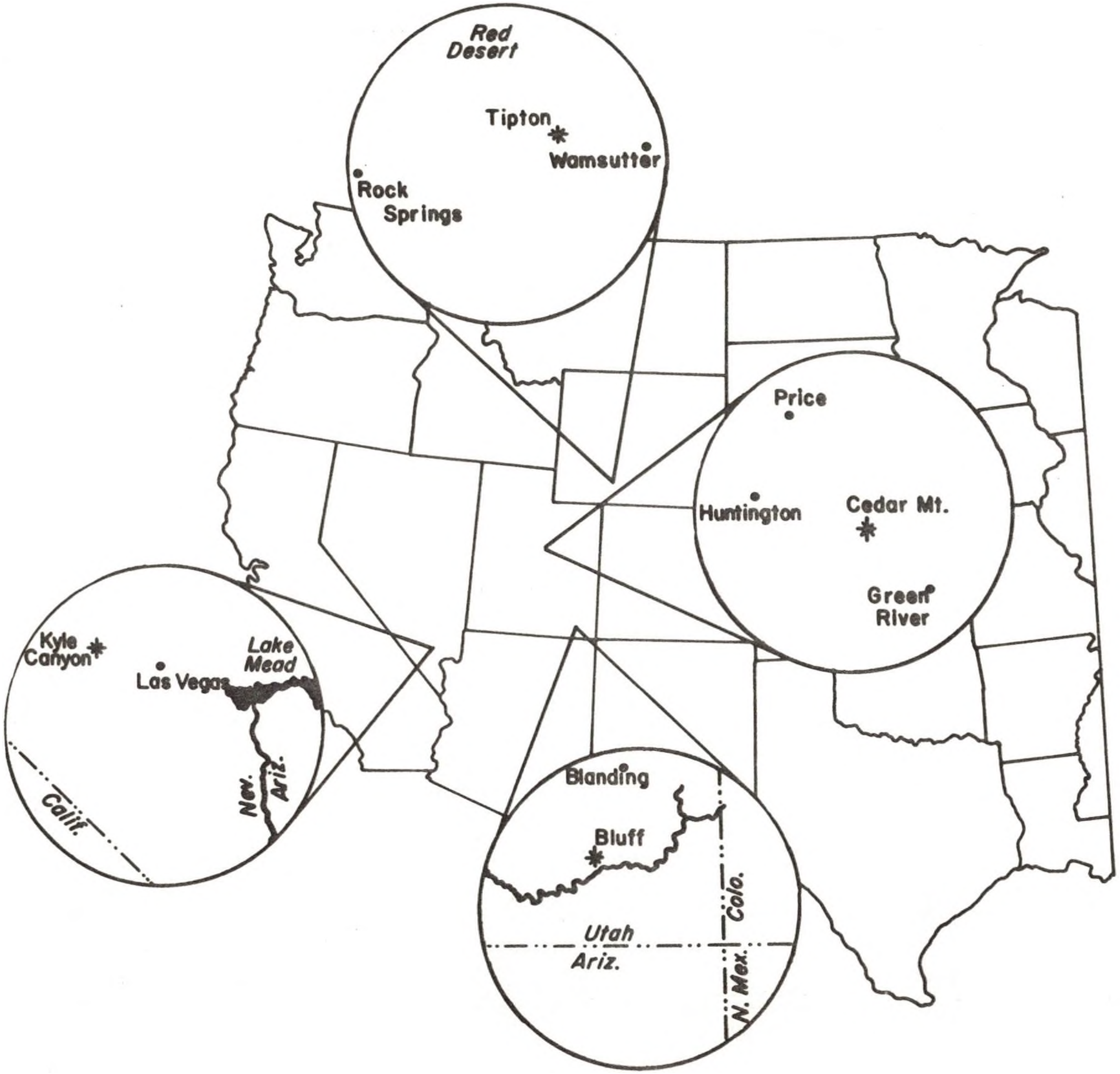

Red Desert
Tipton
Wamsutter
Rock Springs
Price
Huntington
Cedar Mt.
Green River
Kyle Canyon
Las Vegas
Lake Mead
Calif.
Nev.
Ariz.
Blanding
Bluff
Utah
Ariz.
Colo.
N. Mex.

Table 1. Plant species associated with *Atriplex canescens* at the study sites.

Tipton

- *Artemisia arbuscula* var. *nova*
- *Artemisia tridentata*
- *Astragalus kentrophyta*
- *Astragalus megacarpus*
- *Eriogonum ovalifolium*
- *Lappula echinata*
- *Opuntia* sp.
- *Oryzopsis hymenoides*
- *Penstemon arenicola*
- *Psoralea lanceolata*
- *Tetradynia canescens*
- *Chrysothamnus nauseosus*
- *Castelleja linariaefolia*

Cedar Mountain

- *Artemisia dracunculus*
- *Artemisia filifolia*
- *Atriples confertifolia*
- *Bahia oblongifolia*
- *Chrysothamnus nauseosus*
- *Ephedia torreyana*
- *Hilaria mutica*
- *Juniperus osteosperma*
- *Opuntia* sp.
- *Salsola kali*
- *Sarcobatus vermiculatus*
- *Sphaeralcea grossulariaefolia*
- *Sporabolus cryptantdrus*

Bluff

- *Atriplex confertifolia*
- *Gutierrezia sarothrae*
- *Lycium pallidum*
- *Opuntia* sp.
- *Salsola kali*

Kyle Canyon

- *Argemone platyceras*
- *Bromus tectorum*
- *Chrysothamnus grennei*
- *Chrysothamnus nauseosus*
- *Cleome lutea*
- *Cowania mexicana*
- *Eriogonum inflatum*
- *Fallugia paradoxa*
- *Mentzelia laevicaulis*
- *Senecio eremophilus*
- *Sphaeralcea munroana*
- *Yucca baccata*

Fig. 3: Climatograph for Site 1, Tipton, Wyoming.

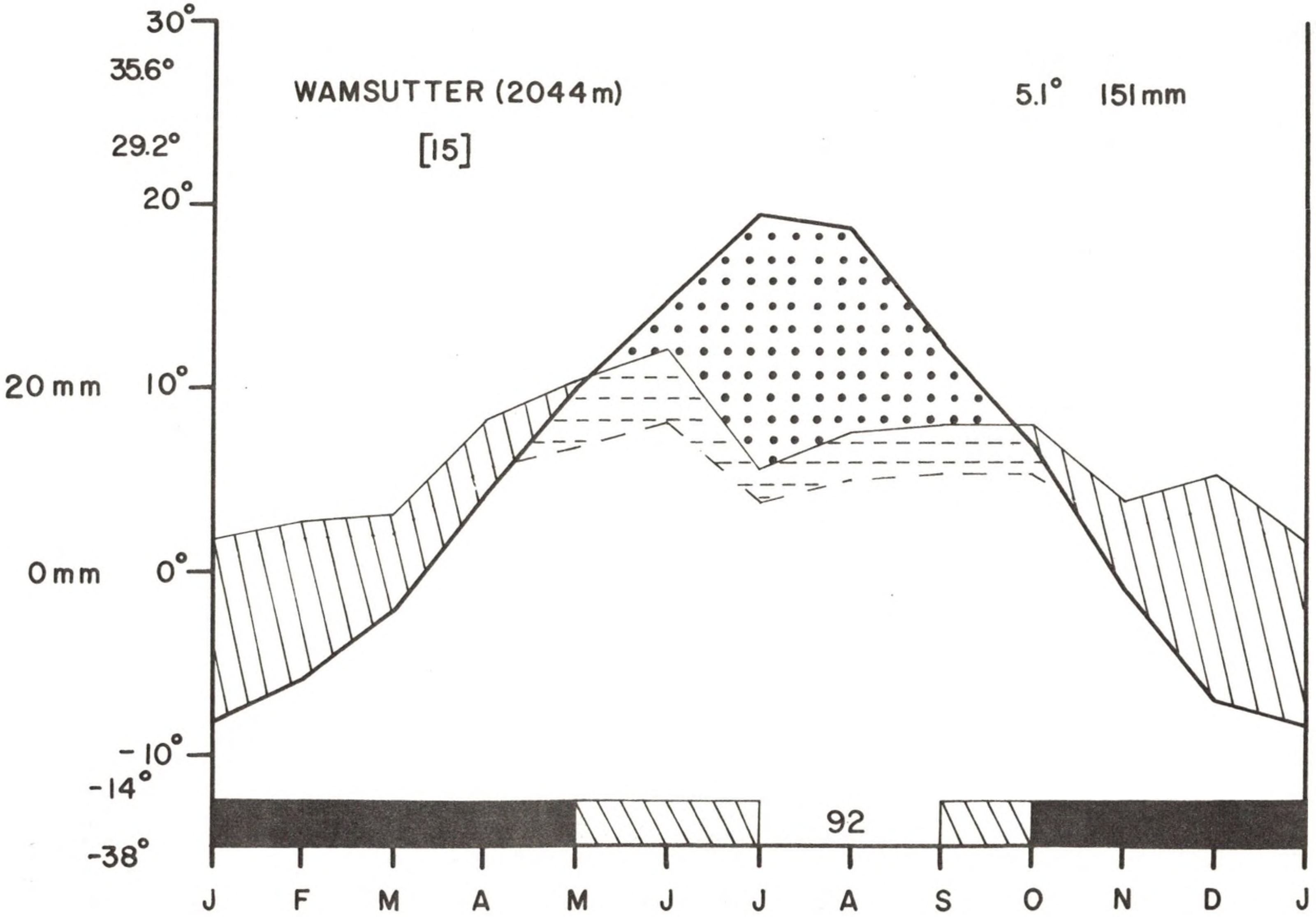

30°
35.6°
29.2°
20°
20 mm
10°
0 mm
0°
-10°
-14°
-38°
WAMSUTTER (2044 m)
[15]
5.1° 151 mm
92
J
F
M
A
M
J
J
A
S
O
N
D
J

Fig. 4: Cold winter community of *Chrysothamnus*, *Artemisia* and *Atriplex* in Wyoming (Site 1, Tipton, Wyoming).

Fig. 5: Climatograph for Site 2, Cedar Mtn., Utah.

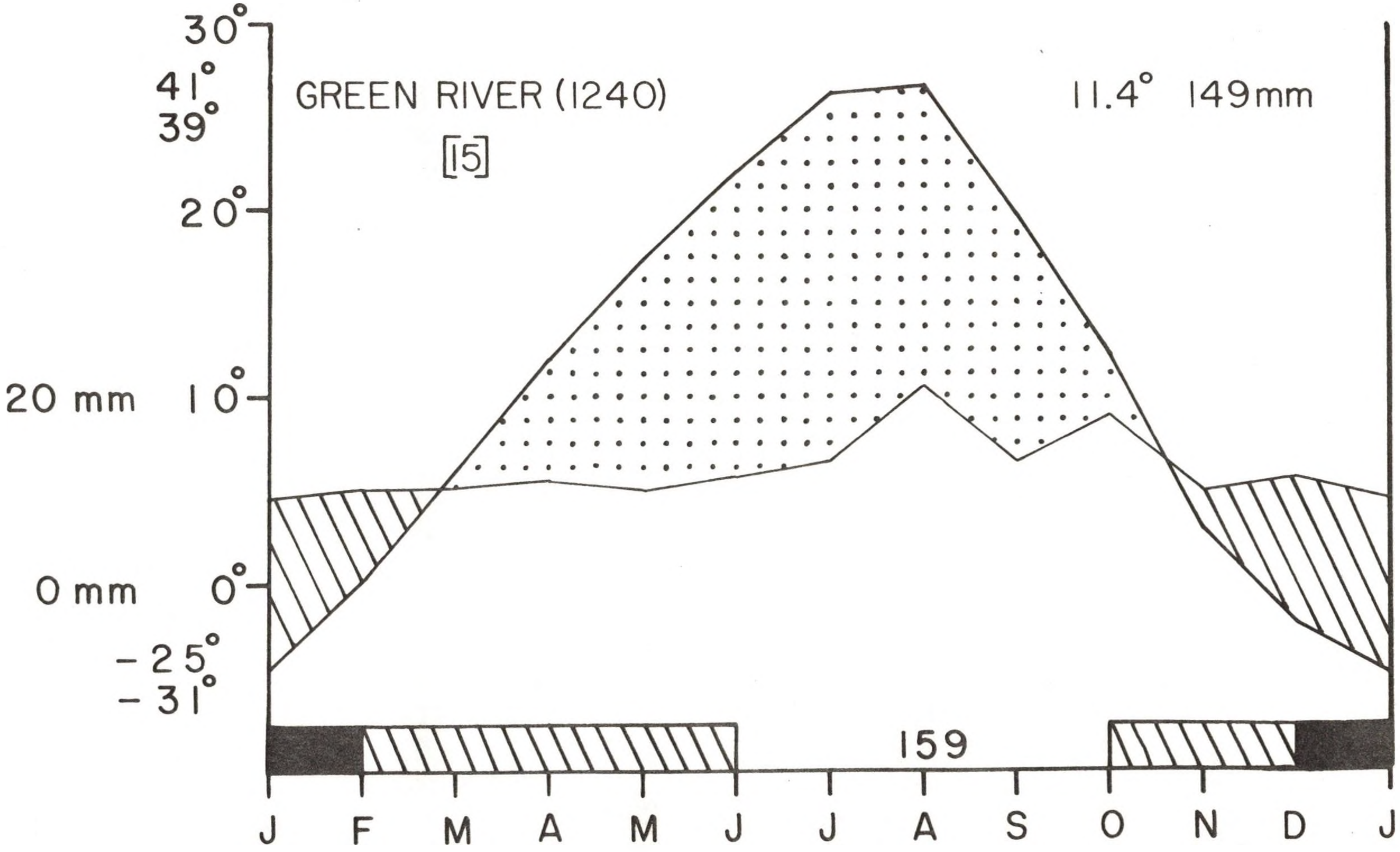

GREEN RIVER (1240)
[15]
11.4° 149mm
30°
41°
39°
20°
20 mm
10°
0 mm
0°
- 25°
- 31°
159
J
F
M
A
M
J
J
A
S
O
N
D
J

Fig. 6: Wadi, or dry streambed community showing sparsely distributed *Artemisia, Atriplex* and *Chrysothamnus* in west-central Utah (Site 2, Cedar Mtn., Utah).

east of Cedar Mountain. Similar to Tipton populations, *A. canescens* at Cedar Mtn. are deciduous. The annual precipitation (149 mm) is similar to that at Tipton; however, wadis (dry streambed communities) such as this site receive supplementary amounts of moisture from run-off waters several times that the amount of rainfall. Percent stoniness of these soils increases to 38% at subsurface depths. These gravelly soils represent dry habitats; even though water penetrates several meters, moisture reserves in the rooting zone are very low.

Bluff - Site 3

The climate in Bluff, Utah ($37^{o}17'$N $109^{o}33'$W) is characteristic of neither warm- or cold-winter desert (Figs. 7 and 8). Although growth is clearly seasonal, production is not restricted to the growing period (146 days), and leaves are maintained throughout the year. Standing snow is ephemeral, thus most of the precipitation is available for plant growth.

Kyle Canyon - Site 4

Kyle Canyon is located 15 km southwest of Desert NWR-Corn Creek Station ($36^{o}26'$N $115^{o}22'$W), and 40 km northwest of Las Vegas, Nevada (Figs. 9 and 10). The site is warm-desert where although growth is seasonal, it continues throughout the year (mean growing period is 212 days). Although precipitation is only 104 mm, the site is located in a canyon where rainfall is supplemented by run-off. All water penetrates surface layers rapidly because the top 40 cm are composed of approximately 86% stones and is readily available for plant growth. The area has never been grazed.

Fig. 7: Climatograph for Site 3, Bluff, Utah.

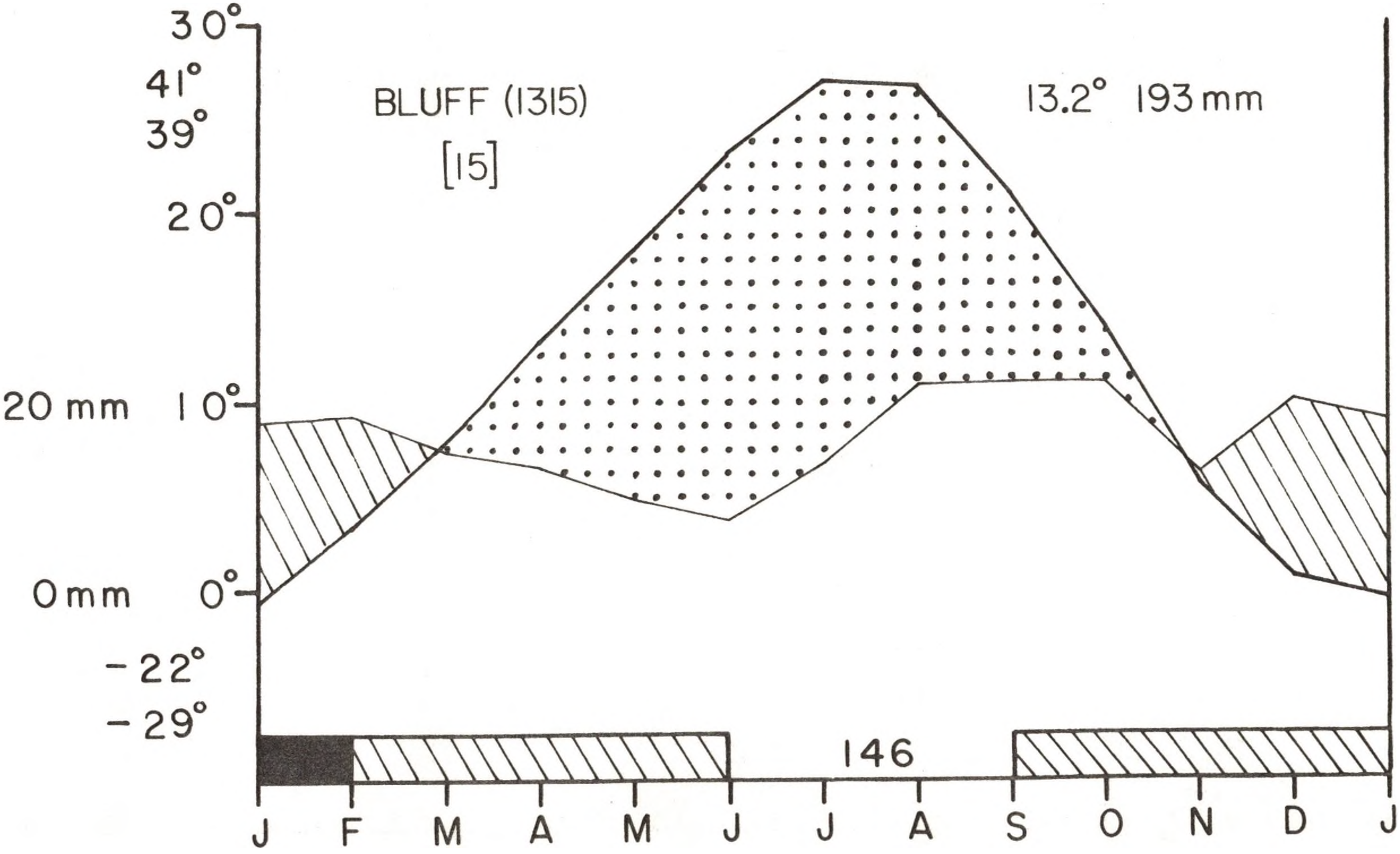

BLUFF (1315)
[15]
13.2° 193 mm
30°
41°
39°
20°
20 mm
10°
0 mm
0°
- 22°
- 29°
146
J
F
M
A
M
J
J
A
S
O
N
D
J

Fig. 8: Dense stand of large *Atriplex canescens* (attains a height of 15 dm) in southeastern Utah (Site 3, Bluff, Utah).

Fig. 9: Climatograph for Site 4, Kyle Canyon, Nevada.

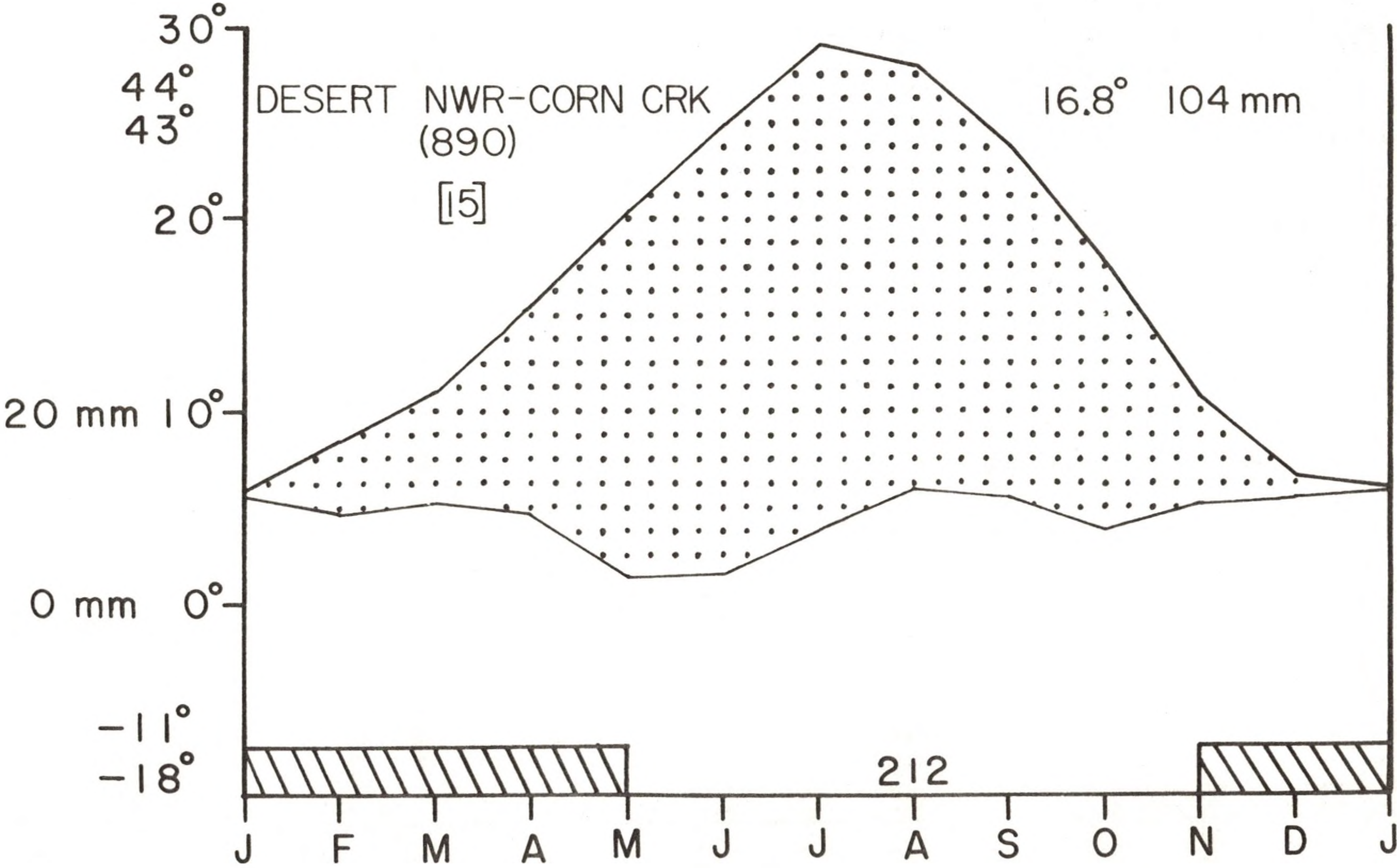

DESERT NWR-CORN CRK
(890)
[15]
16.8° 104 mm
30°
44°
43°
20°
20 mm 10°
0 mm 0°
-11°
-18°
212
J F M A M J J A S O N D J

Fig. 10: Wadi community dominated by *Atriplex* (staminate plant) and *Chrysothamnus* in southern Nevada (Site 4, Kyle Canyon, Nevada).

DATA COLLECTION AND METHODOLOGY

Field Methods

The four study sites were chosen in an effort to include the range of productivity of the species at undisturbed warm and cold winter locations throughout its distribution. The density and coverage of *Atriplex canescens* was measured at randomly selected 15 x 15 m plots at all four sites. Vegetation at each site was recorded. Soils were collected from the study sites during June and September 1977 from beneath the plant canopy at six depths: 0, 5, 10, 15, 30 and 60 cm. For comparison, samples were also obtained from unvegetated sites.

During August, 1978, water potential of *Atriplex canescens* at Tipton was measured by the pressure bomb technique at a nitrogen flow rate of 1 bar sec^{-1} (P.M.S. Instrument Co., Corvallis). Twigs of current year's growth and of equal diameter (2 to 3 mm) were chosen for measurements to eliminate effects of leaf and/or twig age. Plants were chosen at random and repeatedly monitored every 2 hours over a 24-hour period (diel) for several days. Height above ground of the excised twig as well as distance from the central axis of the plant were measured.

Xylem sap was collected in graduated capillary tubes, expelled into sterilized culture tubes and immediately frozen with liquid nitrogen. Pressure was gradually increased beyond the balancing pressure, then stopped and sap collected; the process was repeated until a total of 350 μl was obtained.

Air temperature and relative humidity were monitored with a hygrothermograph, light was measured using a pyroheliometer.

Productivity of *Atriplex canescens* was measured at the four study sites during September 1977 by the harvest method. Plants chosen for harvesting were cut at ground level, placed in bags, and brought to the laboratory. Five plants from Tipton, four from Cedar Mtn., representing the range of plant sizes and both sexes, and one large pistillate plant from Bluff and Kyle Canyon were harvested. Plant material was grouped in three classes. Current year's growth was easily distinguishable as the annual growth past the previous year's terminal node. This tissue was subsequently separated into stems, leaves, and fruits. In an effort to further divide the remaining biomass, middle and old wood age structures were recognized. The middle growth was comprised of all twigs and branches up to a specific size and age; easily distinguishable from the oldest wood. Although the establishment of this age classification was strictly an arbitrary decision made in the field, it proved to be a satisfactory method, repeatable and showing rather surprising intersite consistency. Old wood was that remaining after the harvest of the current and middle growth had been removed.

At the time of plant harvest, leaf litter was collected beneath each shrub.

Laboratory Analyses

Soil samples were passed through a 2 mm sieve, and saturated soil pastes were made (Richards 1954). Saturation percentage of the paste was determined prior to filtration. Measurements of pH and electrical conductivity (E.C.) were taken on the filtrate. Water soluble Na, K, Ca, Mg, Mn and Zn were determined using a Perkin-Elmer Model 503 Atomic Absorption Spectrophotometer (Perkin-Elmer 1977). Alkaline-earth carbonates were determined from acid neutralization (Richards 1954). Soil organic matter was determined by the Walkley-Black Method (Jackson 1958).

Sulfates were measured from a 1:1 soil-water extract as follows. A cation exchange column was prepared by packing the tip of a 10 ml disposable pipette tip with cotton and Amberlite 1R-120 (Analytical Grade) Cation Exchange Resin. The resin was charged using a rinse of 30-40 ml of 1 N HCl in 5 ml portions, and recharged after every 40-60 sulfate samples. Five ml of the water-extracted sample were passed through the column into a 150 ml beaker, followed by a rinse of 5 ml distilled water. To the beaker 1 ml 1000 ppm sulfate standard solution (1.22 gms $NaSO_4 \cdot l^{-1}$), 1 ml of methanol, and 3 drops of 0.1% Sulfonazo III indicator were added. The solution was titrated from a purple to a permanent blue end-point with 0.005 m $BaCl_2$. The addition of 1 ml of 1000 ppm standard was necessary if five drops of titrant were used and the blue color change was permanent. To account for the addition of standard in the final calculation of water-soluble sulfate, an F factor was determined by titrating 1 ml of the stock standard, 5 ml purified water, 8 ml methanol, and 3 drops indicator. The standards should normally use between 1.90 and 2.35 ml of titrant. Sulfate concentrations were calculated as follows:

1. No standard added to sample

$$\text{ppm in soil} = \frac{T_s}{T_{STD}} \times \frac{V_{STD}}{V_s} \times STD \times DF$$

where: Ts = mls of titrant for sample

T_{STD} = mls of titrant for standard

V_{STD} = volume of standard

Vs = volume of sample

STD = concentration of standard

DF = original water to soil ratio

2. Where standard is added to sample

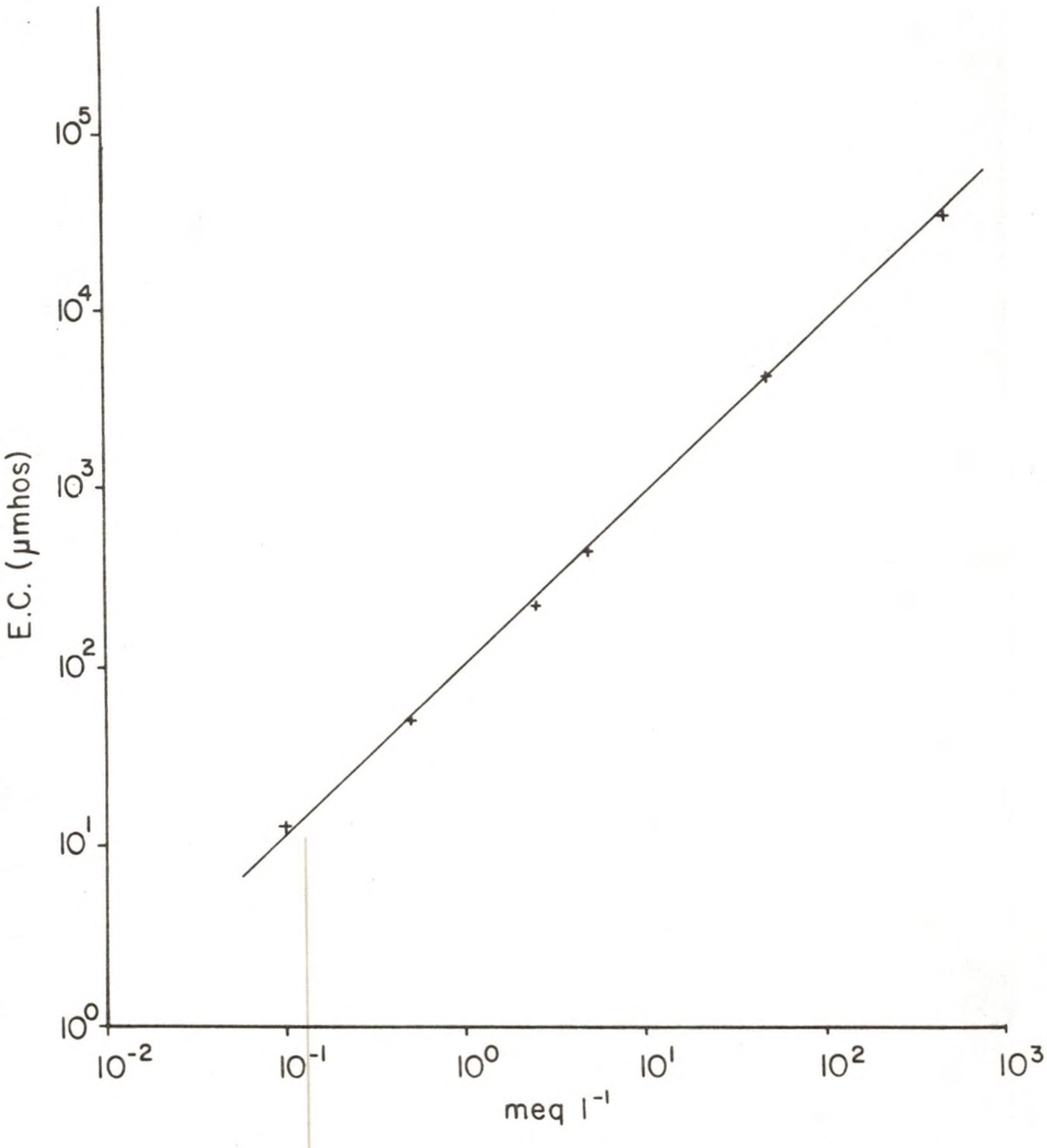
$$\text{ppm in soil} = \frac{T_s - T_{STD}}{T_{STD}} \times \frac{V_{STD}}{Vs} \times \text{STD} \times \text{DF}$$

Olsen's Method was used for the determination of soil phosphorus (Jackson 1958). Total nitrogen was measured by Kjeldahl digestion procedures with method of additions using a Specific Ion NH_4^+ Probe and Mortant Red II (Alizarin) indicator. Water soluble chlorides were analyzed on the extract using an Orion Specific Ion Probe. Particle size analysis was determined hydrometrically (Day 1965).

Osmotic pressure of expressed sap was determined by freezing point depression using an osmometer. Vapor pressure deficits were calculated using tables of water vapor pressures (Oosting 1956).

In order to assess the osmotic components which would be attributable in large part to inorganic constituents, osmotic pressure of the expressed sap was calculated from electrical conductivity measurements. Because the relationship between me 1^{-1} and E.C. is not linear, a synthetic xylem solution was made comprised of the four major cations (8 K, 3 Ca, 2 Mg, 1 Na). A relationship was then established between concentration and electrical conductivity similar to that of the expressed sap (Fig. 11). This figure was then used in conjunction with the known

Fig. 11: Regression line between concentration and electrical conductivity for a synthetic solution of 8 K : 3 Ca : 2 Mg : 1 Na ($Y = 69.790 X + 176.714 + e$).


E.C. (µmhos)
10^0
10^1
10^2
10^3
10^4
10^5
10^{-2}
10^{-1}
10^0
10^1
10^2
10^3
meq l^{-1}

relationship between osmotic pressure and electrical conductivity to assess the inorganic osmotic components (Richards 1954).

Plant material was oven dried at 60°C, weighed, ground and digested using a 5:1 nitric-perchloric digestion solution (Chapman and Pratt 1961). Sodium, K, Ca, Mg, Mn, Zn, Fe, Cu and Li, were measured by atomic absorption spectrophotometry. Total phosphorus and total nitrogen were determined by Olsen's and Kjeldahl methods, respectively, using samples digested in sulfuric acid-hydrogen peroxide. Total oxalates were measured by potassium permanganate titration (Moir 1953).

By digesting glucose and known additions of chloride with a nitric-perchloric and Morgan's Reagent, it was observed that significant amounts of chloride were vaporized. However, it was found that digestion with NaOH did not result in such losses. Plant material (0.5 g) and 10 ml of 30% NaOH were added to a 50 ml erlynmeyer flask to stand overnight. Flasks were warmed gently on a hotplate for 3 hours over low heat. After cooling, the samples were filtered, solutions adjusted to pH 7.0 using concentrated HNO_3 and diluted to 100 ml. Using 25 ml of the solution and no internal strength adjustment, chloride was measured with a specific ion probe using the method of additions; the latter uses 25 ml of 1000 ppm chloride for second reading (Orion Research).

In the laboratory, two groups of leaf litter samples were chosen for analysis. The first group included freshly senesced leaves which had fallen recently. The second froup included leaves from the previous year; although intact, these leaves had undergone initial stages of decomposition. Litter was washed for one minute in distilled water to remove soil contaminants and dried at 60° prior to analysis.

Growth rings of middle and old growth were counted and measured for all plants. Cross sections were made perpendicular to the stem axis, the cut surface sanded, and observed under a dissecting microscope. Rings were counted and radial length was measured with vernier calipers.

RESULTS

Soil Temperature

Surface and subsurface soil temperatures of bare ground and plant canopy soils at Tipton were compared to air temperature (Figs. 12 and 13). Fluctuations in ambient temperature (8.9°C to 31.9°C) represent typical diel ranges during the summer months at the site. Whereas surface temperatures of unvegetated soil varied 30.6° over the period and reached a maximum of 40.3°C, surface temperatures under the plant canopy reached only 21.7°C and varied only 5.9° throughout the 35 hours during which it was measured. However, bare ground soil temperatures at 15 cm averaged 10° less than surface soils, and varied 7°C. Although the variation in soil temperatures at 30 cm in unvegetated soil was equal to that at 15 cm under the plant canopy, vegetated soils at 15 cm averaged 2° cooler than those of bare soil at 30 cm. Soil temperature at 30 cm depth under the plant canopy was the most constant, varying only 1.4°. Coolest and warmest mean soil temperatures were found at 30 cm and surface layers, respectively, in unvegetated soils, and surface layers and at 30 cm, respectively, under the plant canopy.

Particle Size Distribution

Vegetated and unvegetated soils at Tipton contained between 60% and 83% sand, which decreased with depth (Table 2). Silt and clay were found in equal proportions; the soils were sandy loams. Vegetated soils contained higher sand than unvegetated soils. Most soils at Cedar Mtn.

Fig. 12: Air and unvegetated soil temperatures at Tipton from 1000 hrs. 9 August to 2000 hrs. 10 August 1977.

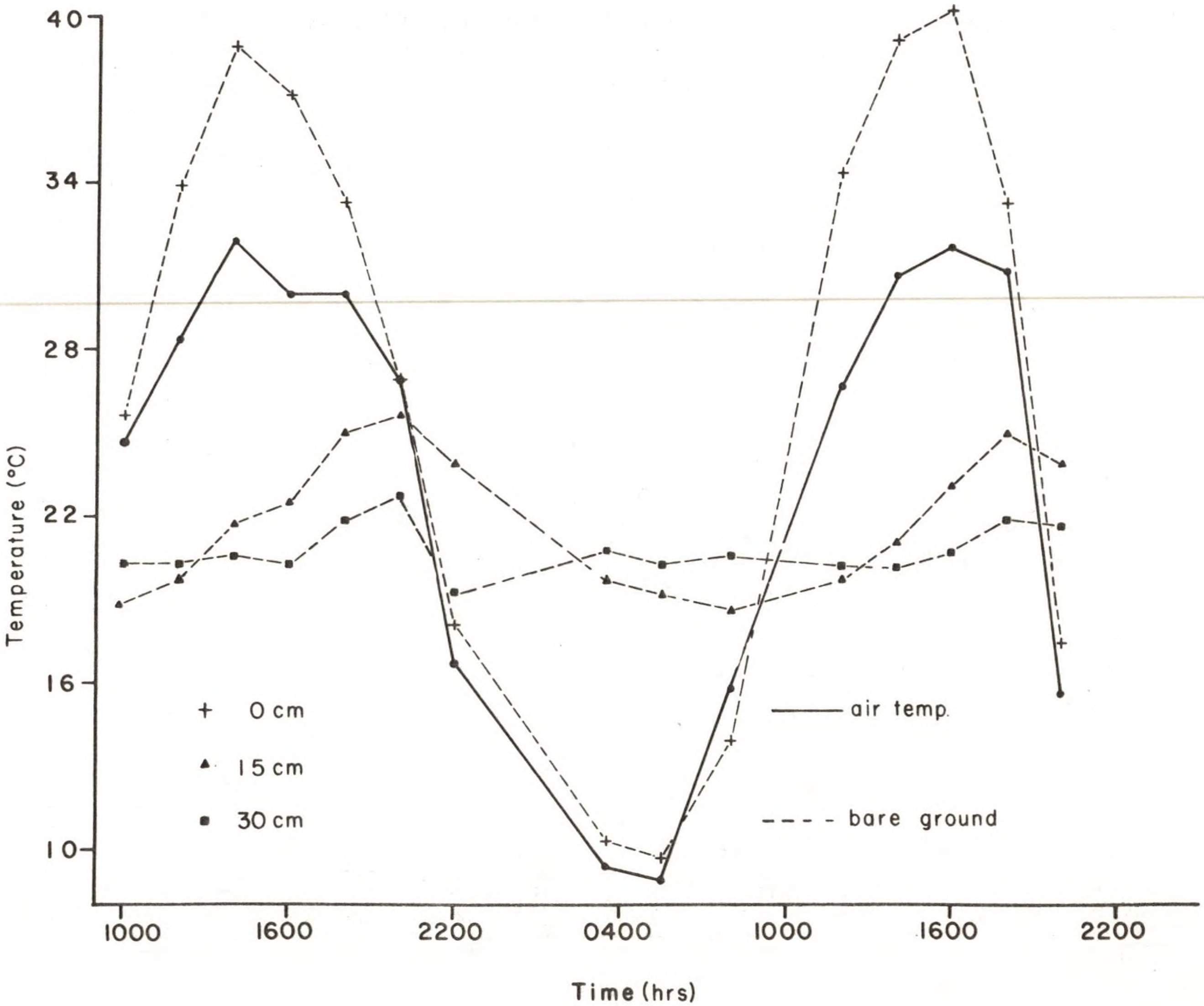

40
34
28
22
16
10
Temperature (°C)
1000
1600
2200
0400
1000
1600
2200
Time (hrs)
+ 0 cm
▲ 15 cm
■ 30 cm
air temp.
bare ground

Fig. 13: Air and vegetated soil temperatures at Tipton from 1000 hrs. 9 August to 2000 hrs. 10 August 1977.

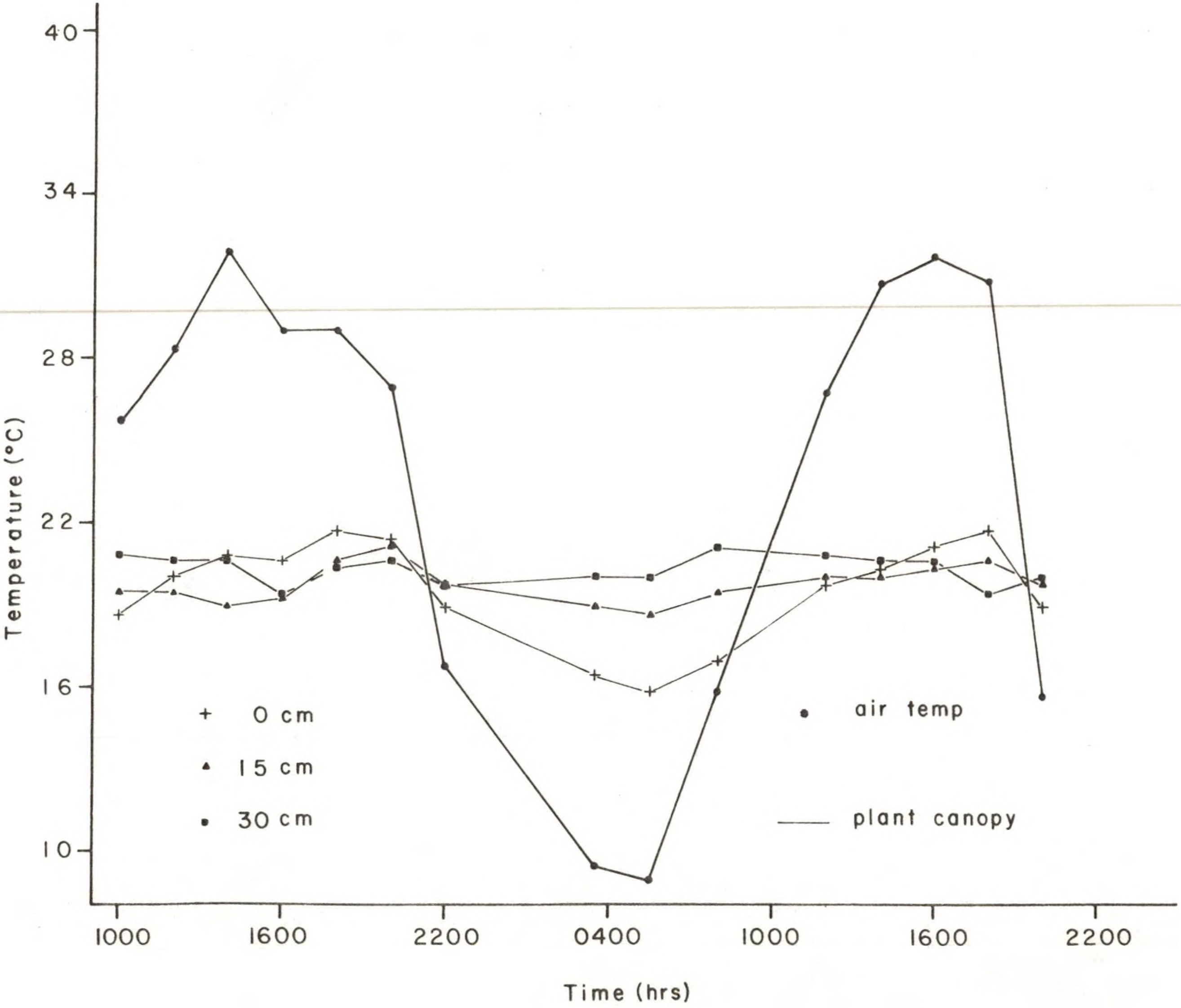

40
34
28
22
16
10
Temperature (°C)
1000
1600
2200
0400
1000
1600
2200
Time (hrs)
+ 0 cm
▲ 15 cm
■ 30 cm
● air temp
— plant canopy

Table 2. Particle size analysis of the sites

	Tipton			Cedar Mountain			Bluff			Kyle Canyon		
Plant	%Sand	%Silt	%Clay	%Sand	%Silt	%Clay	%Sand	%Silt	%Clay	%Sand	%Silt	%Clay
0 cm	83.2	10.2	6.6	74.2	16.9	8.9	84.6	6.1	9.3	72.3	4.3	23.4
5	79.8	12.7	7.5	71.7	16.9	11.4	88.9	6.1	5.0			
10	75.7	8.2	16.1	74.2	14.4	11.4	90.5	5.2	4.3	84.1	4.3	11.6
15	68.3	19.2	12.5	66.7	24.4	8.9	92.3	2.7	5.0	85.7	4.3	10.0
30	59.8	22.7	17.5	66.7	22.0	11.3	91.4	5.2	3.4			
60	67.3	17.7	15.0	85.1	8.6	6.3	83.9	7.7	8.4	90.7	1.8	7.5
Bare												
0 cm	68.2	17.7	14.1	74.9	16.3	8.9	93.2	4.3	2.5	85.7	1.8	12.5
5	64.8	20.2	15.0	79.9	11.2	8.9	93.2	4.3	2.5			
10	59.8	22.7	17.5	84.9	8.7	6.4	93.2	4.3	2.5	85.7	1.8	12.5
15	61.4	20.2	18.4	84.0	9.7	6.4	93.4	3.4	3.2	90.7	1.8	7.5
30	61.4	20.2	18.4	81.5	9.7	8.8	92.5	3.4				
60	60.5	19.5	20.0	78.1	13.0	8.9	92.5	4.3	3.2	93.2	1.8	5.0

were loamy sands, sand content between 67% and 85%. Layers of gravelly-sand deposits usually occurring between 15 and 30 cm were characteristic of these streambed soils. Soils at Bluff were sandy with all but a few samples having less than 90% sand. A distinct increase in sand content and decrease in clay were recorded down the profile at Kyle Canyon. Unvegetated surfaces had slightly higher sand content than did vegetated soils. The texture of soils ranged between loamy-sand and sandy. Stoniness of surface and subsurface layers at Cedar Mountain and Kyle Canyon ranged up to 86.2% of the soil mass. Stoniness did not appear to be important at either Tipton or Bluff.

Saturation Percentage

The percent water saturation of the soils was significantly higher for vegetated than unvegetated soils at Tipton, Cedar Mtn., and Kyle Canyon ($p < .01$) (Fig. 14, Tables 3-11). The mean saturation percentage of vegetated and unvegetated soils ranged from 28.6% and 19.6% at Kyle Canyon to 33.7% and 29.6% at Tipton. There was a slight decrease in saturation percentage with soil depth for vegetated soils.

pH

Atriplex canescens was found growing on moderately alkaline soils with a pH ranging from 7.1 to 8.8 (Tables 2-10). Soil pH differences were not found by depth, either on vegetated or unvegetated soils at any site. The range pH for the soils at each site was: Tipton, 7.1-8.2; Cedar Mtn., 7.5-8.3; Bluff, 7.7-8.2; and Kyle Canyon, 7.8-8.8.

Electrical Conductivity (E.C.)

Electrical conductivity of vegetated surface soils ranged from 2.4 to 3.6 mmhos cm^{-2}, and decreased to less than 1 mmho cm^{-2} below

Fig. 14: Percent water saturation of soils from vegetated and unvegetated soils.

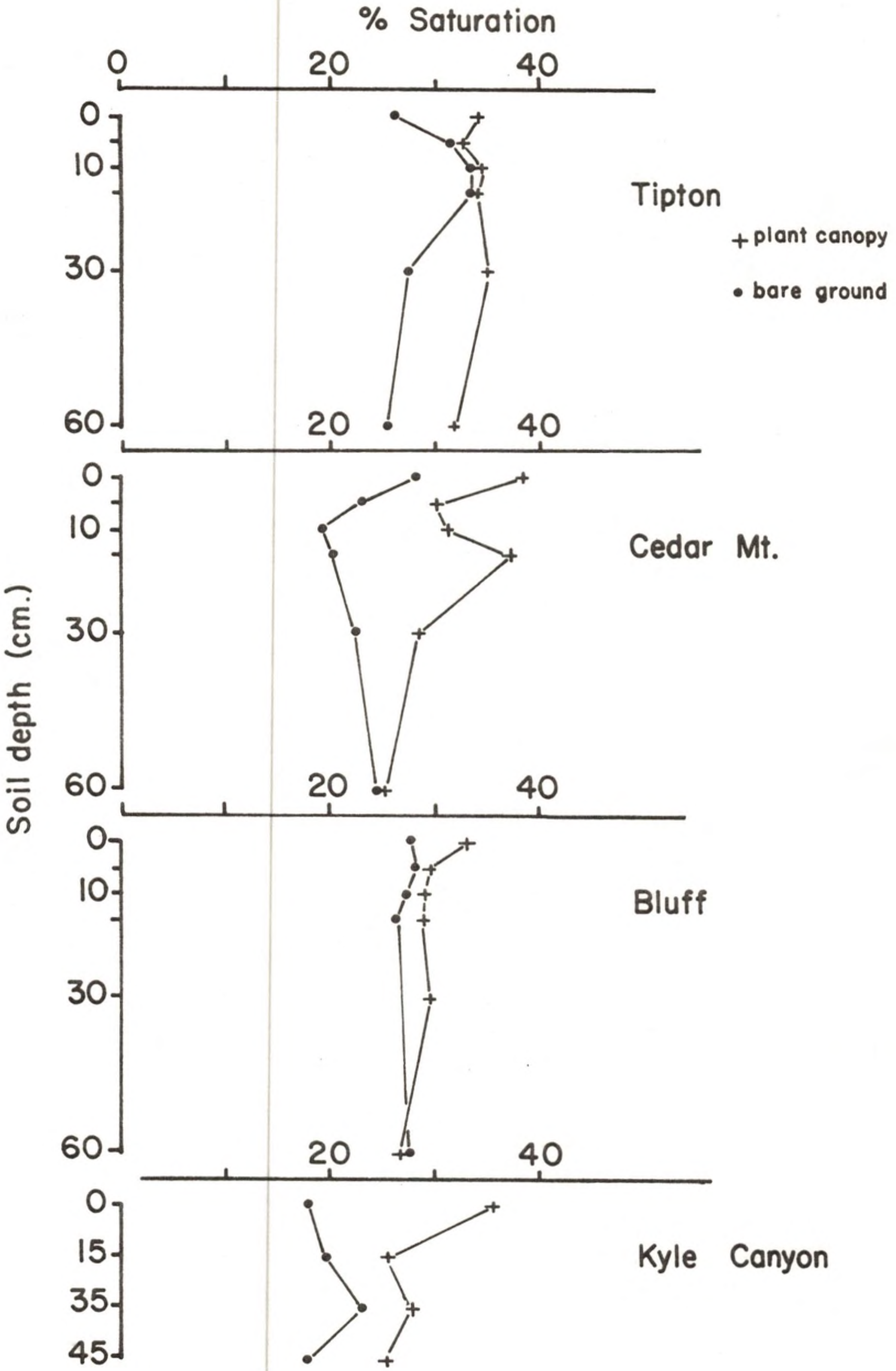

% Saturation
0
20
40
Soil depth (cm.)
0
10
30
60
Tipton
+ plant canopy
• bare ground
20
40
0
10
30
60
Cedar Mt.
20
40
0
10
30
60
Bluff
20
40
0
15
35
45
Kyle Canyon

Table 3. Physical and chemical properties of soils - Tipton

Depth	Alkaline Earth Carbonates (%)		Saturation (%)		pH		E.C. (μmhos)		Cl (ppm)	
cm	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground
September										
0	4.36±0.88	8.37±0.63	34.08	26.12	8.0	7.9	2100	430	300	10
5	6.14±2.18	8.86±0.66	32.74	31.36	8.0	7.8	1350	490	200	9
10	7.84±1.46	8.51±0.98	34.49	33.40	7.9	7.9	970	450	96	7
15	8.44±1.45	7.99±0.44	34.05	33.46	7.9	8.0	700	500	63	7
30	8.36±0.91	7.44±0.13	35.24	27.59	7.7	8.1	560	540	85	9
60	8.03±0.50	7.43±0.25	31.81	25.48	7.9	8.2	580	1000	101	51
June										
0					8.1	8.0	2700	870	490	15
5					8.1	7.9	1100	490	150	10
10					7.9	8.0	760	620	150	10
15					8.0	8.0	1060	640	150	10
30					7.9	7.1	1060	850	230	9
60					8.1	8.2	680	750	108	12

Table 3. (Continued)

Depth	ppm				Organic Matter (%)		N (%)		C/N	
	P		SO_4							
cm	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground
<u>September</u>										
0	13.2	10.8	111.1	33.3	2.33	0.42	.0863±.014	.0343±.003	26.99	12.26
5	8.6	6.6	77.8	38.1	1.19	0.52	.0584±.004	.0337±.003	20.37	15.44
10	7.0	7.6	77.8	19.1	1.02	0.45	.0554±.002	.0294±.005	18.41	15.30
15	7.4	7.0	66.7	28.6	0.87	0.36	.0484±.004	.0262±.005	17.98	13.72
30	6.8	6.8	166.7	19.1	0.67	0.34	.0385±.004	.0216±.002	17.41	15.73
60	7.0	6.6	42.9	66.7	0.40	0.34	.0262±.001	.0199±.003	15.27	17.10
<u>June</u>										
0	16.4	17.0	133.3	27.8	1.64	0.66	.0725	.0403	22.62	16.38
5	13.2	11.6	83.3	16.7	0.99	0.79	.0502	.0363	19.72	21.76
10	10.6	9.8	44.4	22.2	0.59	0.46	.0425	.0363	13.88	12.67
15	8.6	8.2	61.1	33.3	0.99	0.85	.0565	.0425	17.52	20.00
30	10.2	10.2	38.9	27.8	0.66	0.59	.0403	.0282	16.38	20.92
60	7.0	9.8	27.8	22.2	0.59	0.53	.0269	.0269	21.93	19.70

Table 4. Major cation concentrations by depth, using saturation extracts - Tipton.

Depth	me l^{-1}					
	K		Na		Ca	
cm	Bare ground	Plant canopy	Bare ground	Plant canopy	Bare ground	Plant canopy
0	0.34±.04	19.25±5.95	0.46± .03	1.61±1.00	7.68± .28	12.50±3.36
5	0.17±.05	13.04±4.35	0.64± .10	1.27±0.64	4.57±1.50	9.92± .74
10	0.15±.05	7.03±4.54	1.02± .65	1.29±0.70	4.74± .57	8.09±4.11
15	0.15±.03	4.48±4.3	1.68±1.24	1.11±0.49	3.43±1.30	5.88±3.77
30	0.13±.03	1.11±0.94	4.83±2.97	1.08±0.42	2.45± .49	4.25±3.61
60	0.12±.02	0.24±0.05	13.05±8.06	2.26±0.91	2.45± .98	4.66±1.90

Table 4. (Continued)

			ppm			
Depth	Mg (me l^{-1})		Mn		Zn	
cm	Bare ground	Plant canopy	Bare ground	Plant canopy	Bare ground	Plant canopy
0	2.27±.34	30.57±8.23	.43± .25	11.00±6.32	.10± .10	.25±.06
5	1.84±.53	13.92±4.42	.20± .10	2.83±2.0	.27± .29	.15±.06
10	2.44±.13	7.61±3.35	.30± .10	2.13±2.06	.07± .06	.15±.10
15	2.50±.71	4.91±2.49	.30± .20	1.20±1.89	.10±0.	.10±.12
30	2.16±.92	4.36±1.48	.93±1.53	0.43± .33	.10±0.	.13±.05
60	2.00±.96	5.96± .82	.13± .06	0.23± .25	.13± .06	.08±.10

Table 5. Student's *t*-test for vegetated and unvegetated soils at Tipton.

Depth (cm)	Organic Matter	E.C.	% Carbonate	%N	K	Na	Ca	Mg	Mn	Zn
0	10.07**	6.02**	6.67**	6.11**	5.37**	2.33	2.42	5.81**	2.82*	2.54
5	23.75**	5.78**	2.04	9.36**	5.01**	1.64	6.34**	4.59**	2.22	0.81
10	4.70**	3.19*	0.68	9.63**	2.56	0.53	1.37	2.61	1.50	1.27
15	3.75*	2.00	0.51	6.21**	1.70	0.86	1.06	1.60	0.80	0.23
30	3.40*	0.81	1.69	6.33**	1.75	2.58*	1.94	2.23	0.66	0.85
60	1.48	0.74	1.86	3.65*	4.20**	2.75*	1.81	5.89**	0.61	0.92

*p < .01
**p < .05
df = 5

Table 6. Major cation concentrations by depth using soil saturation extracts - Cedar Mountain.

	me 1^{-1}								ppm			
Depth	K		Na		Ca		Mg		Mn		Zn	
cm	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground
September												
0	64.19	1.24	19.13	0.79	31.44	6.79	32.66	1.43	0.20	.10	0.08	.46
5	16.37	2.35	4.78	0.89	6.14	14.42	3.37	1.47	0.09	.07	0.16	.17
10	10.49	2.11	2.78	0.85	4.84	21.31	2.22	1.22	0.07	.07	0.44	.16
15	14.83	1.53	11.13	1.27	49.90	37.93	19.09	1.88	0.15	.09	0.12	.29
30	13.30	0.31	4.09	1.63	35.93	38.18	4.36	2.61	0.23	.10	0.64	.62
60	0.90	0.30	3.74	2.57	44.41	38.67	3.29	4.12	0.23	.14	0.08	.72
June												
0	10.23	0.72	17.83	0.35	12.57	2.59	7.73	0.82	.6	.1	.2	.2
5	6.91	1.53	24.78	0.61	13.72	9.48	6.58	0.90	.3	.1	.2	.1
10	4.48	1.61	17.83	0.65	9.88	32.93	2.88	1.48	.2	.1	.6	.5
15	3.86	0.95	16.09	0.65	15.07	42.42	3.29	1.23	.2	.1	.2	.2
30	0.31	0.15	3.91	1.17	48.90	42.42	1.48	3.78	.1	.1	.2	.2
60	0.38	0.20	2.78	19.57	43.91	38.92	2.06	8.23	.1	.1	.2	.3

Table 7. Physical and chemical properties of soils - Cedar Mountain.

Depth	Alkaline Earth Carbonates (%)		Saturation (%)		pH		E.C. (μmhos)		Cl (ppm)	
cm	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground
<u>September</u>										
0	14.68	12.95	38.35	23.33	7.8	8.3	9100	540	2800	10
5	16.90	13.35	30.24	24.10	8.2	8.3	2300	430	470	9
10	17.55	13.30	31.16	24.84	8.3	8.3	1400	420	200	6
15	22.05	15.60	37.16	25.12	8.1	7.9	5000	1800	1150	7
30	15.40	16.33	28.51	26.96	7.7	7.7	3100	1800	250	4
60	16.75	14.83	25.15	29.70	7.5	8.1	2400	830	210	5
<u>June</u>										
0					8.1	8.2	3000	330	660	19
5					8.2	8.2	3650	730	1000	11
10					8.3	8.0	710	1500	700	8
15					8.1	7.9	800	530	660	7
30					7.8	7.8	680	530	290	11
60					7.7	7.9	600	880	150	95

Table 7. (Continued)

	ppm									
Depth	P		SO_4		Organic Matter (%)		%N		C/N	
cm	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground
September										
0	21.8	10.8	628.6	147.6	1.62	0.44	0.0864	0.0253	18.75	17.39
5	16.2	8.0	147.6	104.8	1.49	0.41	0.0461	0.0159	32.32	25.79
10	14.8	9.0	100.0	95.2	1.49	0.24	0.0498	0.0104	29.92	23.08
15	15.4	7.0	1647.6	1085.7	1.62	0.24	0.0588	0.0077	27.55	31.17
30	7.4	7.4	795.2	1495.2	0.47	0.27	0.0266	0.0084	20.80	32.14
60	6.0	6.4	1475.1	1638.1	0.27	0.20	0.0083	0.0103	32.53	19.42
June										
0	50.6	14.6	277.8	22.2	1.38	0.66	0.0545	0.0200	25.32	33.00
5	21.8	12.2	272.2	100.0	1.45	0.46	0.0436	0.0154	33.26	29.87
10	13.4	9.6	205.6	694.4	0.59	0.33	0.0264	0.0148	22.35	22.30
15	16.0	7.0	216.7	1744.4	0.66	0.46	0.0320	0.0141	20.63	32.62
30	10.0	7.0	1750.0	1855.6	0.46	0.46	0.0192	0.0130	23.96	35.38
60	8.4	6.8	1877.8	2100.0	0.33	0.53	0.0175	0.0154	18.86	34.42

Table 8. Major cation concentrations by depth, using soil saturation extracts - Bluff.

	me l^{-1}								ppm			
Depth	K		Na		Ca		Mg		Mn		Zn	
cm	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground
September												
0	47.83	1.74	2.70	0.48	33.43	5.69	62.52	1.65	2.0	0.8	0.2	0.1
5	23.27	1.69	1.30	0.48	10.48	4.89	13.16	1.48	0.6	0.8	0.2	0.1
10	11.00	1.61	0.70	0.43	3.14	3.39	3.29	1.07	0.6	1.0	0.1	0.1
15	8.70	1.61	0.65	0.35	2.99	2.25	1.73	0.74	0.6	0.8	0.1	0.1
30	3.32	1.79	0.96	0.30	4.79	1.90	1.48	0.66	0.6	0.8	0.1	0.1
60	0.51	1.99	6.09	0.52	7.34	2.50	4.94	0.82	0.6	0.6	0.2	0.1
June												
0	44.5	1.41	1.48	0.48	11.98	5.99	31.26	2.06	2.3	0.3	0.4	0.1
5	18.67	1.23	0.83	0.48	10.98	4.29	7.73	1.65	0.4	0.1	0.3	0.4
10	7.67	1.43	0.57	0.30	10.58	3.99	4.28	1.65	0.2	0.1	0.2	0.2
15	4.35	2.05	0.52	0.22	12.57	4.34	3.87	1.73	0.2	0.1	0.2	0.1
30	3.32	1.84	0.43	0.30	9.48	3.24	3.21	1.73	0.1	0.1	0.3	0.2
60	2.56	2.05	0.48	0.43	6.39	5.64	2.88	2.47	0.1	0.1	0.1	0.1

Table 9. Physical and chemical properties of soils - Bluff.

Depth	Alkaline Earth Carbonates (%)		Saturation (%)		pH		E.C. (μmhos)		Organic Matter (%)	
cm	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground
September										
0	3.15	2.40	32.96	27.68	7.8	7.9	7900	620	2.07	1.60
5	2.85	2.05	29.47	27.90	7.9	7.8	3100	570	0.80	1.40
10	2.85	1.95	28.97	27.25	7.9	7.7	1250	440	0.73	1.20
15	3.03	2.75	29.02	26.28	7.8	7.8	1000	310	0.93	1.27
30	2.70	3.20	29.52		7.9	7.9	700	290	0.80	1.27
60	4.45	3.95	26.68	27.89	7.7	7.8	1100	370	0.87	1.87
June										
0					8.0	8.2	5400	570	1.51	0.39
5					8.1	8.2	2800	490	0.59	0.33
10					8.2	8.1	1700	490	0.33	0.20
15					8.0	7.9	1400	560	0.33	0.26
30					8.0	8.1	1050	480	0.39	0.20
60					7.9	8.0	820	660	0.59	0.46

Table 9. (Continued)

					ppm					
Depth	%N		C/N		Cl		P		SO_4	
cm	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground
September										
0	.0956	.0294	21.65	54.42	1900	230	40.0	10.6	628.6	38.1
5	.0302	.0208	26.49	67.31	570	11	12.8	13.8	138.1	38.1
10	.0158	.0121	46.20	99.17	155	10	6.4	10.0	57.1	42.9
15	.0121	.0106	76.86	119.81	105	7	6.2	9.0	85.7	33.3
30	.0106	.0132	75.47	96.21	85	4	8.4	8.6	57.1	28.6
60	.0121	.0199	71.90	93.97	130	7	8.0	6.8	85.7	28.6
June										
0	.0792	.0264	19.07	14.77	1250	19	6.0	13.2	422.2	33.3
5	.0219	.0110	26.94	30.00	550	15	13.4	14.0	133.3	38.9
10	.0146	.0146	22.60	13.70	440	11	8.6	11.2	94.4	22.2
15	.0110	.0074	30.00	35.14	350	7	8.4	10.0	100.0	11.1
30	.0125	.0100	31.20	20.00	220	7	10.0	11.6	77.8	11.1
60	.0148	.0138	39.86	33.33	105	7	8.0	9.0	33.3	127.8

Table 10. Major soil cation concentrations by depth, using soil saturation extracts - Kyle Canyon.

	me l^{-1}								ppm			
Depth	K		Na		Ca		Mg		Mn		Zn	
cm	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground
0-10	26.60	0.38	0.61	0.30	4.29	5.14	30.44	1.15	1.8	0.8	0.2	0.1
15-20	15.09	0.28	0.48	0.43	3.09	5.09	5.18	1.23	0.8	0.9	0.2	0.1
30-40	9.72	0.18	0.39	0.35	3.69	4.49	3.37	1.15	1.1	0.8	0.1	0.1
45-50	5.63	0.20	0.43	0.30	3.29	4.39	2.22	1.15	0.8	0.9	0.1	0.1

Table 11. Physical and chemical properties of soils - Kyle Canyon.

Depth	Alkaline Earth Carbonates (%)		Saturation (%)		pH		E.C. (μmhos)		Organic Matter (%)	
cm	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground
September										
0-10	49.0	68.25	35.45	17.91	8.8	8.0	3000	390	3.20	1.87
15-30	49.80	68.25	25.50	19.69	8.1	7.8	1550	390	2.27	2.00
30-40	49.85	63.25	27.98	23.14	8.0	7.8	1130	340	1.73	1.60
45-50	49.80	75.38	25.30	17.79	8.0	7.8	730	340	1.07	1.40

Table 11. (Continued)

Depth	%N		C/N		ppm					
					Cl		P		SO_4	
cm	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground	Plant	Bare ground
<u>September</u>										
0-10	0.1447	0.0426	22.11	43.90	105	8	27.6	9.2	523.8	371.4
15-30	0.0692	0.0451	32.80	44.35	31	8	8.6	11.4	152.4	38.4
30-40	0.0417	0.0266	41.49	60.15	25	6	7.4	10.0	85.7	28.6
45-50	0.0266	0.0173	40.23	80.92	14	6	7.0	6.6	66.7	28.6

30 cm. A significant difference between vegetated and unvegetated soils was measured at Tipton for the top 10 cm of soil ($p < .01$) (Fig. 15). Similar trends and values for vegetated soils were found at Cedar Mtn. and Kyle Canyon. Electrical conductivities of all unvegetated soils for the most part were less than 1 mmho cm^{-2}. Although one surface sample from vegetated soil at Bluff was 5.4 mmhos cm^{-2}, this was probably attributable to salts leached from plant litter. Thus, soils from all sites fall below the 4.0 mmhos cm^{-2} level to be considered saline.

Organic Matter

Organic matter of the vegetated soils at Tipton decreased from approximately 2% at the soil surface to 0.4% at a depth of 60 cm (Fig. 16). The values for unvegetated soils by depth ranged from 0.49% to 0.17%. Significant differences between vegetated and unvegetated soils were found at 0, 5 and 10 cm ($p < .01$), and 15 and 30 cm ($p < .05$), but not at 60 cm. Vegetated surface soils at Cedar Mtn. revealed an average of 1.5%. Vegetated soils had greater organic matter content than unvegetated in the top 30 cm of the profile. Values for both soils at 60 cm were between 0.2 and 0.6%. Organic matter distribution at Bluff was not unlike that found at Cedar Mtn. It should be pointed out that unusually high values measured for unvegetated soils were contaminated with charcoal bits from an archeological site at Bluff. Vegetated soils at Kyle Canyon had higher organic matter in the top 30 cm than unvegetated soils, all values at the site were greater than 1.0% with vegetated soils having higher content than the other three sites. The value 3.2%, the highest measured, was at Kyle Canyon.

Fig. 15: Electrical conductivity of vegetated and unvegetated soils.

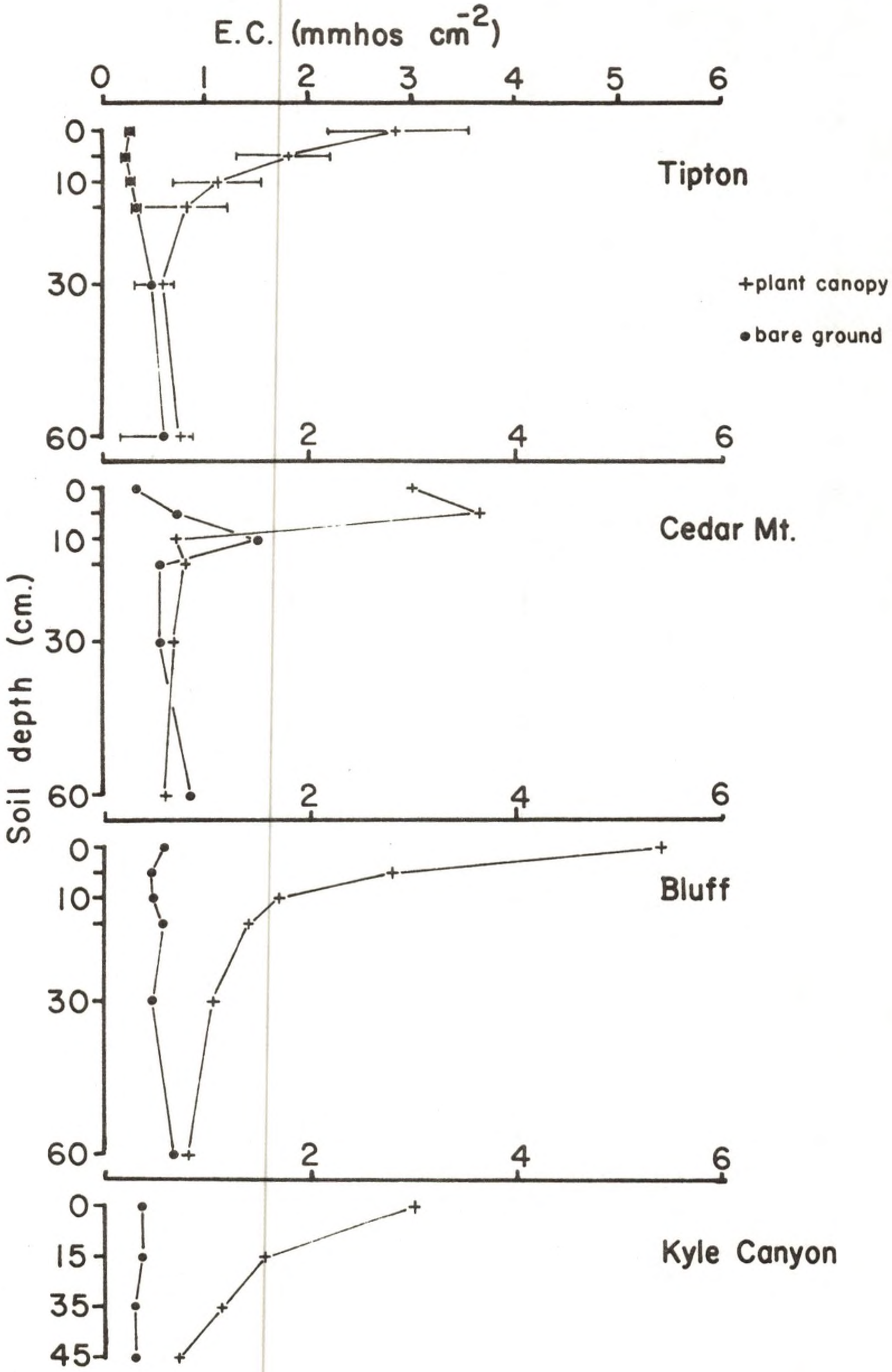
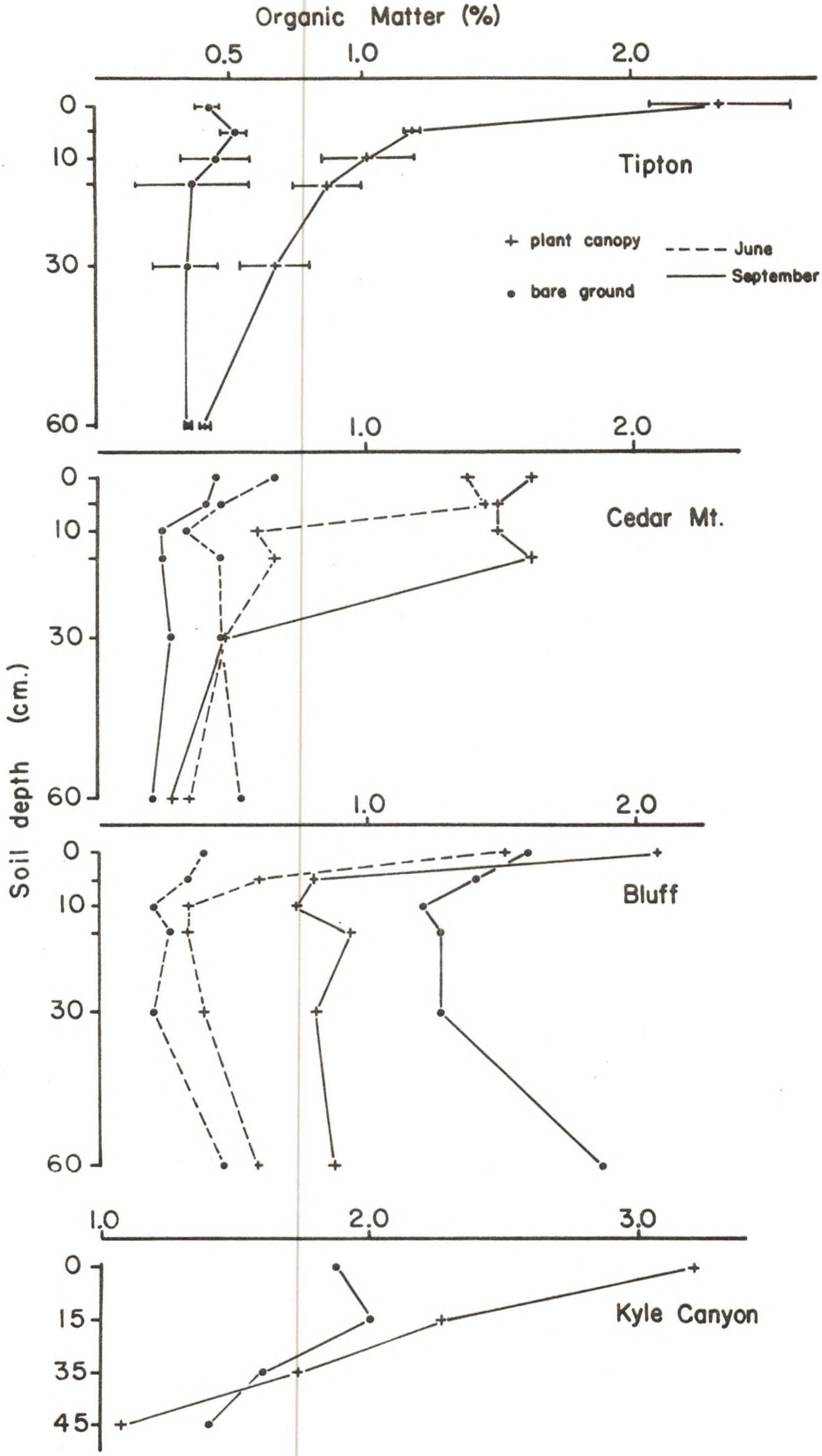

E.C. (mmhos cm^{-2})
0
1
2
3
4
5
6
Soil depth (cm.)
0
10
30
60
Tipton
+plant canopy
• bare ground
Cedar Mt.
Bluff
Kyle Canyon
15
35
45

Fig. 16: Organic matter content of vegetated and unvegetated soils.


Organic Matter (%)
0.5
1.0
2.0
3.0
Soil depth (cm.)
0
10
15
30
35
45
60
Tipton
Cedar Mt.
Bluff
Kyle Canyon
+ plant canopy
● bare ground
June
September

Total Nitrogen

Significant differences in total soil nitrogen between vegetated and unvegetated soils were measured at all depths at Tipton ($p < .01$). Nitrogen content of vegetated soils gradually decreased from less than 0.1% at the surface to near 0.02% at 60 cm (Fig. 17). Unvegetated soils were generally less than 0.04% at all depths. Cedar Mtn. and Bluff were not unlike Tipton in their profile characteristics and concentrations of total nitrogen. Samples of vegetated soils collected in September had slightly higher values in the top profile layers than did the June samples. There was less discrepency between vegetated and unvegetated soils at Bluff than either at Tipton or Cedar Mtn. The highest soil nitrogen content (0.145%) was recorded at Kyle Canyon, where vegetated soils were clearly more concentrated than unvegetated soils. Nitrogen values below 50 cm at all sites were less than 0.03%.

The relationship between percent organic matter and percent total nitrogen was calculated for soils at each site and for all soils collectively (Fig. 18, Table 12), and can be compared to other experimental regressions (Jackson 1958, Killingbeck and Wali 1978).

Carbon/Nitrogen Ratios

Carbon/nitrogen ratios for vegetated and unvegetated soils at Tipton ranged between 12.26% and 26.99%. Ratios at Cedar Mtn. were slightly higher than those at Tipton ranging between 17.39% and 35.38%. The occurrence of carbon fragments in some samples at Bluff, Utah, coupled with decreasing concentrations of total nitrogen in the profile, resulted in abnormally high carbon/nitrogen ratios for two soil profiles. Carbon/nitrogen ratios at Bluff were for the most part within

Fig. 17: Total nitrogen of vegetated and unvegetated soils.

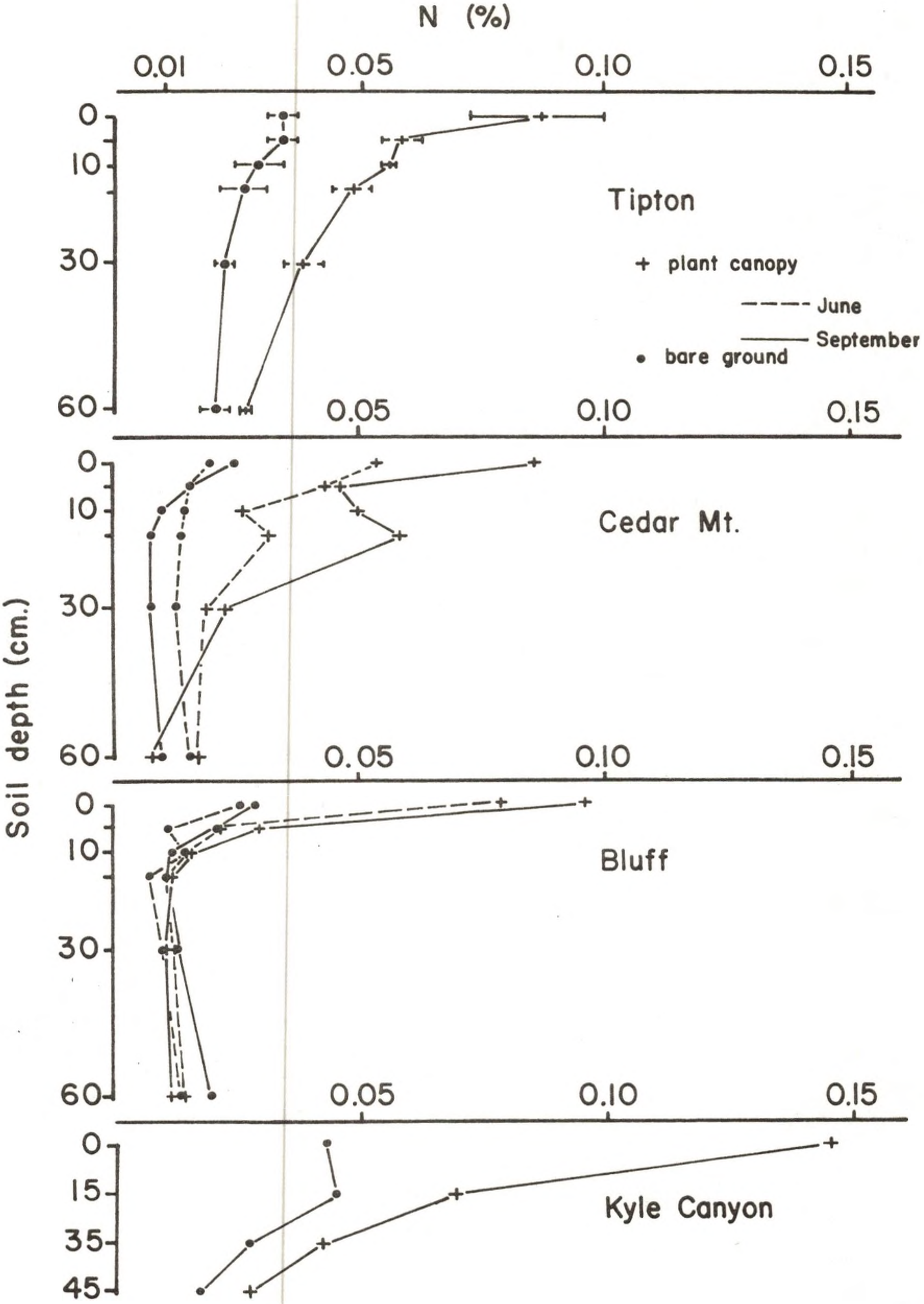

N (%)
0.01
0.05
0.10
0.15
Soil depth (cm.)
0
10
30
60
Tipton
+ plant canopy
June
September
• bare ground
Cedar Mt.
Bluff
0
15
35
45
Kyle Canyon

Fig. 18: Relationship between total nitrogen and organic matter for all soils.

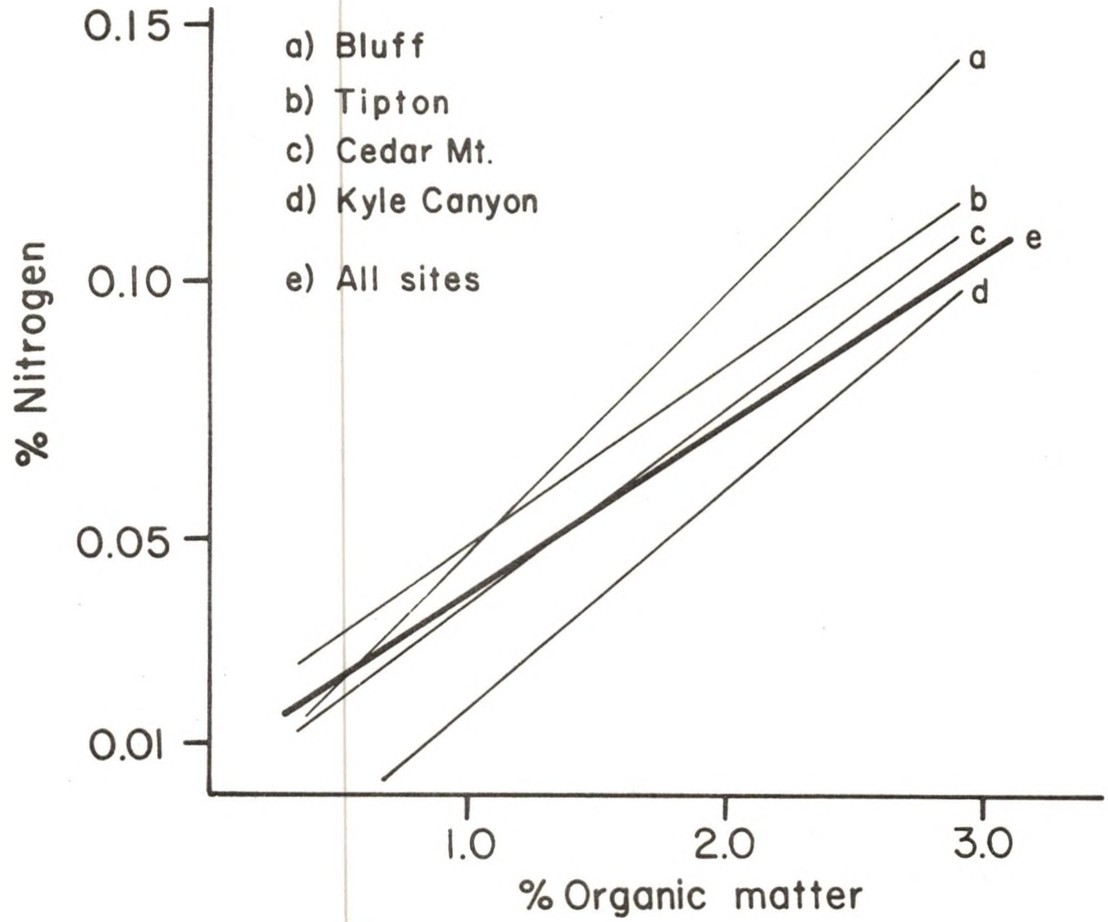

0.15
0.10
0.05
0.01
% Nitrogen
1.0
2.0
3.0
% Organic matter
a) Bluff
b) Tipton
c) Cedar Mt.
d) Kyle Canyon
e) All sites
a
b
c
e
d

Table 12. Relationships between organic matter (%) and total nitrogen (%) in soils.

Site	Equation*	r^2	Sy·x	S_0	S_1
Tipton	$Y = 0.0358 X + 0.0129 + e$	0.899	0.0057	0.0021	0.0025
Cedar Mtn.	$Y = 0.0374 X + 0.0007 + e$	0.878	0.0072	0.0024	0.0029
Bluff	$Y = 0.0508 X - 0.0036 + e$	0.900	0.0064	0.0028	0.0051
Kyle Canyon	$Y = 0.0430 X - 0.0263 + e$	0.802	0.0199	0.0151	0.0081
All Sites	$Y = 0.0333 X + 0.0058 + e$	0.745	0.0125	0.0023	0.0023

*Y = % Total Nitrogen; X = % Organic Matter; $Y = a_0 + a_1 x$;
Sy·x = standard error of estimate of y on x
S_0 = standard error of the regression coefficient a_0
S_1 = standard error of the regression coefficient a_1

the range of values recorded at Cedar Mtn. Higher C/N ratios at lower depths may be attributable to slow decomposition as was found at Kyle Canyon where C/N ratios increased from 43.9 to 80.9% in unvegetated soil profiles.

Calcium

Vegetated samples had slightly higher calcium concentrations than unvegetated soils at Tipton; however, a significant difference between the two ($p < .01$) was found only at 5 cm (Fig. 19). Mean values for these soils ranged between 4.25 me 1^{-1} and 12.50 me 1^{-1} for vegetated soils and between 2.45 me 1^{-1} and 7.68 me 1^{-1} for bare ground soils. Unlike the profile distribution at Tipton, calcium concentrations at Cedar Mtn. increased dramatically between the surface and 30 cm, where values for vegetated and unvegetated soils ranged between 35.93 me 1^{-1} and 48.90 me 1^{-1}. Vegetated surface samples contained more calcium than unvegetated soils. Soils outside the plant canopy at Bluff were similar in calcium content to unvegetated Tipton soils. However, vegetated soils were slightly more concentrated than those at Tipton ranging from 33.43 me 1^{-1} at the surface to 6.39 me 1^{-1} at 60 cm. Little change in the profile distribution of calcium was measured at Kyle, where unvegetated soils were slightly more concentrated than vegetated soils, and where both had calcium values > 6 me 1^{-1}.

Magnesium

Profile distributions of magnesium from vegetated and unvegetated soils at Tipton were very similar to those of potassium and electrical conductivity (Fig. 20). Values for vegetated soils steadily decreased from 30.6 me 1^{-1} at the surface to 4.4 me 1^{-1} at 30 cm. Little varia-

Fig. 19: Water soluble calcium of vegetated and unvegetated soils.

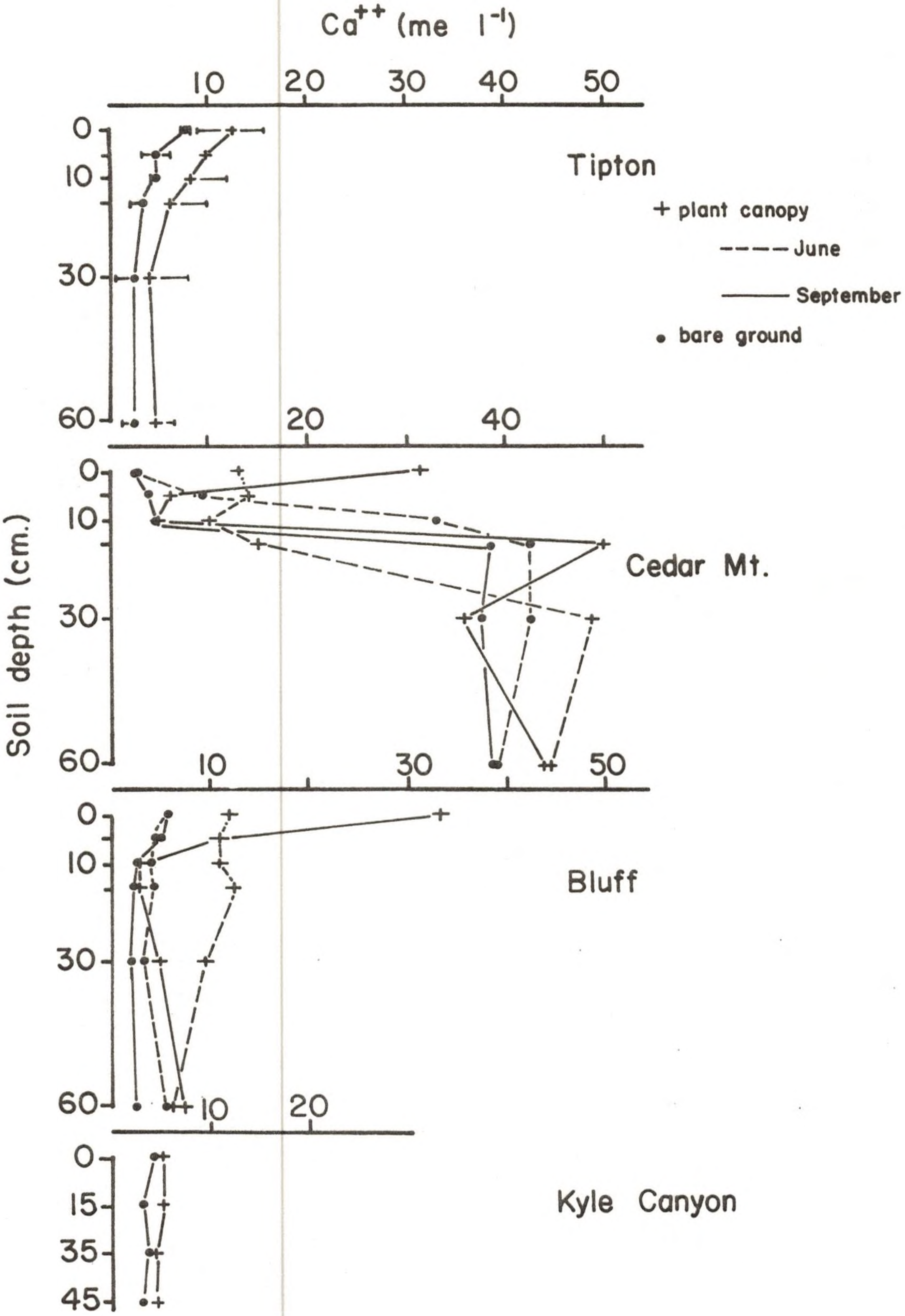
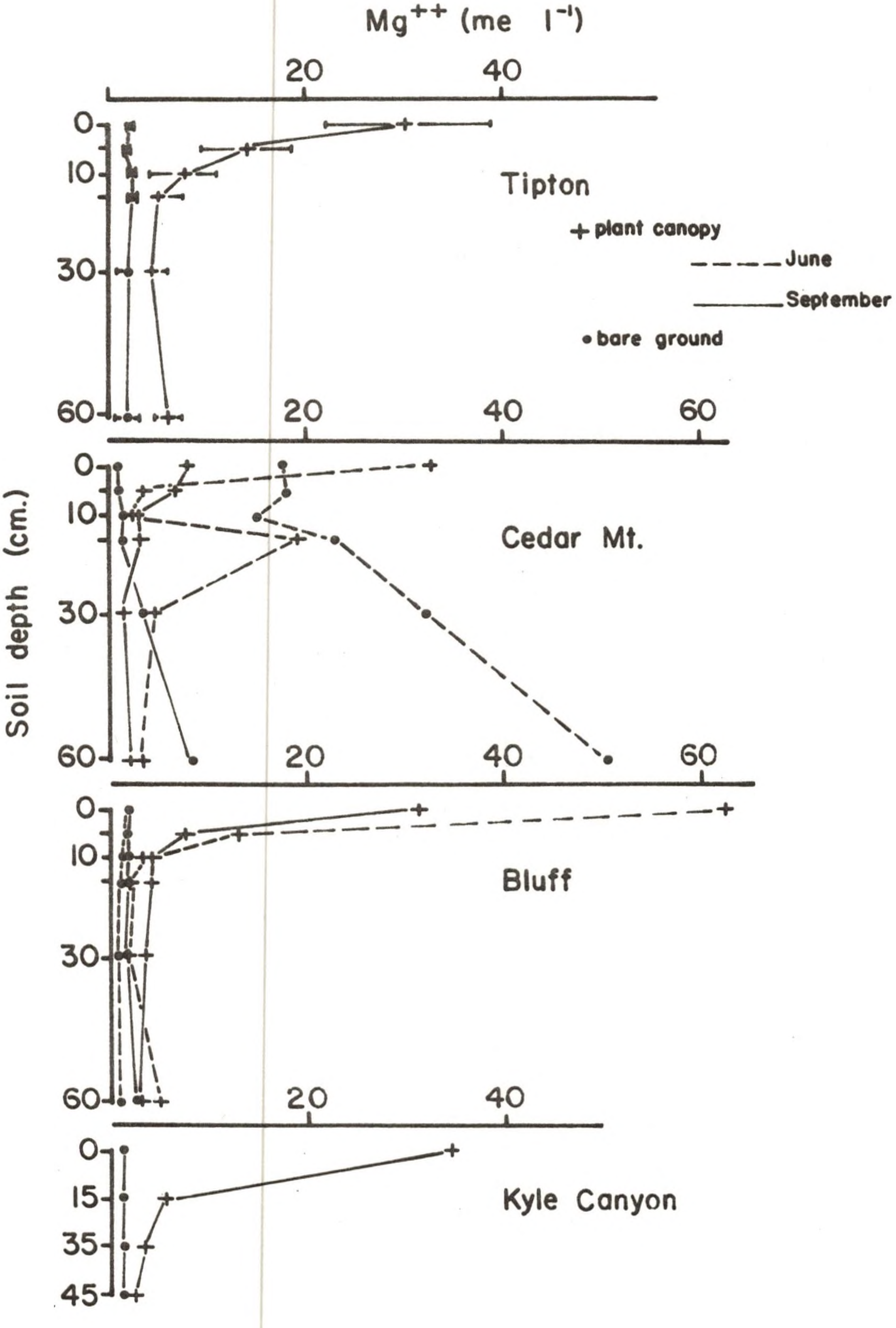

Ca⁺⁺ (me l⁻¹)
10
20
30
40
50
Tipton
+ plant canopy
June
September
• bare ground
Cedar Mt.
Bluff
Kyle Canyon
Soil depth (cm.)
0
10
30
60
15
35
45

Fig. 20: Water soluble magnesium of vegetated and unvegetated soils.


Mg++ (me l-1)
20
40
0
10
30
60
Tipton
+ plant canopy
June
September
• bare ground
20
40
60
0
10
30
60
Cedar Mt.
Soil depth (cm.)
20
40
60
0
10
30
60
Bluff
20
40
0
15
35
45
Kyle Canyon

tion in magnesium concentration was found with depth for unvegetated soils where depth means were no greater than 2.5 me 1^{-1}. Magnesium content at Cedar Mtn. seemed to increase and decrease with depth for unvegetated soils and vegetated soils, respectively. Values of vegetated soils at Cedar Mtn. were similar to those at Tipton; however, large differences in magnesium content of unvegetated soils were found: ranging from 0.82 me 1^{-1} to 17.5 me 1^{-1} at the surface, to 8.23 and 50.5 me 1^{-1} at 60 cm. The highest surface concentration (62.52 me 1^{-1}) was recorded under a canopy at Bluff. This value aside, vegetated and unvegetated profiles at this site and Kyle Canyon were not unlike those measured at Tipton.

Potassium

Water soluble potassium concentrations were higher on vegetated than unvegetated soils at all sites; a gradual decrease down the profile was measured for vegetated soils (Fig. 21). Significant differences in potassium concentrations between vegetated and unvegetated soils at Tipton were measured at 0, 5 and 60 cm ($p < .01$).

Sodium

The greatest changes in sodium concentrations at Tipton were found in unvegetated soils where values increased from 0.46 me 1^{-1} at the soil surface to 13 me 1^{-1} at 60 cm (Fig. 22). Even though the variations found at lower depths were large, sodium concentrations of unvegetated soils were significantly greater ($p < .05$) than vegetated soils at 30 and 60 cm. Similar to vegetated soils at Bluff, soil concentrations under the plant canopy at Tipton initially decreased from the surface and seemed to accumulate slightly at the lower depths. Like those at

Fig. 21: Water soluble potassium concentrations of vegetated and unvegetated soils.

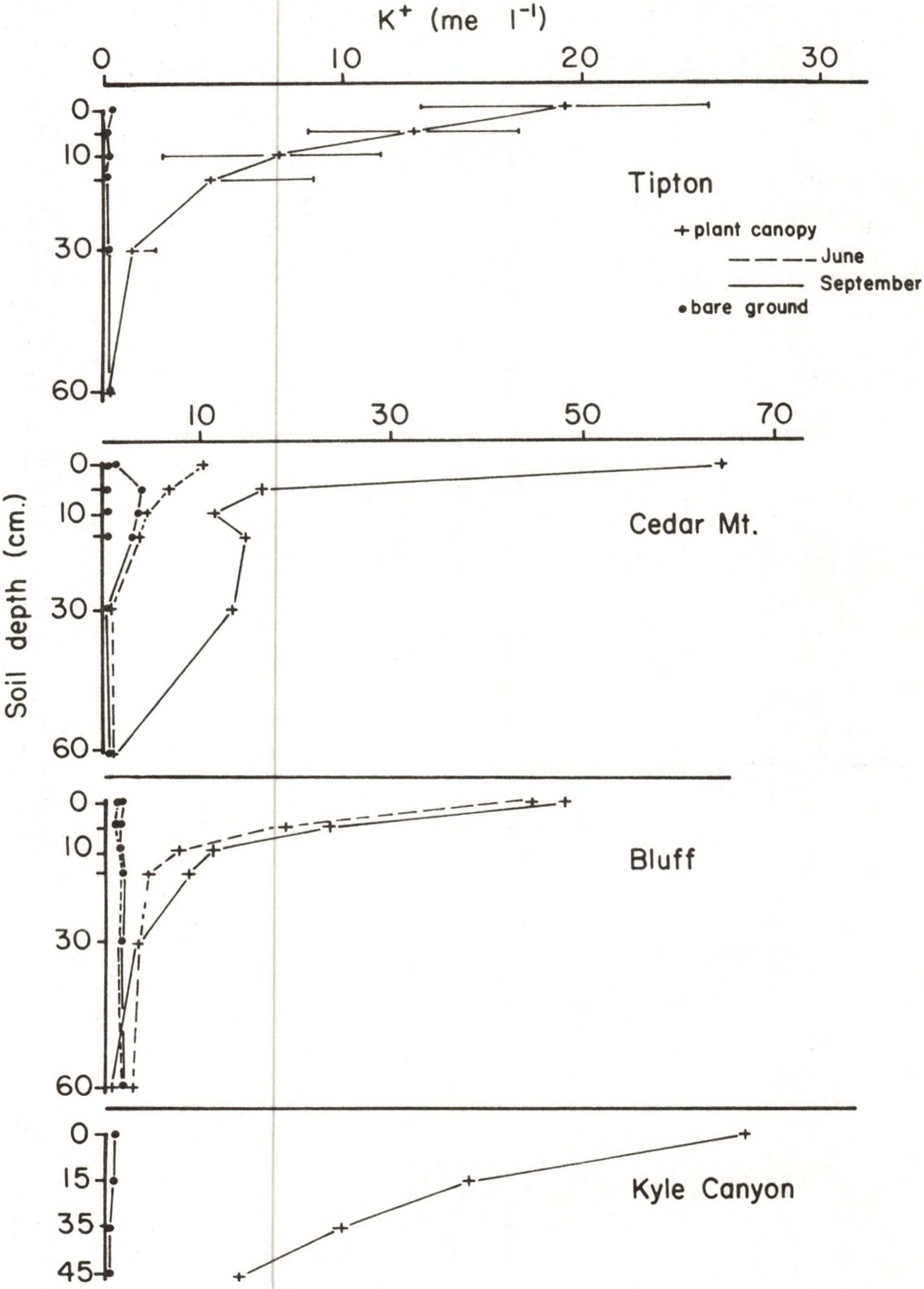
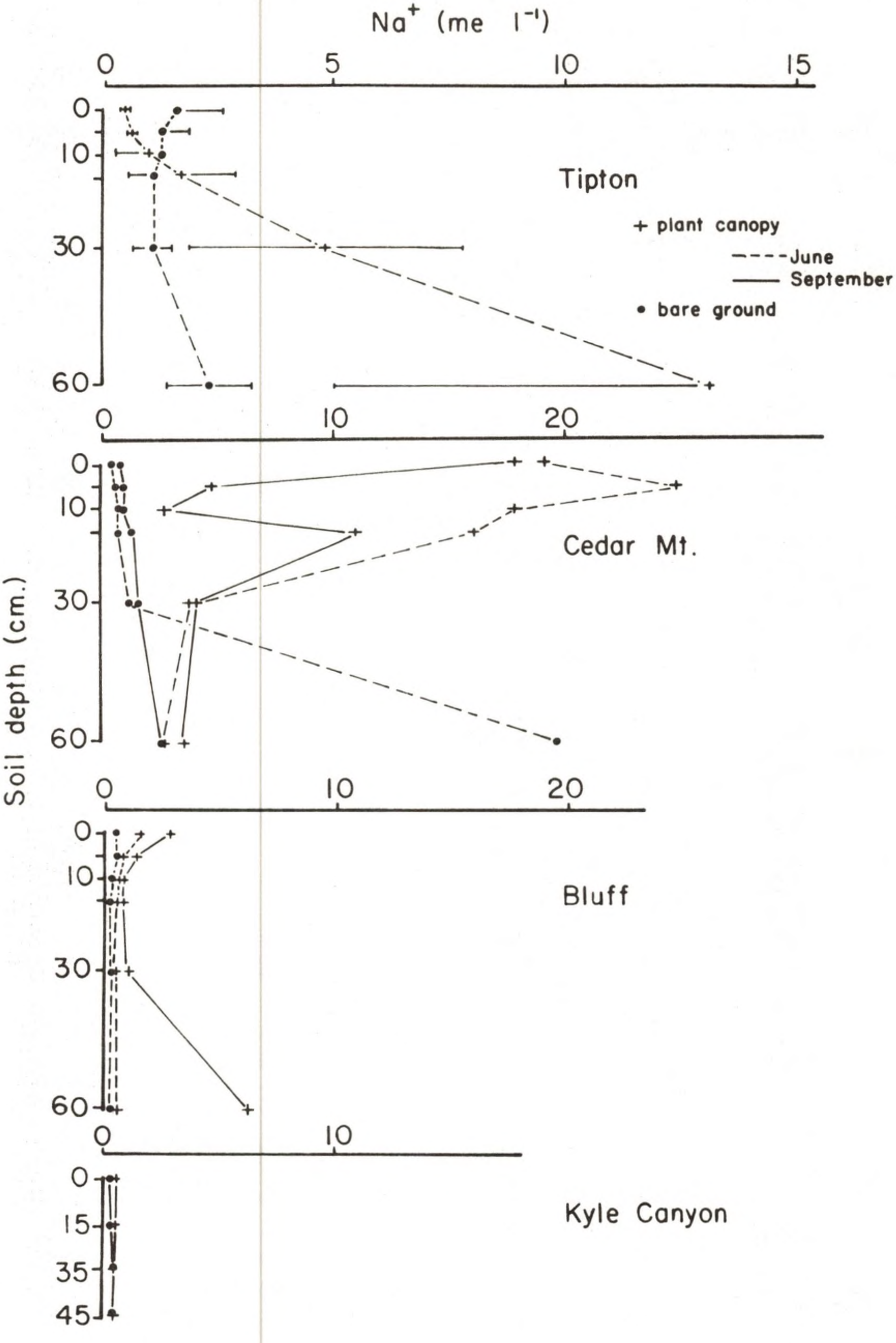

K⁺ (me l⁻¹)
0
10
20
30
Tipton
+ plant canopy
June
September
• bare ground
0
10
30
60
10
30
50
70
Cedar Mt.
Soil depth (cm.)
0
10
30
60
Bluff
0
10
30
60
Kyle Canyon
0
15
35
45

Fig. 22: Water soluble sodium of vegetated and unvegetated soils.


Na$^+$ (me l^{-1})
0
5
10
15
Tipton
+ plant canopy
- - - - June
——— September
• bare ground
Cedar Mt.
20
Bluff
Kyle Canyon
Soil depth (cm.)
0
10
30
60
15
35
45

Tipton, sodium values of unvegetated soils at Cedar Mtn. gradually increased with depth. Concentrations under the plant canopy at Cedar Mtn. were higher than vegetated soils at the other sites, generally decreasing from 20 me 1^{-1} at the surface to less than 4 me 1^{-1} at 60 cm. Unvegetated profiles from Bluff and all profiles at Kyle Canyon had sodium concentrations less than 1 me 1^{-1}.

Manganese

Significant differences in manganese levels between vegetated and unvegetated soils at Tipton were found only at the soil surface ($p < .05$) (Fig. 23). Manganese content of vegetated surface soils at the site (mean = 11.0 ppm) was the highest recorded. Values of vegetated soils from the other sites were less than 2.5 ppm and decreased with profile depth. Manganese concentrations of unvegetated soils at all sites were less than 1.0 ppm and for the most part decreased with depth.

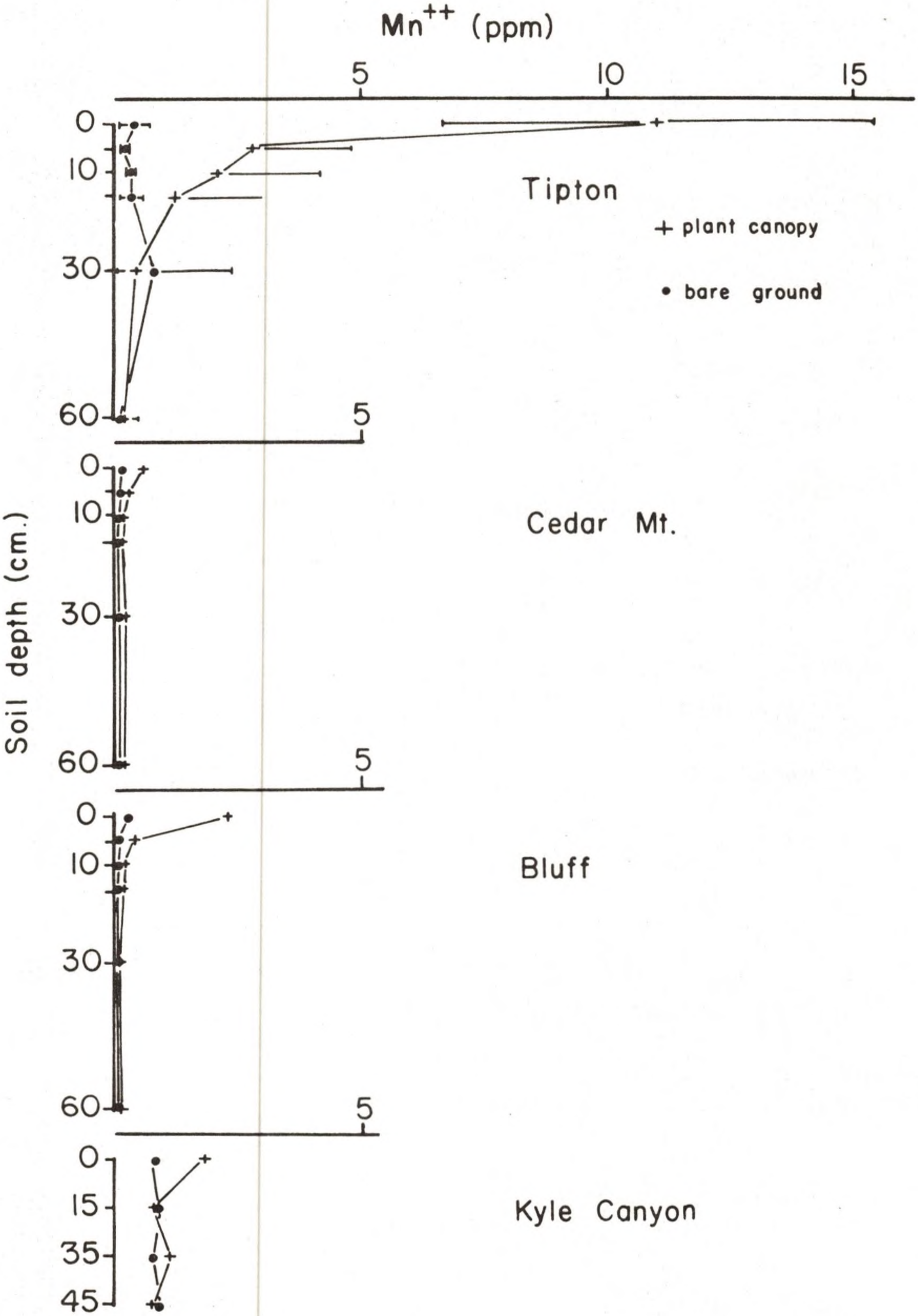
Zinc

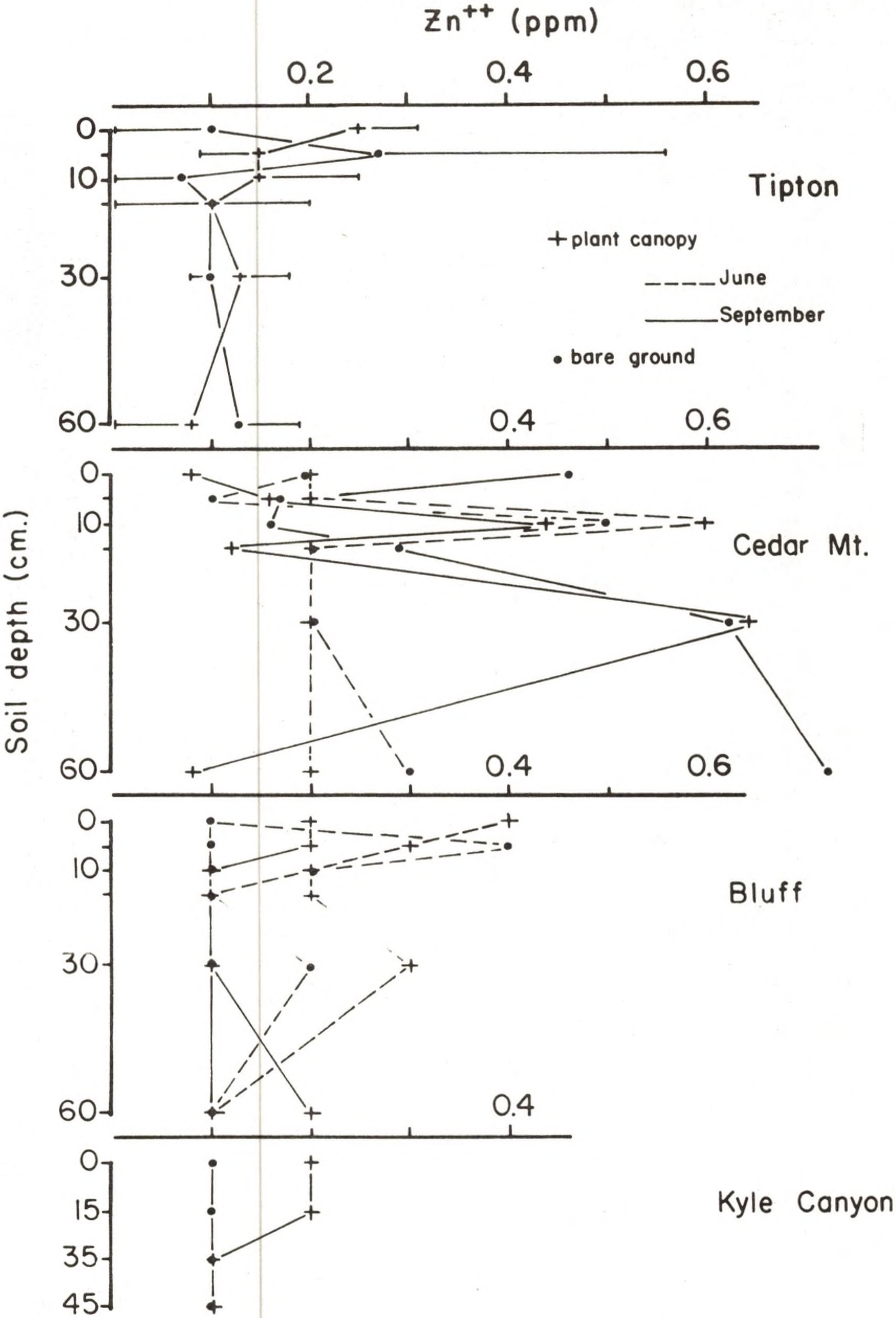
Zinc content of soils from all sites was > 0.1 ppm, however, in Tipton soils no zinc was detected in several unvegetated soils (Fig. 24). The majority of soils at the site ranged between 0.1 and 0.3 ppm. Both vegetated and unvegetated soils at Cedar Mtn. had zinc values ranging from 0.1 to 0.7 ppm. Zinc content of Bluff soils was between 0.1 and 0.4 ppm, while soils at Kyle Canyon had up to 0.2 ppm zinc.

Phosphorus

Phosphorus content of all soils generally decreased with depth showing site-specific similarities down the profiles of vegetated and

Fig. 23: Water soluble manganese concentrations of vegetated and unvegetated soils.


Mn^{++} (ppm)
5
10
15
0
10
30
60
Tipton
+ plant canopy
• bare ground
5
0
10
30
60
Cedar Mt.
Soil depth (cm.)
5
0
10
30
60
Bluff
5
0
15
35
45
Kyle Canyon


Zn++ (ppm)
0.2
0.4
0.6
Soil depth (cm.)
0
10
30
60
Tipton
+ plant canopy
June
September
• bare ground
0.4
0.6
Cedar Mt.
0.4
0.6
Bluff
0.4
Kyle Canyon
15
35
45

unvegetated soils (Fig. 25). Concentrations at Tipton ranged from 6.6 to 17.0 ppm. Higher phosphorus concentrations for vegetated soils were found consistently only at Cedar Mtn. While unvegetated soils at the site were similar to those at Tipton, vegetated soils in the top 15 cm had phosphorus values generally greater than 15 ppm. Below 5 cm, all soils at Bluff ranged between 6.2 and 14.0 ppm, not unlike values for similar depths at Kyle Canyon.

Alkaline Earth Carbonates

All soils analyzed were calcareous, values recorded were always greater than 1.95%. Large differences in percent carbonates were found among sites (Fig. 26). Surface soils at Tipton had significantly lower levels on vegetated than unvegetated soils ($p < .01$). The concentrations of unvegetated soils decreased with depth and ranged from 7.43% to 8.86%. Surface soils from vegetated sites increased with depth from 4.4% to 8.4% and below 15 cm were greater than unvegetated soils. Bare ground carbonates at Cedar Mtn. were greater than vegetated soils, in both groups of samples carbonates increased to a depth of 15 cm. The highest value measured at Cedar Mtn. was 22.05%. Concentrations, trends and percentages in the soil profiles were similar for vegetated and unvegetated soils at Bluff, Utah. Carbonate percentages for all soils at this site ranged between 1.95% to 4.45%. Vegetated soils with values between 2.70% and 3.15% were slightly higher than unvegetated soils in the top 15 cm. The highest values of carbonates measured were at Kyle Canyon where a substantial quantity of free lime was present in the form of lime concretions. Values for vegetated soils ranged between 49.0% and 49.85% of the soil, while unvegetated soils ranged from 63.25% and 75.38%.

Fig. 25: Phosphorus concentrations of vegetated and unvegetated soils.

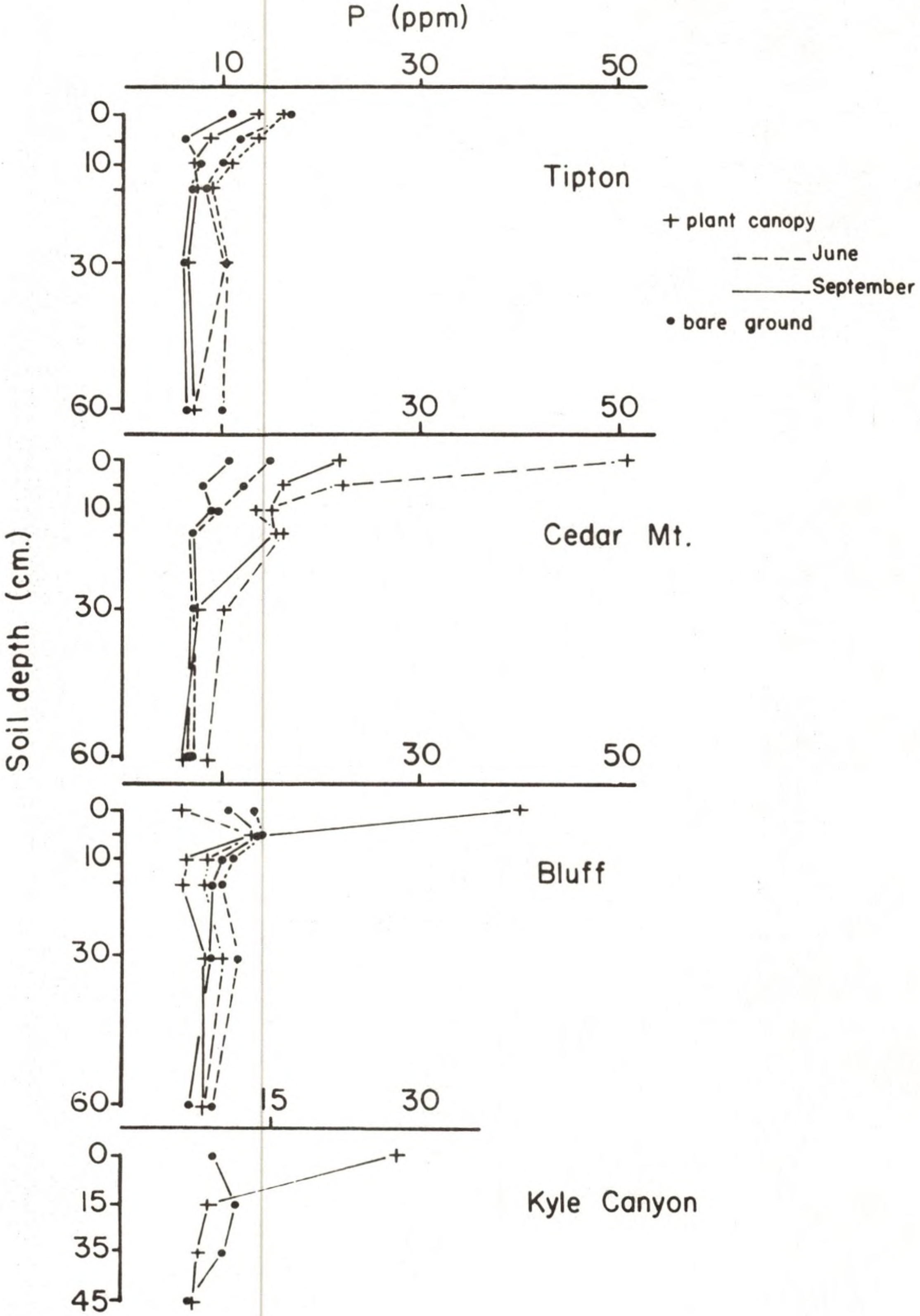
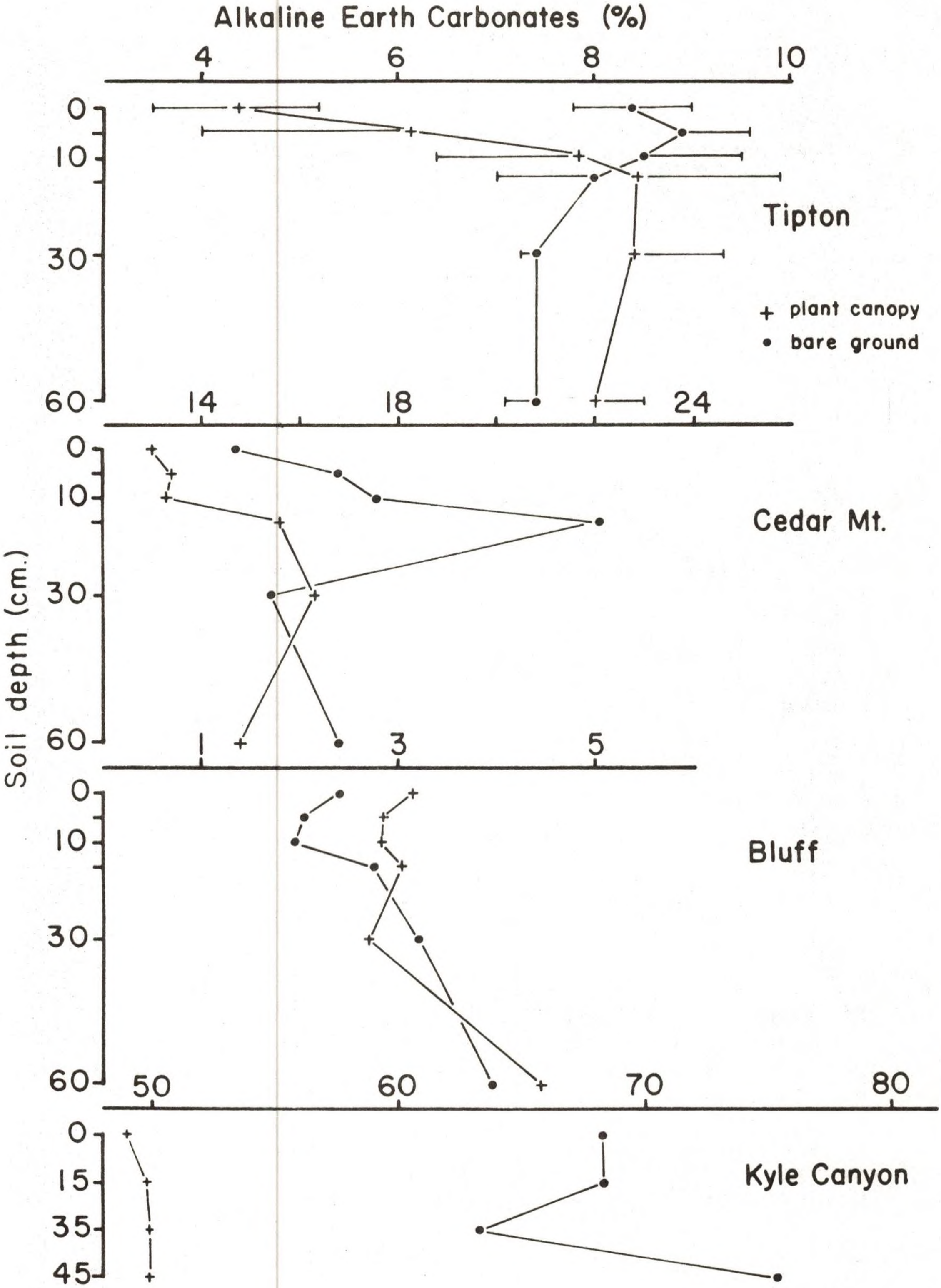

P (ppm)
10
30
50
Soil depth (cm.)
0
10
30
60
Tipton
+ plant canopy
June
September
• bare ground
30
50
0
10
30
60
Cedar Mt.
30
50
0
10
30
60
Bluff
15
30
0
15
35
45
Kyle Canyon

Fig. 26: Alkaline earth carbonate concentrations of vegetated and unvegetated soils.


Alkaline Earth Carbonates (%)
4
6
8
10
0
10
30
60
Tipton
+ plant canopy
• bare ground
14
18
24
0
10
30
60
Cedar Mt.
Soil depth (cm.)
1
3
5
0
10
30
60
Bluff
50
60
70
80
0
15
35
45
Kyle Canyon

Chloride

Chloride concentrations at Tipton were in all cases higher in vegetated than unvegetated soils (Fig. 27). Surface samples under the plant canopy had concentrations ranging from 300 to 500 ppm, which rapidly decreased to 200 ppm at 5 cm, and to 100 ppm at 60 cm. Bare ground soil samples had values below 15 ppm with the exception of one 60 cm sample at 51 ppm. Chloride concentrations in the top 15 cm of soil under the plant canopy at Cedar Mtn. were up to 100 times greater than concentrations in bare ground soils. Surface samples ranged from up to 2800 ppm on vegetated soils compared to 19 ppm on unvegetated soils. Concentrations steadily decreased below 15 cm on unvegetated soils to near 200 ppm at 60 cm. With the exception of one sample, chloride concentrations of unvegetated soils remained below 20 ppm. The differences between and range among vegetated and unvegetated soils at Bluff were similar to those measured at Cedar Mtn. Values of chloride in vegetated soils ranged between 1000 and 2000 ppm at the soil surface, decreasing steadily to 100 ppm at 60 cm. Unvegetated soil chloride concentrations were less than 20 ppm, except for a surface sample of 230 ppm probably from contamination. Concentrations at 60 cm were 10 times less on unvegetated than vegetated soils. Concentrations of chloride at the surface and by depth on vegetated soils at Kyle Canyon were considerably less than those from other sites. Concentrations at the surface were 105 ppm, decreasing to less than 15 ppm at 50 cm. All chloride values at the site on unvegetated soils were less than 10 ppm.

Sulfate

Sulfate values for soils at Tipton decreased with depth; all but one soil had less than 135 ppm (Fig. 28). Vegetated soils had higher

Fig. 27: Water soluble chloride concentrations of vegetated and unvegetated soils.

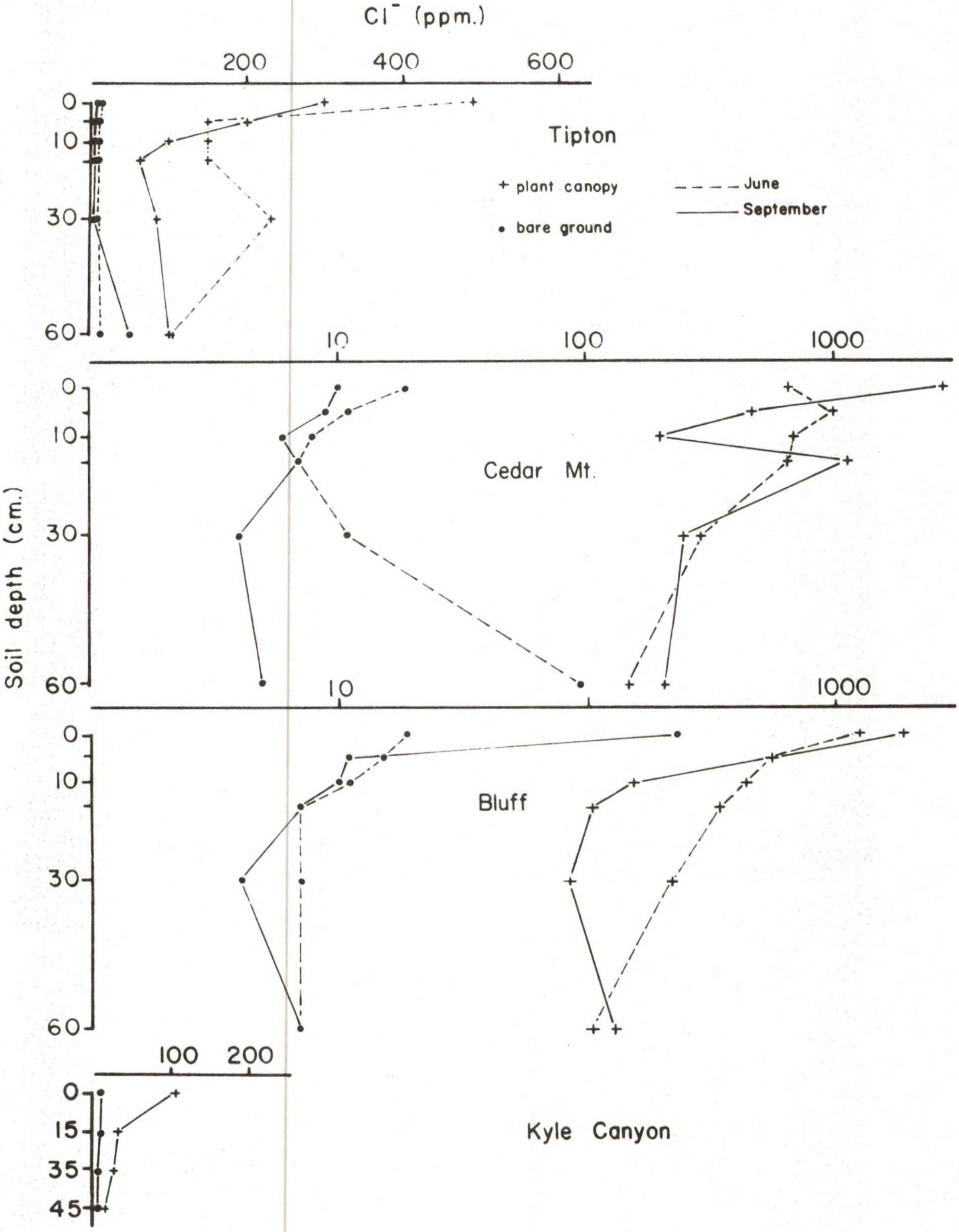
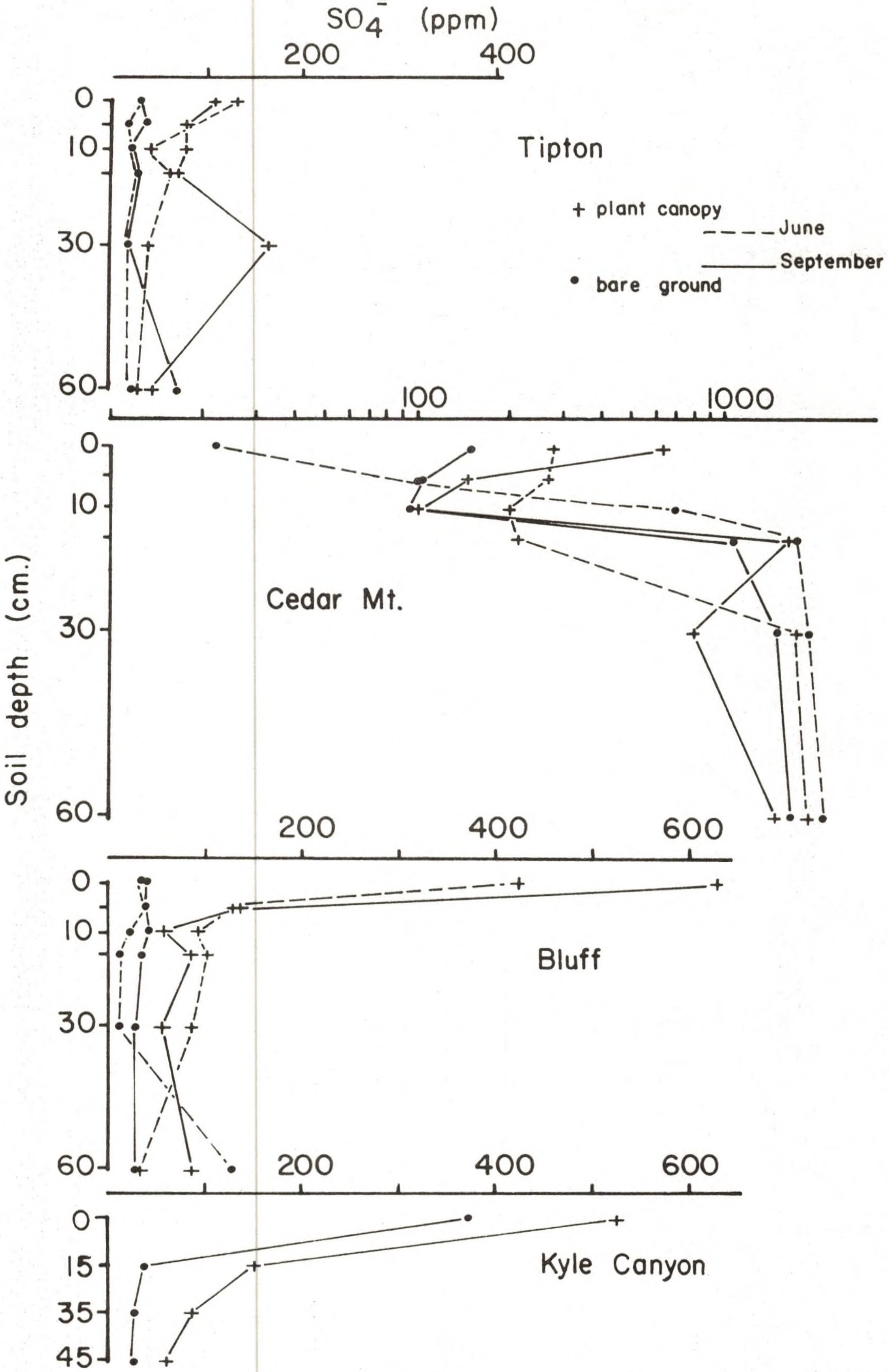

Cl⁻ (ppm.)
200
400
600
0
10
30
60
Tipton
+ plant canopy
• bare ground
June
September
10
100
1000
0
10
30
60
Cedar Mt.
Soil depth (cm.)
10
1000
0
10
30
60
Bluff
100
200
0
15
35
45
Kyle Canyon

Fig. 28: Sulfate concentrations of vegetated and unvegetated soils.


SO$_4^=$ (ppm)
200
400
0
10
30
60
Tipton
+ plant canopy
– – – – June
———— September
• bare ground
100
1000
Cedar Mt.
Soil depth (cm.)
200
400
600
Bluff
200
400
600
0
15
35
45
Kyle Canyon

values in the top 30 cm than unvegetated soils. All soils at Cedar Mtn. showed a dramatic increase in sulfate between 10 cm (100 ppm) and 60 cm (1500 to 2100 ppm). Surface samples of vegetated soils at the site were similar to those at Bluff ranging between 278 and 629 ppm. Below 5 cm, soil sulfate concentrations at Bluff were similar to those at Tipton and ranged from 11 ppm to 138 ppm. Both vegetated (524 ppm) and unvegetated (371 ppm) soils at Kyle Canyon decreased with soil depth from the surface.

Growth and Ring Analysis

Growth ring counts indicated that plants from all sites were over 100 years old. The mean age of old wood selected for growth rate estimation ranged from 41.3 ± 13.4 years at Kyle Canyon, to 71.3 ± 32.6 years at Cedar Mtn. (Table 13). The radial length of old wood ranged from 1.614 ± 0.65 cm at Tipton, to 2.589 ± 1.18 cm at Cedar Mtn. The highest growth rate of old tissue was 0.394 ± 0.03 mm/yr at Kyle Canyon. The growth rate of old wood from Bluff was also greater than either Tipton or Cedar Mtn.; however, no significant differences between sites in growth rates of old growth were found.

Mean middle growth ranged from 12.0 ± 2.4 years at Tipton to 21.8 ± 6.0 years at Bluff. Growth rates of middle wood ranged from 0.258 ± 0.03 mm/yr at Cedar Mtn. to 0.362 ± 0.02 mm/yr at Kyle Canyon. There were no significant differences in growth rates between old and middle growth at Tipton or Kyle Canyon, however, middle and old growth rates were significantly different at both Cedar Mtn. and Bluff ($p < .01$). The growth rate of middle wood at Tipton was significantly greater than that at Cedar Mtn. ($p < .01$), but not at Kyle Canyon. No differences in

Table 13. Age and growth rates of *Atriplex canescens*.

	Old n	Age (years)	Radial Length (cm)	Growth Rate (mm/yr.)	Middle n	Age (years)	Radial Length (cm)	Growth Rate (mm/yr.)
Tipton	8	44.1±15.9	1.614±0.648	a* A† 0.364±0.086	6	12.0±2.4	0.392±0.070	a A 0.330±0.033
Cedar Mtn.	7	71.3±32.6	2.589±1.184	a A 0.363±0.030	6	18.7±4.6	0.483±0.130	b B 0.258±0.014
Bluff	6	58.5±23.1	2.263±1.331	a A 0.371±0.052	6	21.8±6.0	0.611±0.195	b B 0.277±0.026
Kyle Canyon	6	41.3±13.4	1.635±0.576	a A 0.394±0.032	7	19.0±3.9	0.689±0.142	a A 0.362±0.022

*Means in the vertical column followed by the same lower case letter are not significantly different at the 5% level of probability by students *t*-test.

†Means in the horizontal row followed by the same upper case letter are not significantly different at the 5% level of probability by students *t*-test.

middle growth rates were found between Cedar Mtn. and Bluff. The highest and lowest growth rates for both middle and old wood were found at Kyle Canyon and Cedar Mtn., respectively.

Atriplex canescens was found to develop several stem branches above ground as do many shrubs. The central portion of the below ground basal stem dies and separates from within and segregates eventually into several radial arcs (Fig. 29). These arcs either constitute a portion of the main canopy or, in time, become the basal stem of a separate adult plant (Fig. 30). Both are common in fourwing saltbush. In other species, senescing individuals give rise to sprouting satellite shrubs resulting in a ring of plants which can be maintained as a clone for thousands of years (Vasek 1980).

A close association was observed between the presence of the ephemeral grass *Oryzopsis hymenoides*, and the distribution of *Atriplex canescens* and *Artemisia tridentata* at Tipton (Fig. 31a, b, c).

Biomass Production and Productivity

With the exception of plants at Tipton, all plants measured showed greater variation in diameter than height (Tables 14 and 15). Elliptical volume represented the physical space occupied by the crowns of Tipton plants, whereas cylindrical volume was chosen for the measurement of crown volume at the other sites. Although significant differences between height, diameter, and volume of pistillate and staminate plants was found only at Kyle Canyon ($p < .01$) (Table 16), the largest plant measured at each site was pistillate. The size of plants increased from Tipton to Kyle Canyon; however, Bluff was found to have the largest mean plant size. Tipton and Cedar Mtn. had more pistillate plants, while Kyle

Fig. 29: Cross section of the tap root of *Atriplex canescens* from Kyle Canyon (94 years old).

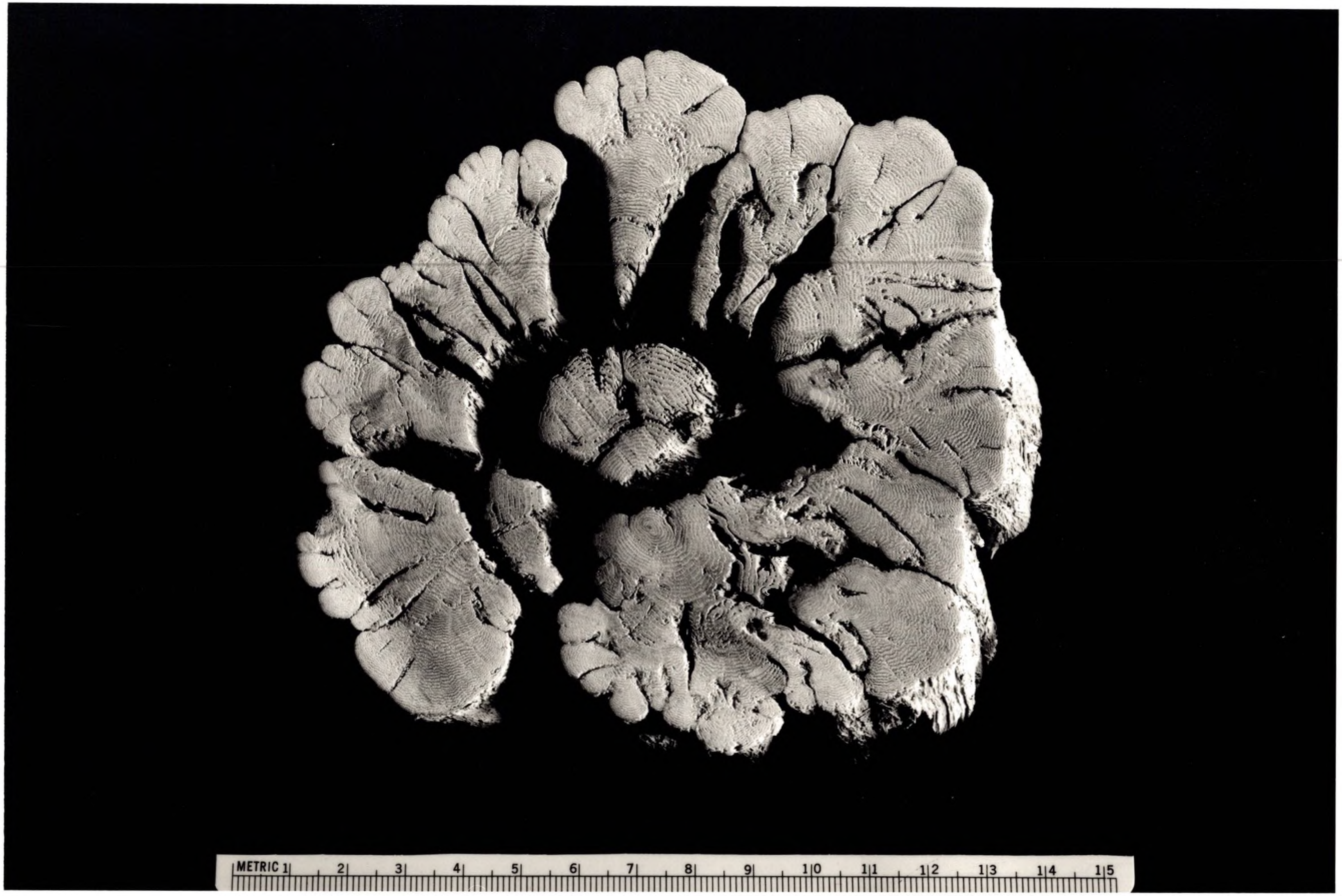

METRIC 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15

Fig. 30: Cross sections: top - arc-stem, above ground, of *Atriplex canescens* at Cedar Mountain (112 years old); bottom - basal stem (bole) of *Atriplex canescens* at Bluff (105 years old).

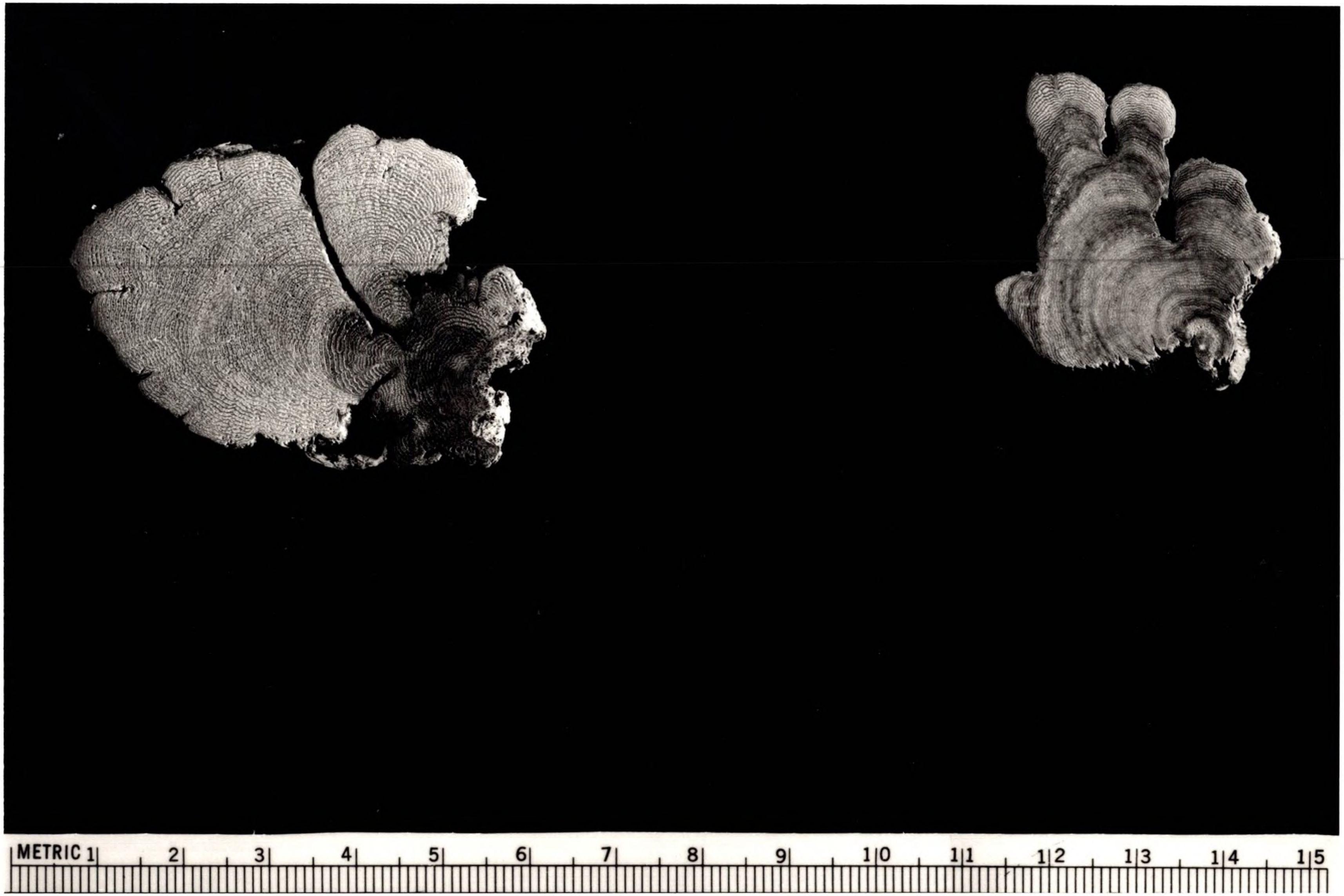
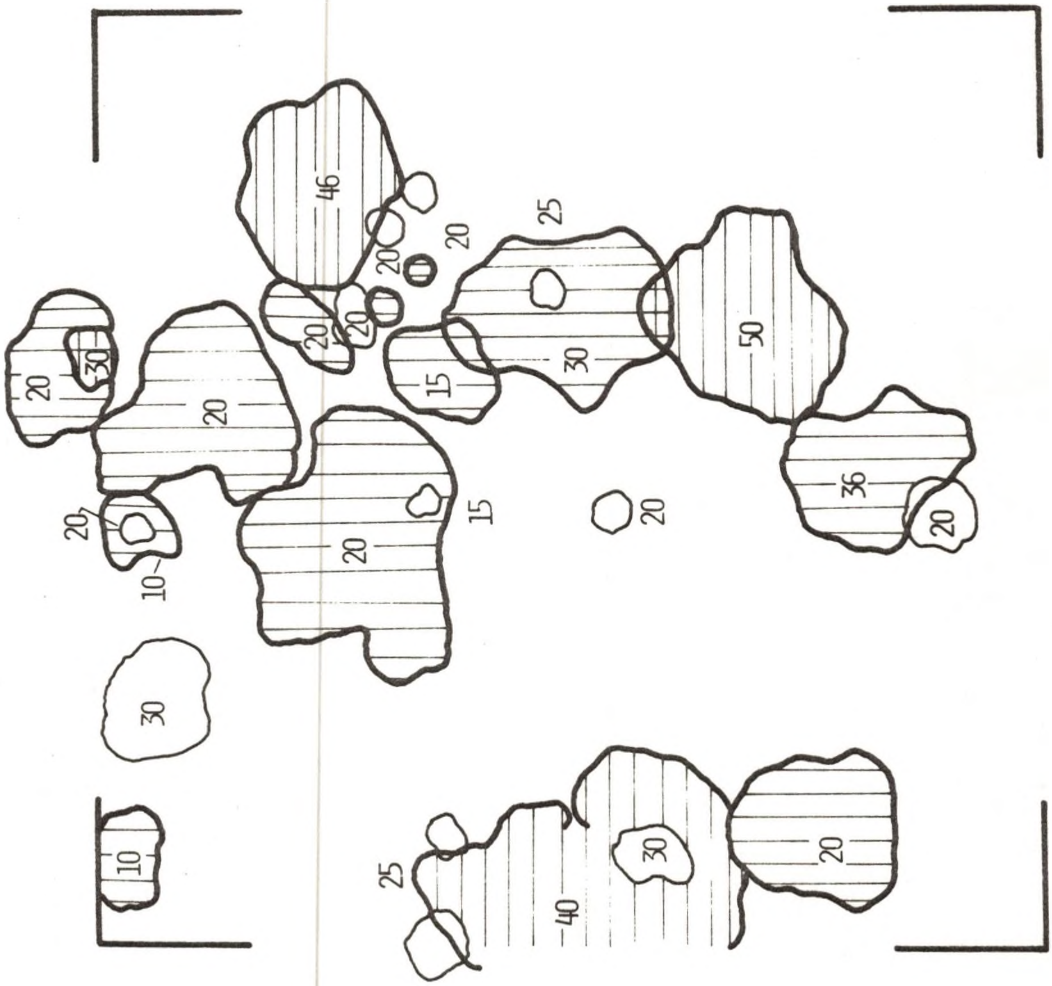

METRIC 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15

Fig. 31 (a-c): Distribution (10 m^2 plot) and height (numbered, cm) of *Atriplex canescens* (horizontal lines), *Artemisia tridentata* (vertical lines) and *Oryzopsis hymenoides* (open) at Tipton.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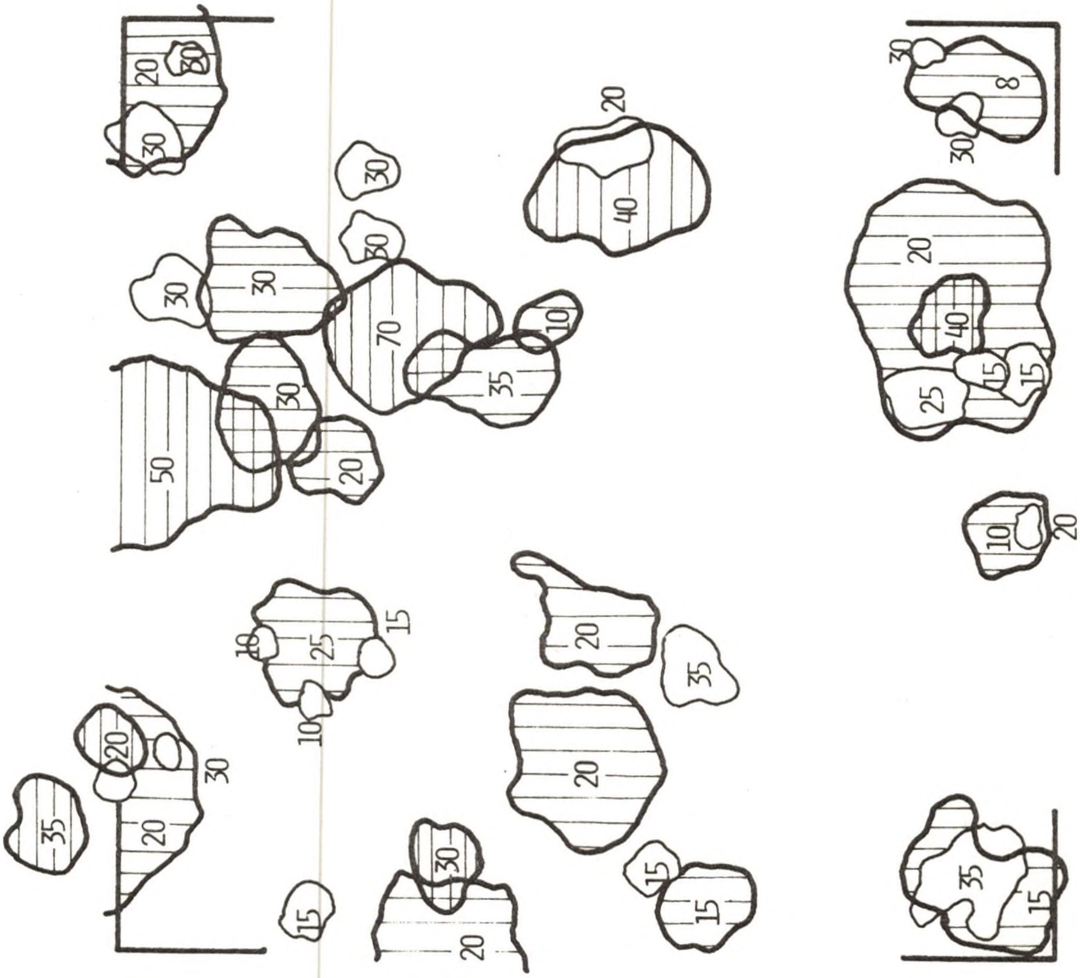
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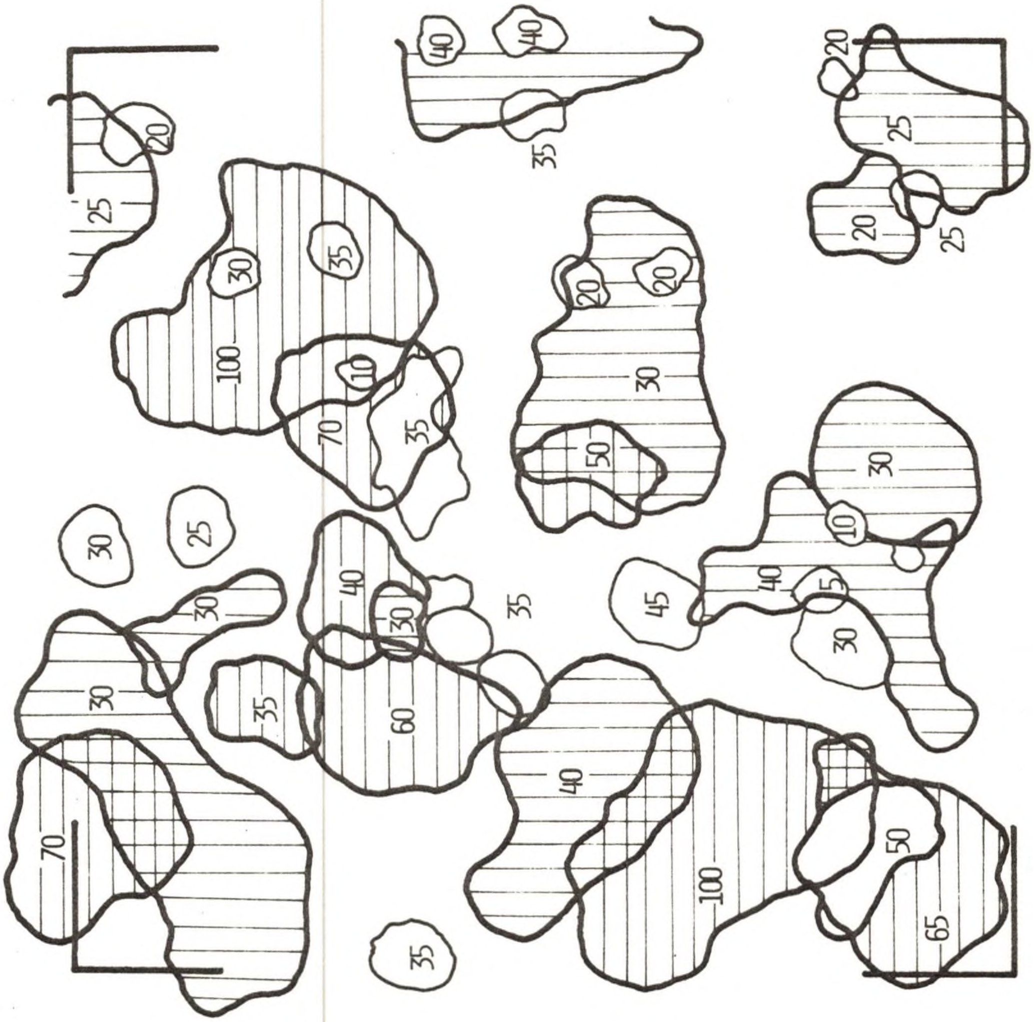
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Table 14. Size, volume and cover of plants.

	Plot size	n	♀/♂	Largest Plant (cm, m^3)	Mean (cm)	Mean Volume (m^3)	Plants ha^{-1}	% coverage
S_1 Tipton	15m x 15m	23	15/8=1.88/1	100 160 v= (2.01) ♀	h= 64±15.3 D_1= 99±7.95 D_2= 70±6.88	0.62± .48	1.022 x 10^3	7.9
S_2 Cedar Mtn.	25m x 25m	25	14/11=1.27/1	120 263 v= (6.52) ♀	h= 92±13.7 D= 135±63.8	1.77±2.11	400 plants ha^{-1}	5.7
S_3 Bluff	25m x 25m	47		130 300 v= (9.18) ♀	h= 135±18.7 D= 255±36.9	7.05±2.19	752 plants ha^{-1}	38.4
S_4 Kyle Canyon	25m x 25m	44	19/25=1/1.32	167 445 v=(26.04) ♀	h= 121±39.0 D= 236±110.5	7.71±7.77	704 plants ha^{-1}	15.41
					h= 51±41.2 D= 82±77.6	1.37±4.38	304 ♀ 400 ♂	

Table 15. Plant size statistics for Tipton (15 m x 15 m plot).

	cm		
	♀	♂	Both Sexes
n	15.0	8.0	23.0
$H\bar{X}$	65.8	59.5	63.6
HSX	12.0	20.4	15.3
$HS\bar{X}$	3.1	7.2	3.2
$D_1\bar{X}$	107.13	83.88	99.04
D_1SX	31.51	46.66	38.12
$D_1S\bar{X}$	8.14	16.50	7.95
$D_2\bar{X}$	68.47	73.50	70.22
D_2SX	26.62	44.54	32.98
$D_2S\bar{X}$	6.87	15.75	6.88
Volume m^3	$.66m^3 \pm .40$	$.53m^3 \pm .63$	$.62m^3 \pm .48$
H ♂H ♀:	t = 0.94	df = 21 (ns)	
D_1♂ D_1♀ :	t = 1.43	df = 21 (ns)	
D_2♂ D_2♀ :	t = 1.01	df = 21 (ns)	

Canyon the staminate. Sex ratios at Bluff were not recorded. The highest number of plants ($1022\ ha^{-1}$) and lowest densities ($400\ ha^{-1}$) of *Atriplex canescens* were recorded at Tipton and Cedar Mtn., respectively. The largest coverage of all sites by the species was 38% of the ground space at Bluff, the lowest of 5.7% was at Cedar Mtn. Although the densities of plants at Bluff and Kyle Canyon were similar, the coverage at Kyle Canyon appeared less due to the wide range of plant size.

Table 16. Plant size statistics for Kyle Canyon (25 m x 25 m).

♂H	$\bar{X}$ = 50.76	SX = 41.2;	$S\bar{X}$ = 8.24	t = 5.73**	df = 42
♀H	$\bar{X}$ = 120.95;	SX = 38.95;	$S\bar{X}$ = 8.93		
♂D	$\bar{X}$ = 82.16;	SX = 77.55;	$S\bar{X}$ = 15.51	t = 5.42**	df = 42
♀D	$\bar{X}$ = 235.74	SX = 110.54;	$S\bar{X}$ = 25.36		
♂V	$\bar{X}$ = 1.37;	SX = 4.38;	$S\bar{X}$ = 0.88	t = 3.43**	df = 42
♀V	$\bar{X}$ = 7.71;	SX = 7.77;	$S\bar{X}$ = 1.78		
Both Sexes	H = 81.07 cm ± 53.10				
	D = 148.5 cm ± 120.				
	V = 4.11 m^3 ± 6.79				

The mean total plant biomass of the four harvested plants from Tipton was 3.2 kg (Table 17). The middle component (B_m) was the largest for each plant averaging 53% of the total plant weight. The contribution of old biomass (B_o) varied from 13% of the smallest plant to 41% for the largest plant. Both pistillate plants had smaller B_o but greater B_c (current biomass) than the two staminate individuals measured resulting in a B_o/B_c ratio near 1 for the site. The compactness of the male plant is evident from comparisons of plants 2 and 4. An increase in diameter and height of 20 and 3 cm, respectively, for the pistillate plant resulted in estimates of 42% increase in volume and 234% increase in total biomass.

Of the two staminate plants measured at Cedar Mtn., plant 3 had a diameter 16 cm greater and a height 12 cm less than plant 1. Yet plant 3 had over twice the standing total biomass; this is attributable chiefly to its age, and thus much higher values for B_o and B_m. The pistillate

Table 17. Plant size and biomass statistics for *Atriplex canescens*.

	cm		V				
	D	H	(m^3)	B_c[a]	B_m[b]	B_o[c]	B_t[d]
Tipton							
♂	150	100	2.01	874 g (16%)	2243 g (42%)	2201 g (41%)	5.32 kg
♂	140	83	1.28	976 g (20%)	2793 g (59%)	1005 g (21%)	4.77 kg
♀	100	60	0.47	425 g (31%)	775 g (57%)	174 g (13%)	1.37 kg
♀	120	80	0.90	431 g (31%)	759 g (55%)	235 g (17%)	1.43 kg
$\overline{X}$	130 ± 25.82	80.75 ± 16.4	1.17 ± .65	676.5 g ± 289.9	1642.5 g ± 1035.6	903.75 g ± 943.9	3.22 kg ± 2.12
Cedar Mtn.							
♂	112	100	0.98	472 g (38%)	499 g (40%)	280 g (22%)	1.25 kg
♀	263	120	6.52	1563 g (10%)	6124 g (39%)	8154 g (51%)	15.84 kg
⚥	128	88	1.13	349 g (13%)	1407 g (51%)	1016 g (37%)	2.77 kg
$\overline{X}$	168 ± 83	103 ± 16	2.88 ± 3.16	795 g ± 668	2677 g ± 3019	3150 g ± 4349	6.62 kg ± 8.02
Bluff							
♀	288	140	9.12	5.11 kg (31%)	6.31 kg (38%)	4.97 kg (30%)	16.39 kg
$\overline{X}$	255 ± 37	135 ± 19	7.05 ± 2.19				

Table 17. (Continued)

	cm		V				
	D	H	(m^3)	B_c[a]	B_m[b]	B_o[c]	B_t[d]
<u>Kyle Canyon</u>							
♀	295	170	11.62	4.99 kg (31%)	5.403 kg (34%)	5.595 kg (35%)	15.99 kg
$\bar{X}$ ♀	236 ± 111	121 ± 39	7.71 ± 7.77				
$\bar{X}$ ♂	82 ± 78	51 ± 41	1.37 ± 4.38				

a current biomass, net annual production; b middle growth; c old growth; d total standing biomass.

plant sampled was one of the larger plants at the site. The high B_o/B_c and B_o/B_m values for this plant in comparison to the two staminate plants raises the mean B_o value for the site to 47%, which is considerably higher than the other three sites. The $\%B_o$ and $\%B_m$ on an average for the three plants were 37% and 43% respectively. In any case, the $\%B_o$ was greater than for Tipton, whereas B_m and B_c were lesser.

The biomass values for the plants at Bluff and Kyle Canyon appear similar. The plant at Bluff had a more dense growth form, being smaller than the plant at Kyle Canyon, yet had a larger biomass--owing to the larger $\%B_m$. The B_c for both Bluff and Kyle Canyon were identical and at least 50% larger than the mean values for Tipton and Cedar Mtn. The B_c values of the two pistillate plants at Tipton were 31% each.

The percent twigs (%T) comprised the largest portion of annual production for the male and female plants from Tipton (Table 18). The percent annual production of leaves (%L) was similar for each plant. The %T for the staminate plant was considerably larger than for the pistillate plant. Fruit production represented approximately one third of the annual growth.

The $\%B_c$ of total biomass was much less for the two plants at Cedar Mtn. than for Tipton plants; yet the %L for the male and female plants was similar to the values recorded from Tipton. The %T occupied the largest portion of annual production for the plants at Cedar Mtn. while %F accounted for the least (21%). The %T/%L ratio for both plants was identical (1.5).

The %T of the Bluff pistillate plant was 37%, similar to the pistillate plants of Tipton and Cedar Mtn. The %L and %F accounted for the smallest (22%) and the largest (41%) portions of the B_c, respectively.

Table 18. Components of Current Productivity for *Atriplex canescens*.

			g			%		
			Leaves	Fruit	Twigs	Leaves	Twigs	Fruit
Tipton	♂	Plant 2	160.4	--	288.5	36	64	--
Tipton	♀	Plant 4	43.2	43.0	51.6	31	38	31
Cedar Mtn.	♀	Plant 2	101.1	67.6	147.0	32	47	21
Cedar Mtn.	♂	Plant 3	104.5	--	155.0	40	60	--
Bluff	♀		96.5	181.0	165.8	22	37	41
Kyle Canyon	♀		53.0	362.0	127.0	10	23	67

The results were similar at Kyle Canyon; however, the %L (10%) and %F (67%) were the smallest and largest components of the four sites. Although $\%B_c$ from Tipton, Bluff, and Kyle Canyon were identical, there was an increase percentage expenditure for reproduction over these sites.

Data from the four plants weighed from Tipton were used to develop regression equations using the least squares method where plant biomass (kg) was used as the dependent variable and crown volume (m^3) as the independent variable. Linear relationships for B_t, B_o, B_m, and B_c are shown in Table 19. The mean plant volume for Tipton (0.62 m^3) was used in these equations in order to compute a mean site value for productivity. The data obtained showed that the average plant weight ($B_t\bar{x}$) was 1.69 kg and had an annual production ($B_c\bar{x}$) comprising 24% of the standing biomass of 0.40 kg $plant^{-1}$ yr^{-1}. Middle biomass was the largest component accounting for over one-half of the biomass. This mean plant production in conjunction with plant density, estimates the standing biomass (1.727×10^3 kg ha^{-1}) and net annual production (0.409×10^3 kg $plant^{-1}$ yr^{-1}) for *Atriplex canescens* at Tipton, Wyoming.

Plant volume was found to be equally satisfactory in predicting B_t, B_o, B_m and B_c (Table 20). The mean plant volume (1.77 m^3) similarly resulted in the biomass components for a hypothetical plant weighing 4 kg and having a standing net annual productivity of 0.51 kg. Unlike Tipton, B_o accounted for the largest portion of the plant (47%), and B_c the least (13%). Since the density of the species at Cedar Mtn. is nearly one-third that at Tipton, and B_c represents only 13% of B_t of the mean plant weight, the annual production at Cedar Mtn. (0.203×10^3 kg ha^{-1} yr^{-1}) is approximately one-half that for Tipton, despite the larger mean plant size at Cedar Mtn. (4 kg $plant^{-1}$ compared to 1.69 kg $plant^{-1}$).

Table 19. Estimation of productivity and biomass by regression methods for *Atriplex canescens* at Tipton, Wyoming.

$B_T = -0.07 + 2.84X_v + e$	$r^2 = 0.88^{**}$	$Sy \cdot x = 0.95$	$S_o = 0.71$	$S_1 = 0.61$
$B_o = -0.31 + 1.11X_v + e$	$r^2 = 0.88^{**}$	$Sy \cdot x = 0.36$	$S_o = 0.27$	$S_1 = 0.24$
$B_m = 0.13 + 1.27X_v + e$	$r^2 = 0.71^{**}$	$Sy \cdot x = 0.72$	$S_o = 0.54$	$S_1 = 0.47$
$B_c = 0.12 + 0.45X_v + e$	$r^2 = 0.78^{**}$	$Sy \cdot x = 0.21$	$S_o = 0.16$	$S_1 = 0.14$

$$\text{density} = \frac{23 \text{ plants}}{(15 \text{ m}^2)} \quad \frac{10{,}000 \text{ m}^2}{\text{ha}} = 1.022 \text{ X } 10^3 \text{ plants ha}^{-1}$$

mean crown volume = 0.62 m^3

B_T = 1.69 kg/plant	$1.727 \text{ X } 10^3$ kg/ha
B_o = 0.38 kg/plant	$0.388 \text{ X } 10^3$ kg/ha
B_m = 0.92 kg/plant	$0.940 \text{ X } 10^3$ kg/ha
B_c = 0.40 kg/plant/yr	$0.409 \text{ X } 10^3$ kg/ha-yr

$B_m/B_o = 2.42$ $B_m/B_c = 2.30$ $B_o/B_c = 0.95$

Table 20. Estimation of productivity and biomass by regression methods for *Atriplex canescens* at Cedar Mtn., Utah.

$B_T = -0.38 + 2.48\ X_v$	$r^2 = 0.99^{**}$	$Sy \cdot x = 0.67$	$S_o = 0.44$	$S_1 = 0.13$
$B_o = -0.46 + 1.31\ X_v$	$r^2 = 0.99^{**}$	$Sy \cdot x = 0.51$	$S_o = 0.33$	$S_1 = 0.10$
$B_m = -0.03 + 0.94\ X_v$	$r^2 = 0.99^{**}$	$Sy \cdot x = 0.38$	$S_o = 0.25$	$S_1 = 0.08$
$B_c = 0.11 + 0.23\ X_v$	$r^2 = 0.98^{**}$	$Sy \cdot x = 0.13$	$S_o = 0.08$	$S_1 = 0.02$

$$\text{density} = \frac{25\text{ plants}}{625\text{ m}^2} \quad \frac{10{,}000\text{ m}^2}{\text{ha}} = 400\text{ plants ha}^{-1}$$

mean crown volume = 1.77 m^3

$B_T = 4.00$ kg/plant	$1.600 \times 10^3\text{ kg ha}^{-1}$
$B_o = 1.86$ kg/plant	$0.744 \times 10^3\text{ kg ha}^{-1}$
$B_m = 1.64$ kg/plant	$0.656 \times 10^3\text{ kg ha}^{-1}$
$B_c = 0.51$ kg/plant/yr	$0.203 \times 10^3\text{ kg ha}^{-1}\text{ yr}^{-1}$

$B_m/B_o = 0.88$ $\quad B_m/B_c = 3.22$ $\quad B_o/B_c = 3.65$

Production estimates for Bluff and Kyle Canyon were based initially on the single harvested plant (Table 21). However, these values are an overestimation, since the volumes for these two plants are not representative of all plants at each site. To calculate a more reasonable estimation of production for the two sites the following were used: data from all plants weighed, and mean plant statistics from Tables 19 and 20. These data (Table 22) were incorporated into a species-specific predictive model for *Atriplex canescens.* The resultant equations show linear relationships predicting biomass (B_T, B_o, B_m and B_c) for the species over an extensive range (Table 23). All r^2 values were greater than or equal to 0.90.

Using these equations (Table 23, Fig. 32) and a mean plant volume of 7.05 m^3, the mean plant biomass components for Bluff were calculated (Table 24). From these values, the total standing biomass for Bluff (8.550 X 10^3 kg ha^{-1}), and the net annual productivity (2.482 X 10^3 kg ha^{-1} yr^{-1}) appeared to be in all cases to be at least 20% less than the values estimated in Table 21.

Since a significant size difference between the two sexes was found at Kyle Canyon, separate volumes and densities (staminate plants: 1.37 m^3, 400 plants ha^{-1}; pistillate plants: 7.71 m^3, 304 plants ha^{-1}) were used in the equations from Table 23 for the estimation of productivity for the site (Table 24). The resultant mean plant weight for pistillate and staminate plants was 12.33 kg and 3.25 kg, respectively. These predicted biomass values times their respective densities, in addition, yielded an overall B_T for the site of 5.048 X 10^3 kg ha^{-1}, an annual production of 1.332 X 10^3 kg ha^{-1} yr^{-1}. These values show that the calculations based on the single pistillate plant harvested were

Table 21. Biomass (kg) and productivity (kg ha^{-1} yr^{-1}) estimates for Bluff and Kyle Canyon based on single plant.

	Volume	Density	B_T	B_o	B_m	B_c
Bluff	9.12	752 plants ha^{-1}	16.39	4.97	6.31	5.11
			12.325×10^3	3.737×10^3	4.745×10^3	3.843×10^3
Kyle Canyon	11.62	704 plants ha^{-1}	15.99	5.60	5.403	4.99
			11.257×10^3	3.942×10^3	2.804×10^3	3.513×10^3

Table 22. Biomass values used to generate species-specific prediction equations for four study sites.

	$V(m^3)$	kg				
		B_T	B_o	B_m	B_c	
Tipton $\bar{X}$	1.17	3.22	0.904	1.643	0.677	Volume and biomass values are from the means of the 4 plots measured and weighed.
$\widehat{\text{Tipton}}$	0.62	1.69	0.38	0.92	0.40	The 0.62 is the mean volume for plants measured; $\bar{X}v$ is then used to solve predicative equations.
Cedar Mtn. $\bar{X}$	2.88	6.62	3.15	2.68	0.80	Volume and biomass values from 3 plants weighed.
$\widehat{\text{Cedar Mtn.}}$	1.77	4.01	1.86	1.63	0.52	Mean volume of <u>all</u> measured plants; $\bar{X}v$ used in site 2 prediction equations.
Bluff	9.12	16.39	4.97	6.31	5.11	Actual values from the 1 plant measured.
Kyle Canyon	11.62	15.99	5.60	5.403	4.99	Actual values for the 1 plant measured.

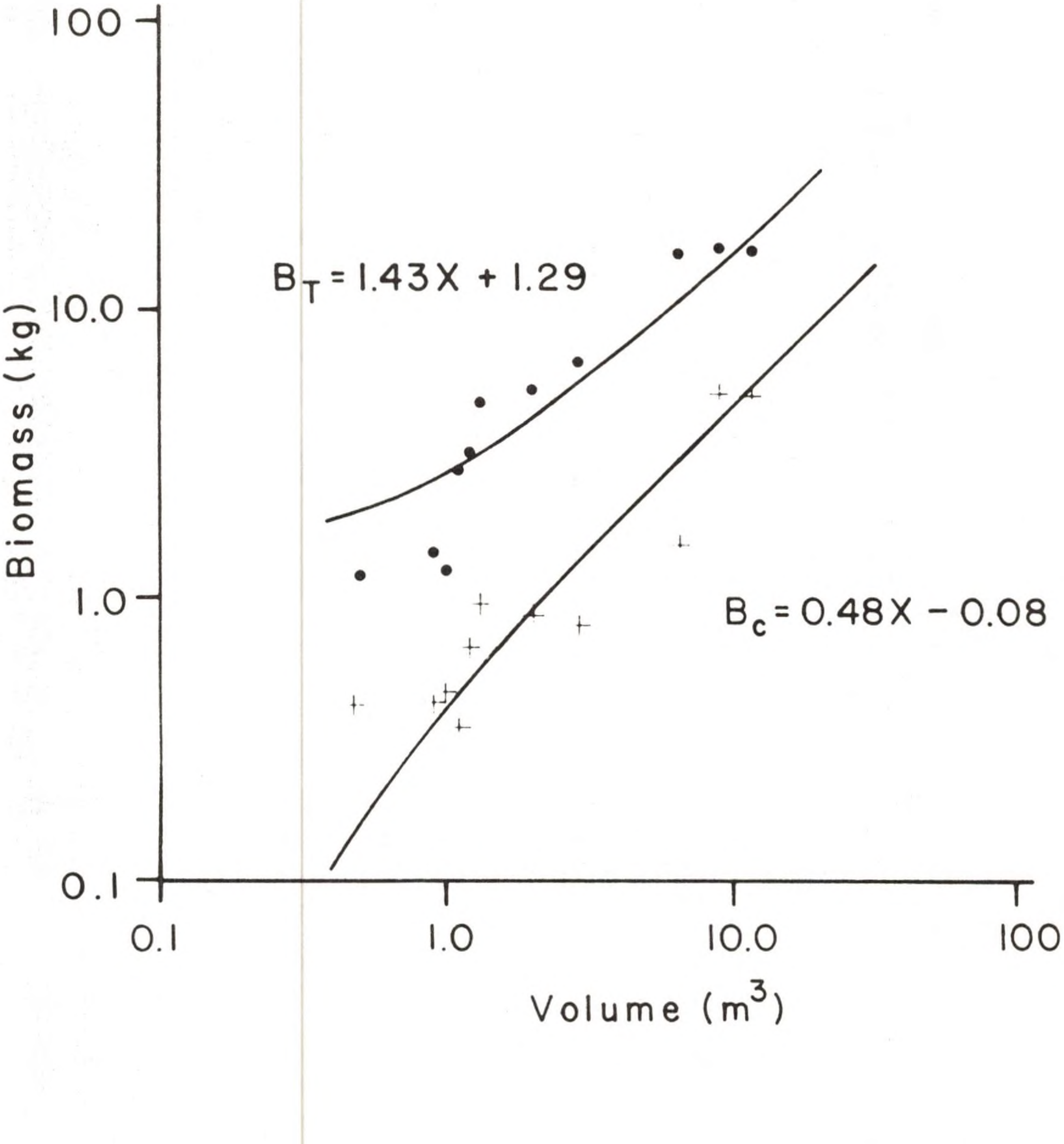
Table 23. Species-specific prediction equations of productivity and standing biomass of *Atriplex canescens*.

$B_T = 1.29 + 1.43\ Xv + e$	$r^2 = 0.96$	$Sy{\cdot}x = 1.51$	$S_o = 0.77$	$S_1 = 0.13$
$B_o = 0.60 + 0.47\ Xv + e$	$r^2 = 0.92$	$Sy{\cdot}x = 0.71$	$S_o = 0.36$	$S_1 = 0.06$
$B_m = 0.77 + 0.49\ Xv + e$	$r^2 = 0.90$	$Sy{\cdot}x = 0.80$	$S_o = 0.41$	$S_1 = 0.07$
$B_c = -0.08 + 0.48\ Xv + e$	$r^2 = 0.96$	$Sy{\cdot}x = 0.51$	$S_o = 0.26$	$S_1 = 0.05$

Species-specific power curve relationships for production of *Atriplex canescens*.

$B_T = 2.66\ X^{0.78} + e$	$r^2 = 0.99^{**}$
$B_o = 0.82\ X^{0.87} + e$	$r^2 = 0.91^{**}$
$B_m = 1.38\ X^{0.67} + e$	$r^2 = 0.88^{**}$
$B_c = 0.47\ X^{0.94} + e$	$r^2 = 0.90^{**}$

Fig. 32: Predictive relationship between total crown volume and standing total biomass (or net annual productivity) for *Atriplex canescens* from the four study sites.



100
10.0
1.0
0.1
Biomass (kg)
0.1
1.0
10.0
100
Volume (m^3)
$B_T = 1.43X + 1.29$
$B_c = 0.48X - 0.08$

Table 24. Mean productivity and biomass of *Atriplex canescens* at Bluff and Kyle Canyon.

		kg			
	V(m^3)	B_T	B_o	B_m	B_c
Bluff	7.05	11.37	3.91	4.22	3.30
Kyle Canyon ♂	1.37	3.25	1.24	1.43	0.58
Kyle Canyon ♀	7.71	12.33	4.19	4.52	3.62

more of an overestimation than were the values for Bluff. Estimated biomass and productivity data for all sites (Table 25) as well as the relationships between the various plant components (Table 26) were recorded. The production from these equations can be compared to estimations based on production from a single plant harvested (Table 27).

Seed production was estimated using seed weight per 500 seeds, seed mass per plant (= %F X $B_c\overline{x}$), and assuming an equal sex ratio. The calculated weight of seeds on the plants weighed from each site was: Tipton, 133.61 g; Cedar Mtn., 328.23 g; Bluff, 2.10 kg; Kyle Canyon, 3.34 kg (Table 28). However, the calculated weight of seeds on a plant of mean size was: Tipton, 124.0 g; Cedar Mtn., 107.1 g; Bluff, 1.35 kg; Kyle Canyon, 2.34 kg (Table 28). Because the %F for plants at Cedar Mtn. was less than that for Tipton, the mean plant at Tipton had a greater production per plant of seeds (5.46×10^3 seeds) than did plants from Cedar Mtn. (4.86×10^3 seeds). The calculated yields of seeds for Tipton and Cedar Mtn. were 63.36 kg ha^{-1} and 21.42 kg ha^{-1}, respectively. Pistillate plants at Bluff and Kyle Canyon yielded not only a much larger quantity of seeds per plant (6.54×10^4 seeds and 1.56×10^5 seeds), but also a dramatic increase in yield per hectare (507.6 kg ha^{-1} and 855.4 kg ha^{-1}). The largest expected yield per plant from any site was for Kyle Canyon (5.33×10^5 seeds) (Table 29).

Plant Analyses

Concentrations of the cations K, Ca, Mg, Na (in that order) decreased from leaves, fruits, twigs, middle, and old growth (Tables 30-33). Potassium values of leaf tissue ranged from 2.82% at Cedar Mtn. to 6.05% at Tipton. Leaves and fruit had at least twice as much potassium

Table 25. Net annual productivity and standing biomass of *Atriplex canescens* at study sites, from species-specific prediction relationships.

	kg ha^{-1}			B_c
	B_T	B_o	B_m	(kg ha^{-1} yr^{-1})
Tipton	1.727×10^3	0.388×10^3	0.940×10^3	0.409×10^3
Cedar Mtn.	1.600×10^3	0.744×10^3	0.656×10^3	0.203×10^3
Bluff	8.550×10^3	2.940×10^3	3.173×10^3	2.482×10^3
Kyle Canyon	5.048×10^3	1.770×10^3	1.946×10^3	1.332×10^3

Table 26. Biomass ratios and percentages of plant components from prediction equations.

	$\frac{B_m}{B_o}$	$\frac{B_m}{B_c}$	$\frac{B_o}{B_c}$	%		
				B_o	B_m	B_c
Tipton	2.42	2.30	0.95	22	54	24
Cedar Mtn.	0.88	3.22	3.65	47	40	13
Bluff	1.27	1.23	0.97	30	38	31
Kyle Canyon	0.97	1.08	1.12	35	34	31

Table 27. Predicted biomass values for largest plants at the sites.

	m^3	kg			
		B_c	B_m	B_o	B_T
Tipton*	2.01	.874	2.243	2.201	5.32 kg
Cedar Mtn.*	6.52	1.563	6.124	8.154	15.84 kg
Bluff	9.18	4.33 kg	5.27 kg	4.91 kg	14.42 kg
Kyle Canyon	26.04	12.42 kg	13.53 kg	12.84 kg	38.53 kg

*Actual plant weights.

Table 28. Top: Seed biomass and production based on single plant harvested.
Bottom: Seed biomass and production estimated for plant of mean size.

		Wt. of 500 Seeds	Seed wt.	Calculated wt. of seeds per plant
Tipton	(511 ♀ ha^{-1})	11.36 g	44.01 seeds g^{-1}	133.61 g
Cedar Mtn.	(200 ♀ ha^{-1})	11.02 g	45.37 seeds g^{-1}	328.23 g
Bluff	(376 ♀ ha^{-1})	10.32 g	48.45 seeds g^{-1}	2.10 kg
Kyle Canyon	(352 ♀ ha^{-1})	7.80 g	64.10 seeds g^{-1}	3.34 kg
Tipton*		11.36 g	44.01 seeds g^{-1}	124.0 g
Cedar Mtn.*		11.02 g	54.37 seeds g^{-1}	107.1 g
Bluff*		10.32 g	48.45 seeds g^{-1}	1.35 kg
Kyle Canyon*	(304 ♀ ha^{-1})	7.80 g	64.10 seeds g^{-1}	2.43 kg
Kyle Canyon*	(352 ♀ ha^{-1})	7.80 g	64.10 seeds g^{-1}	2.43 kg

*The calculated wt. of seeds on the plants obtained from seeds per plant.

Table 28. (Continued)

		Calculated no. of seeds per plant	Wt. of seeds / ha	# seeds ha^{-1}
Tipton	(511 ♀ ha^{-1})	$5.88x10^{3}$ seeds	68.27 kg ha^{-1}	$3.00x10^{6}$ seeds ha^{-1}
Cedar Mtn.	(200 ♀ ha^{-1})	$14.89x10^{3}$ seeds	65.65 kg ha^{-1}	$2.98x10^{6}$ seeds ha^{-1}
Bluff	(376 ♀ ha^{-1})	$101.7\ x10^{3}$ seeds	$7.88x10^{2}$ kg ha^{-1}	$3.82x10^{7}$ seeds ha^{-1}
Kyle Canyon	(352 ♀ ha^{-1})	$2.14x10^{5}$ seeds	$1.18x10^{3}$ kg ha^{-1}	$7.53x10^{7}$ seeds ha^{-1}
Tipton*		$5.45x10^{3}$ seeds	63.36 kg ha^{-1}	$2.79x10^{6}$ seeds ha^{-1}
Cedar Mtn.*		$4.86x10^{3}$ seeds	21.42 kg ha^{-1}	$0.97x10^{6}$ seeds ha^{-1}
Bluff*		$6.54x10^{4}$ seeds	507.6 kg ha^{-1}	$2.46x10^{7}$ seeds ha^{-1}
Kyle Canyon*	(304 ♀ ha^{-1})	$1.56x10^{5}$ seeds	738.72 kg ha^{-1}	$4.74x10^{7}$ seeds ha^{-1}
Kyle Canyon*	(352 ♀ ha^{-1})	$1.56x10^{5}$ seeds	855.4 kg ha^{-1}	$5.49x10^{7}$ seeds ha^{-1}

*The calculated wt. of seeds on the plants obtained from seeds per plant.

Table 29. Expected yield of seeds from the largest plant at each site.

	Size	Wt. of 500 seeds	Seed wt.	Calculated wt. of seeds per plant	Calculated no. of seeds per plant
Tipton	(2.01 m^3)	11.36 g	44.01 seeds g^{-1}	274.3 g	1.21×10^4 seeds
Cedar Mtn.	(6.52 m^3)	11.02 g	45.37 seeds g^{-1}	640.4 g	2.91×10^4 seeds
Bluff	(9.18 m^3)	10.32 g	48.45 seeds g^{-1}	1.77 kg	8.58×10^4 seeds
Kyle Canyon	(26.04 m^3)	7.80 g	64.10 seeds g^{-1}	8.32 kg	5.33×10^5 seeds

Expected seed yield from largest plant (volume put into the 4-site equations).
Wt. of seeds = $(\%F)\ (Bc\bar{X})$.

Table 30. Cation and anion concentrations of *Atriplex canescens* - Tipton.

	CATIONS								
	% dry weight				ppm				
	Na	K	Ca	Mg	Mn	Zn	Li	Fe	Cu
Leaves	0.13±.17	5.36±.50	1.65±.32	1.20±.27	88±29	25±18	2	240	8
Fruit	0.03±.01	4.50±.07	0.81±.09	0.62±.08	39± 4	22± 1	1		
Twigs	.01±.01	1.28±.16	0.46±.13	0.29±.04	56±12	20± 9	0		
Middle	.01±0	0.50±.10	0.28±.04	0.19±.01	88±16	29±22	0		
Old	.02±0	0.48±.03	0.30±.11	0.20±.03	125±30	12± 5	0		

	ANIONS			
	% dry weight			ppm
	N	Cl	Oxalate	P
Leaves	2.05	1.96	1.56±.32	875± 50
Fruit	0.95	1.80	0.76±.08	525±247
Twigs	0.82	1.07	0.39±.08	488±125
Middle	0.61	0.78		213± 48
Old	0.78	0.55		311± 68

Table 31. Cation and anion concentrations of *Atriplex canescens* - Cedar Mtn.

CATIONS

	% dry weight				ppm				
	Na	K	Ca	Mg	Mn	Zn	Li	Fe	Cu
Leaves	0.77±1.03	4.61±1.55	2.06±.26	0.73±.14	48± 8	37±12	5	3800	10
Fruit	0.11	4.10	1.11	0.48	24	41	3		
Twigs	0.07± .08	1.21± .21	0.82±.07	0.20±.05	32± 9	15± 6	1		
Middle	0.03± .02	0.47± .07	0.52±.09	0.16±.03	59±16	23± 3	0		
Old	0.03± .02	0.35± .11	0.86±.29	0.16±.04	89±29	15± 4	0		

ANIONS

	% dry weight			ppm
	N	Cl	Oxalate	P
Leaves	1.93	2.14	1.48±0.13	817±236
Fruit	1.93	1.96	0.70	650
Twigs	0.67	1.23	0.59±0.08	383±153
Middle	0.58	0.66		167± 29
Old	0.67	0.47		252± 31

Table 32. Cation and Anion Concentrations of *Atriplex canescens* - Bluff.

CATIONS

	% dry weight				ppm				
	Na	K	Ca	Mg	Mn	Zn	Li	Fe	Cu
Leaves	0.03	3.83	1.80	0.92	27	26	6	240	11
Fruit	0.02	3.10	1.65	0.82	35	21	5		
Twigs	0.01	1.26		0.24	27	43	1		
Middle	0.01	0.75	0.46	0.22	42	31	0		
Old	0.01	0.48	1.06	0.25	101	21	0		

ANIONS

	% dry weight			ppm
	N	Cl	Oxalate	P
Leaves	1.61	2.35	1.19	1550
Fruit	1.37	2.14	0.70	800
Twigs	1.00	0.83	0.41	700
Middle	0.78	0.59		250
Old	1.00	0.38		216

Table 33. Cation and Anion Concentrations of *Atriplex canescens* - Kyle Canyon.

CATIONS

	% dry weight				ppm				
	Na	K	Ca	Mg	Mn	Zn	Li	Fe	Cu
Leaves	0.01	2.96	2.87	1.82	36	72	1	160	7
Fruit	0.01	2.55	1.83	1.17	27	21	1		
Twigs	0.01	1.23	0.73	0.36	12	10	1		
Middle	0.01	0.69	0.46	0.25	29	29	0		
Old	0.01	0.45	0.17	0.19	37	8	0		

ANIONS

	% dry weight			ppm
	N	Cl	Oxalate	P
Leaves	1.93	0.36	2.22	1300
Fruit	1.52	0.47	1.57	1050
Twigs	0.82	0.34	0.65	650
Middle	0.58	0.33		250
Old	0.64	0.31		270

than other plant parts. Calcium content of the leaves was less variable, ranging from 1.32 to 2.87% whereas values for magnesium were between 0.65 and 1.82% dry weight. Highest levels of both calcium and magnesium were found at Kyle Canyon. Sodium content of leaves was less than the other major cations and exhibited large intrasite variation, ranging from 0.04 to 1.95% at Cedar Mtn.

The highest levels of manganese on a per plant basis were found in middle and old growth, which in many cases were 50% higher than leaf concentrations. Manganese content of leaves from all plants ranged from 27 to 122 ppm, and old growth concentrations from 37 to 166 ppm. Although the mean iron content of leaves from Tipton, Bluff, and Kyle Canyon was 213 ppm, iron levels in plants from Cedar Mtn. rose to a level of 0.38% dry weight. Zinc concentrations were not always the highest in leaf tissue, but usually least in old growth. Values of zinc in leaf tissue ranged from 12 to 72 ppm. Trace amounts of lithium were detected in leaf tissue, levels were below 10 ppm in all cases. Leaf concentrations of copper from all sites were between 7 and 11 ppm dry weight.

Total phosphorus decreased in the same manner as the plant parts of major cations. With the exception of one plant, middle growth from all plants had the lowest values, approximately one quarter of leaf percentages. Plants from Bluff and Kyle Canyon had higher total phosphorus concentrations. Leaf concentrations of phosphorus from all sites ranged from 550 to 1550 ppm.

The greatest total nitrogen was found in leaf tissue, with values ranging from 1.61 to 2.05% dry weight. Similar to the behavior of phosphorus, the lowest concentrations of nitrogen were found in middle growth, ranging from 0.51 to 0.78%.

Large variations between sites were measured for leaf content of chloride. Highest value 2.35%, and lowest value 0.36%, were measured at Bluff and Kyle Canyon, respectively. A significant correlation was found between chloride leaf content and the sum of major cations ($r = 0.88$, $p < .05$). Leaf chloride content was inversely related to the total oxalate content in both leaves ($r = -0.98$, $p < .01$), and fruit ($r = -0.99$, $p < .01$). Oxalic acid content of leaves ranged from a low of 1.19% at Bluff to 1.93 and 2.22% at Tipton and Kyle Canyon, respectively.

The total contribution from the four major cations ranged from 264.75 me 100 g^{-1} at Bluff to 396.06 me 100 g^{-1} at Kyle Canyon (Table 34).

The four anions accounted for a total contribution ranging from 93.06 me 100 g^{-1} dry weight at Kyle Canyon, to 125.96 me 100 g^{-1} dry weight at Cedar Mtn. On the basis of the major cations and anions analyzed, the resultant cation/anion ratios from all sites ranged from 2.19 at Bluff to 3.97 at Kyle Canyon.

Low potassium/sodium ratios were found for unvegetated soils in comparison to ratios of these cations in above ground plant parts (Table 35). Although sodium in most cases was equal to or greater than potassium in the soil, very little sodium was measured in leaf and woody tissues. Calcium dominated unvegetated soils at all sites and high calcium/sodium ratios were found in both soils and plants.

Calcium showed the largest decrease of the four cations (Ca, Mg, K, Na) from fresh leaf tissue to new litter, ranging from a 38% decrease at

Table 34. Major cations and anions in *Atriplex canescens* leaf tissue.

	me 100 g^{-1} dry wt.					me 100 g^{-1} dry wt.				
	Na	K	Ca	Mg	Σcations[a]	Cl	N	P	Organic	Σanions[b]
Tipton	5.65	137.08	82.34	98.72	323.79	55.28	33.06	0.90	35.45	124.69
Cedar Mtn.	33.49	117.90	102.79	60.05	314.23	60.36	31.13	0.84	33.63	125.96
Bluff	1.30	97.95	89.82	75.68	264.75	66.28	25.77	1.60	27.04	120.89
Kyle Canyon	0.43	75.70	143.21	149.72	369.06	10.15	31.13	1.34	50.44	93.06

[a] Cations as Na, K, Ca, Mg

[b] Anions as Cl, NO_3, H_2PO_4, C_2O_4

Table 35. Cation ratios of unvegetated soil and tissue of *Atriplex canescens*.

	K/Na	Ca/Na
Tipton		
soil (top 15 cm)	0.31	7.97
leaves	41.23	12.69
middle	50.00	28.00
old	24.00	15.00
Cedar Mtn.		
soil (top 15 cm)	2.26	16.87
leaves	5.99	2.68
middle	15.67	17.33
old	11.67	28.67
Bluff		
soil (top 15 cm)	3.65	10.13
leaves	127.67	60.00
middle	75.00	46.00
old	48.00	106.00
Kyle Canyon		
soil (top 20 cm)	0.89	13.84
leaves	296.00	287.00
middle	69.00	46.00
old	45.00	17.00

Cedar Mtn., to a 58% reduction at Kyle Canyon (Table 36). Further loss of calcium from new litter was not calculated due to the contamination of old litter by soil solution at all sites but Kyle Canyon where the calcium loss through old litter was 62%. Less than 20% of the initial fresh leaf potassium content remained in old litter from Tipton. Similarly, between 69% and 76% of the potassium was lost from fresh leaf tissue at the other sites. The majority of this loss occurred during the decomposition of new litter. No other element measured appeared to be at the same rate. Losses in magnesium on the other hand, occurred predominantly prior to or immediately after litter fall. Content of magnesium in old litter represented between a 23% and 37% loss from live leaves at Tipton and Kyle Canyon, respectively. Similarly, less than half of the total leaf nitrogen remained in new litter except at Bluff where 1.44±0.05% represented only an 11% reduction from fresh tissue. Little loss of sodium from either fresh leaf or new litter was measured at any site. The reported 78% loss of sodium from fresh leaves at Cedar Mtn. may need closer examination since this loss was calculated by comparing the averages of plants with wide ranges in sodium concentrations to a fewer number of litter samples. On a per plant basis, the largest loss in sodium from fresh tissue through old litter was 8%. Differences in phosphorus content of fresh leaves in comparison to new litter ranged from a 30% decrease at Tipton (875 to 610 ppm) to 52% at Bluff (1550 to 746 ppm). Calculations of phosphorus mobilization from new litter because of contamination in old litter.

Similarities in losses of major cations from fresh leaf to new litter were observed between Tipton and Cedar Mtn., and between Bluff and Kyle Canyon. The latter two sites had higher losses of K, Ca and

Table 36. Comparison of live leaf tissue and leaf litter of *Atriplex canescens*.

	% dry weight					
	Na	K	Ca	Mg	N	P
Tipton						
Fresh leaf	0.13±0.17	5.36±0.50	1.65±0.32	1.20±0.27	2.05	0.09±.01
New litter	0.16±0.14	4.12±0.38	0.94±0.13	1.02±0.22	0.82±.20	0.06±.02
Old litter	0.06±0.04	1.09±0.32	1.43±0.15	0.93±0.12	0.92±.19	0.08±.01
Cedar Mtn.						
Fresh leaf	0.77±1.03	4.61±1.55	2.06±0.26	0.73±0.14	1.93	0.08±.02
New litter	0.17±0.14	3.72±0.16	1.27±0.08	0.55±0.04	0.77±.14	0.04±.01
Old litter	0.14±0.09	1.26±0.06	1.37±0.13	0.49±0.03	0.86±.21	0.08±.01
Bluff						
Fresh leaf	0.03	3.83	1.80	0.92	1.61	0.16
New litter	0.04±0	2.43±0.21	0.81±0.07	0.70±0.03	1.44±.05	0.07
Old litter	0.04±0	1.20±0.31	1.32±0.08	0.65±0.01	1.72±.21	0.12
Kyle Canyon						
Fresh leaf	0.01	2.96	2.87	1.82	1.93	0.13
New litter	0.01±0	1.72±0.20	1.20±0.03	1.22±0	0.94±.03	0.07
Old litter	0.01±0.01	0.70±0.08	1.09±0.18	1.14±0	1.32±.10	0.12

Mg, at or prior to leaf fall. Reduction from fresh leaf tissue for Tipton and Cedar Mtn., and Bluff and Kyle Canyon, respectively, compared thus: Potassium, 21.0±2.8% and 39.5±3.5%; Calcium, 40.5±3.5% and 56.5±2.1%; and Magnesium, 20.0±7.1% and 28.5±6.4%.

The nutrient content of new litter was calculated for individual plants using leaf harvest values (Table 37). Not only does potassium represent the largest portion of any of the six elements in the new litter, but also the highest rate of mineral return. Values of K^+ for the two plants at Tipton ranged from 3.94 g yr^{-1} to 11.12 g yr^{-1}. The largest amount of potassium mobilized from leaf litter was 13.92 g $plant^{-1}$ yr^{-1} at Bluff, while single plants from Cedar Mtn. and Kyle Canyon returned 11.80 and 5.09 gK^+ yr^{-1}, respectively.

Water Potential (ψ)

Water potential was found to be independent of plant size, age or sex, proximity to other plants, and of the spacial location and orientation of the twig sampled. Repeated excisions from individual plants had not effect on ψ. Water potential extremes at the site for the species were -15.5 and -45.1 bars (Fig. 33 and Appendix A). The maximum diel fluctuations for all individuals measured was 26 bars (mean = 21.9).

Rates of ψ change exceeded 12 bars hr^{-1} during periods of rapidly moving storm systems over the site. Minimum readings were at dawn when air and soil temperatures were the lowest; maximum readings coincided with the greatest atmospheric evaporative demand. Regressions of environmental variables are shown in Table 38. All individuals initially responded linearly to the effects of vapor pressure deficit, followed by a declining slope which intersected the linear equation at about one-half the range of ψ (Fig. 34).

Table 37. Ionic content of new litter.

		g					
		Na	K	Ca	Mg	N	P
Tipton							
Plant 2	(315 g)	1.13	14.24	3.02	3.65	2.03	0.24
Plant 4	(134 g)	0.25	5.01	1.29	1.37	1.18	0.09
Cedar Mtn.							
Plant 2	(500 g)	1.50	17.90	6.10	2.60	4.49	0.27
Bluff							
Plant 1	(1124 g)	0.42	27.30	9.10	7.87	16.19	0.84
Kyle Canyon							
Plant 1	(499 g)	0.05	8.58	5.99	6.09	4.71	0.35

Fig. 33: Fluctuations in water potential of *Atriplex canescens* for a 48-hour period, Aug. 9-11, 1978. Curves delineate the range of values for the site.

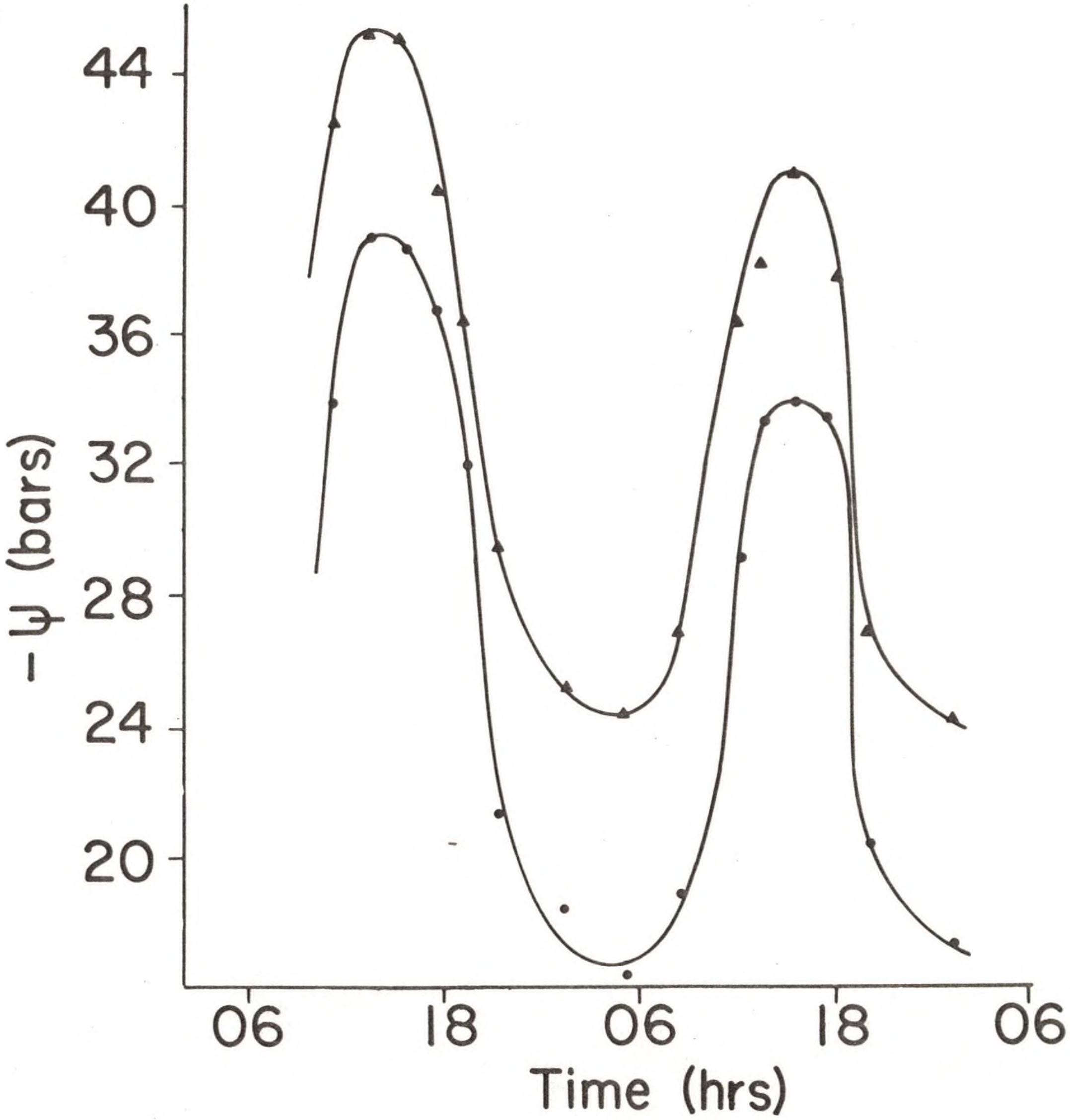
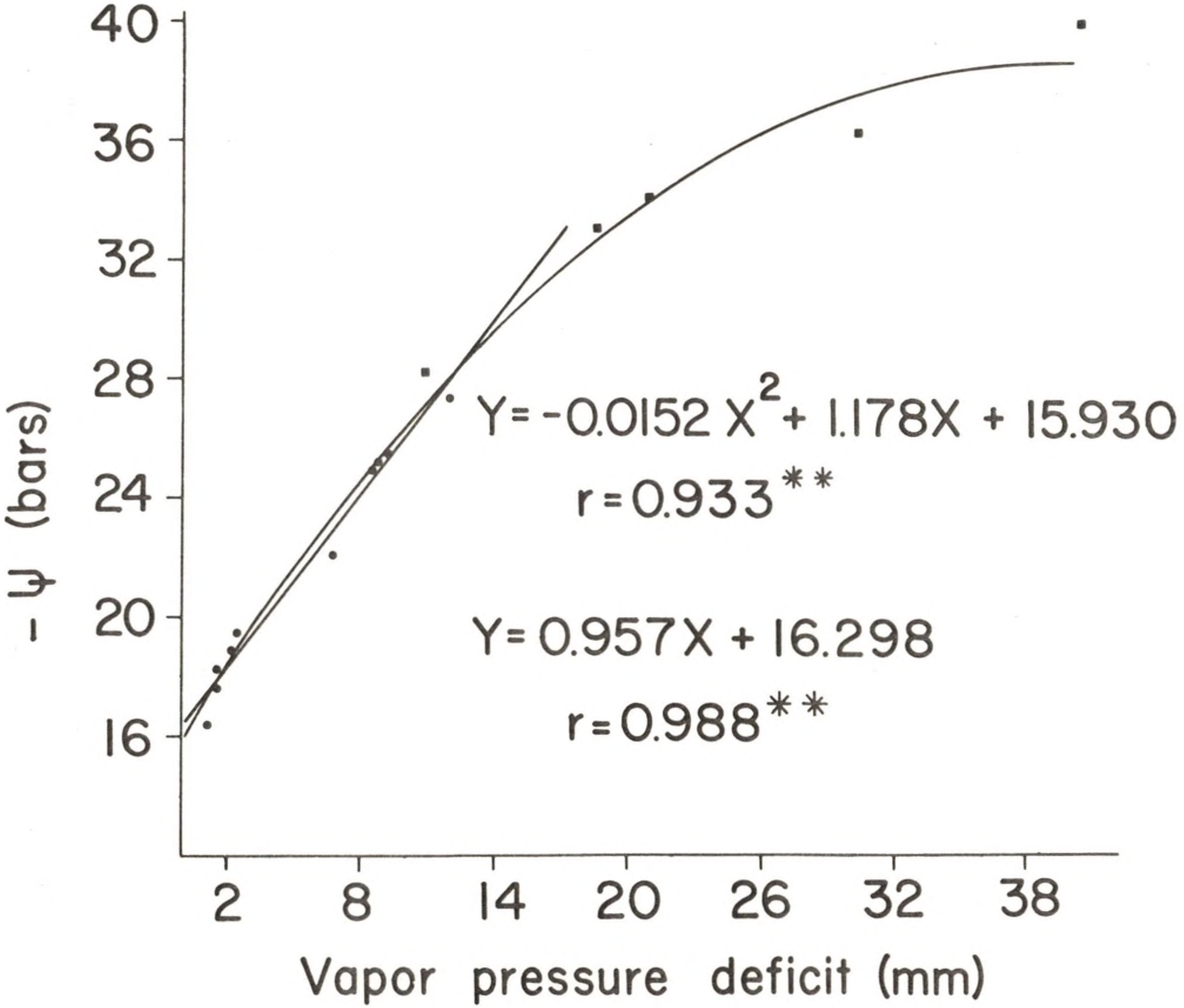

44
40
36
32
28
24
20
$-\psi$ (bars)
06
18
06
18
06
Time (hrs)

Table 38. Relationships between water potential and environmental variables.

Quadratic Equations for a Single Plant	Multiple R for a Single Plant	Multiple R for all plants (Z scored)
$Y = -0.275\ A^2 + 1.0940\ A + 17.88$	0.833**	0.899**
$Y = 1.161\ B^2 - 0.272\ B + 13.60$	0.891**	0.943**
$Y = 0.598\ C^2 - 1.506\ C + 37.58$	-0.939**	-0.931**
$Y = -0.487\ D^2 + 1.384\ D + 16.64$	0.933**	0.956**

Y = water potential (bars); A = light (cal $\text{cm}^{-2}\ \text{min}^{-1}$); B = temperature (^{o}C); C = relative humidity (%); D = vapor pressure deficit (mm Hg).

Fig. 34: Linear and quadratic relationships between water potential and vapor pressure deficit.


40
36
32
28
24
20
16
- ψ (bars)
2
8
14
20
26
32
38
Vapor pressure deficit (mm)
$Y = -0.0152X^2 + 1.178X + 15.930$
$r = 0.933^{**}$
$Y = 0.957X + 16.298$
$r = 0.988^{**}$

Osmolality of expressed sap in relation to the time of day is shown in Fig. 35. Sap expressed at high ψ was up to three times more concentrated than sap at low potentials. In all cases, the rate of sap expression increased with decreasing pressure potential. The mean osmolality of the sap was 31 milliosmoles corresponding to an osmotic pressure of 0.76 bar. Electrical conductivity readings, representing inorganic components only, gave a mean of 1.31 μmhos cm^{-1} corresponding to an osmotic effect of 0.47 bar. The mean sum of four major cations (Ca, Mg, K and Na) is 13.45 me 1^{-1} (Table 39), which equates to approximately 1.25 μmhos cm^{-2} or 0.45 bar. These four cations contributed 59% of mean osmolality; however, K and Cl were the dominant ions. The relationships between the changing osmolality of the sap and the concentration of major individual ions are distinct (Fig. 36).

Fig. 35: Representative diel trends in osmolality of expressed xylem sap.

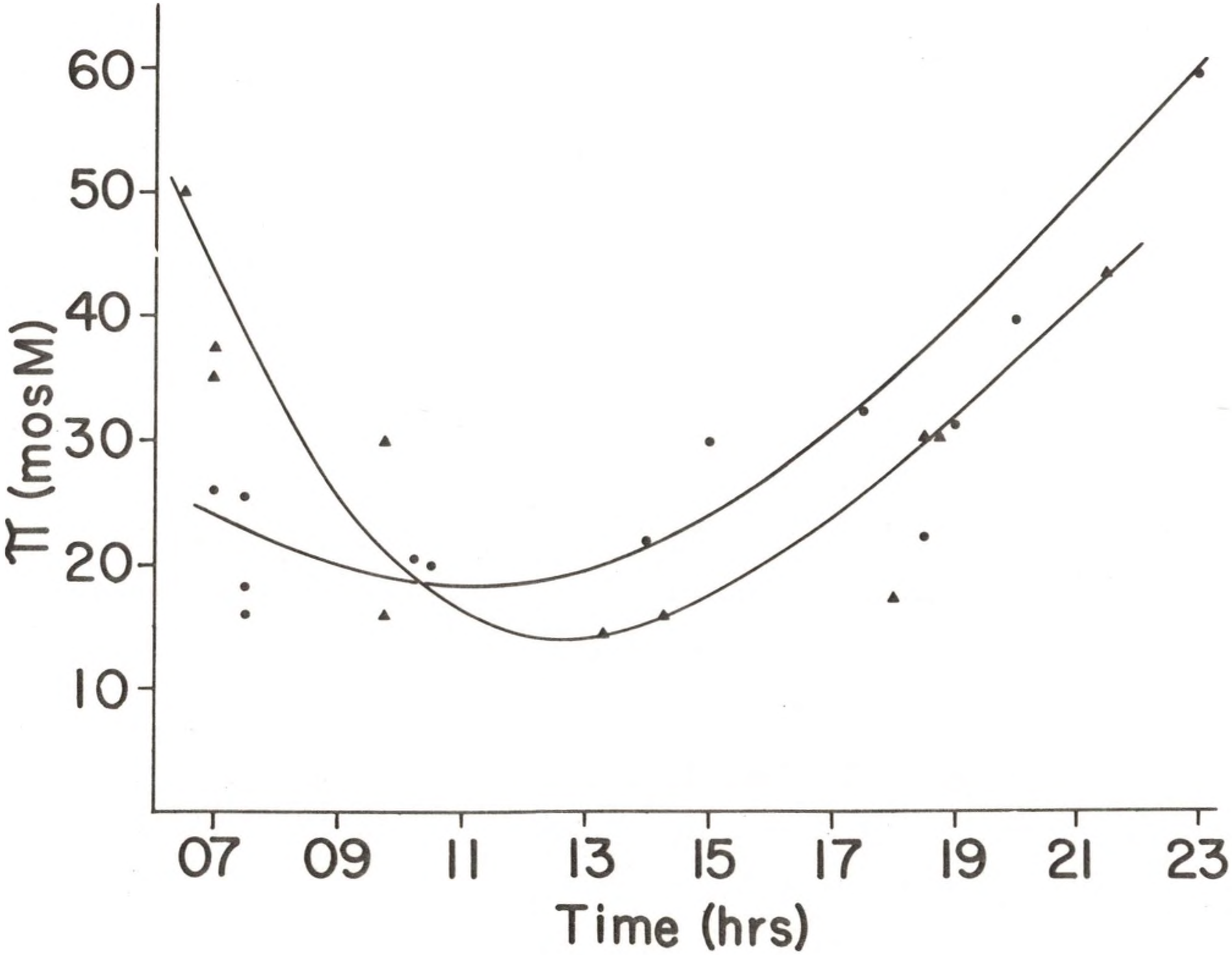
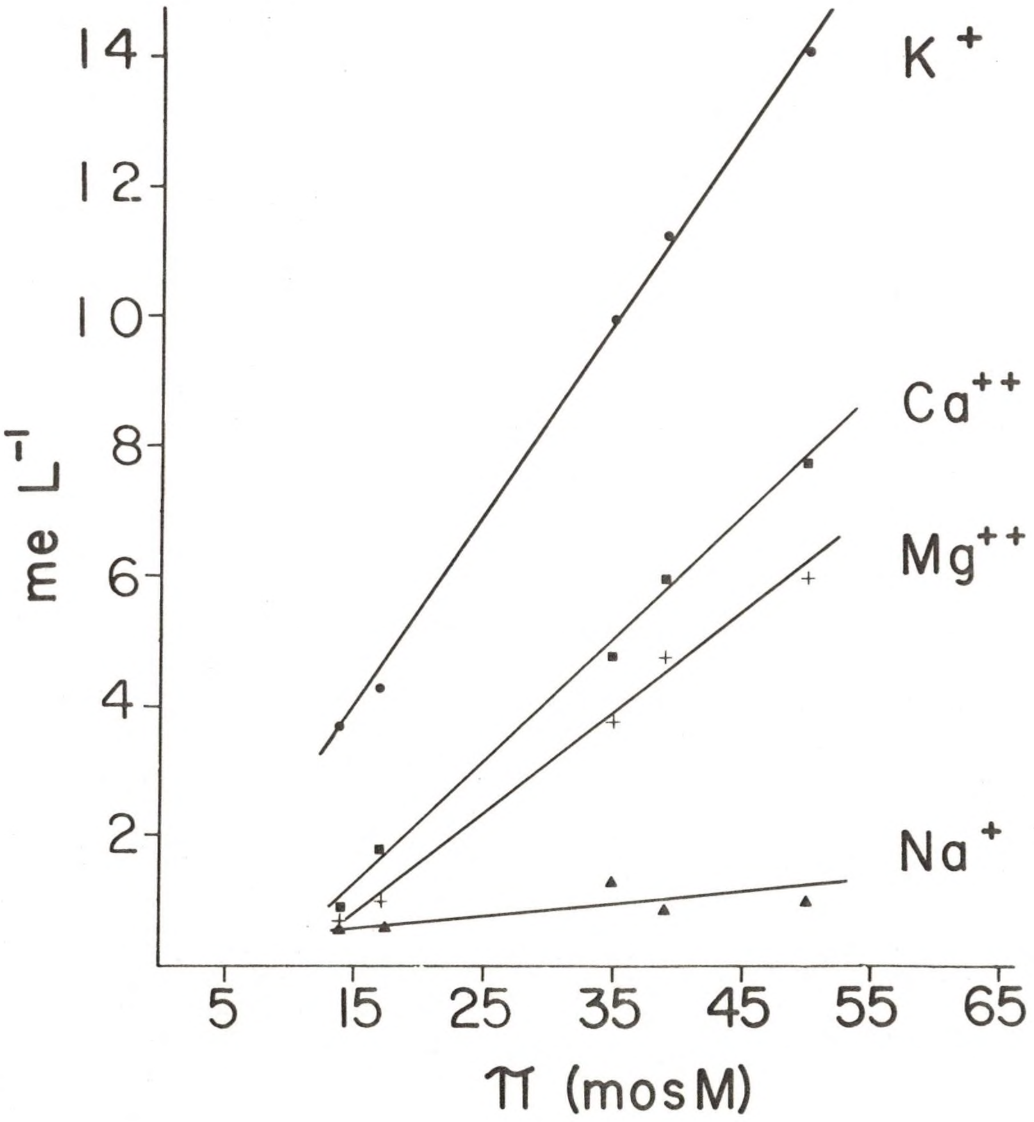

60
50
40
30
20
10
π (mosM)
07
09
11
13
15
17
19
21
23
Time (hrs)

Table 39. Physical-chemical characteristics of xylem sap.

								$me\ l^{-1}$					
Plant No.	Date	Time	$-\psi$(bars)	π(mosmls)^a	π(bars)^a	π(bars)^b	% Inorganic	Ca	K	Na	Mg	Σcations	Cl
1	8/21/78	1200	39.28	40	0.98								
	8/22/78	0730	22.74	38	0.93								
	8/22/78	1800	36.87	28	0.68								
	8/23/78	1100	34.80	22	0.54								
	8/23/78	2000	31.01	43	1.05								
2	8/21/78	1400	35.84	34	0.33								
4	8/21/78	1630	36.18	50	1.22								
	8/21/78	2000	21.36	40	1.10	0.84	76.48	3.29	13.66	2.87	2.47	22.29	9.87
	8/21/78	2300	19.99	61	1.49								
	8/22/78	0700	17.57	27	0.66								
	8/22/78	1730	32.39	38	0.93								
	8/22/78	2215	20.33	36	0.88	0.69	79.02	3.24	9.85	0.78	2.55	16.42	6.70
	8/23/78	0730	17.23	26	0.63								
	8/23/78	1015	28.26	21	0.51	0.33	64.11	0.90	6.27	0.39	0.82	8.38	3.67
	8/23/78	1500	35.15	30	0.73	0.38	52.39	1.95	7.54	0.57	1.56	11.53	4.68
	8/23/78	1900	27.91	33	0.80	0.53	65.78	3.04	4.96	0.35	2.30	10.65	8.85
	8/24/78	0730	19.30	16	0.39	0.37	93.52	1.30	4.60	0.52	1.07	7.49	4.30
	8/24/78	1015	30.32	20	0.49	0.38	77.89	1.00	5.98	0.17	1.15	8.30	5.57
	8/24/78	1400	37.22	22	0.54	0.38	71.45	1.45	5.93	0.39	1.23	9.00	3.67
	8/24/78	1830	29.63	20	0.49	0.35	71.25	1.40	5.98	0.22	1.15	8.75	4.30
	8/25/78	0730	19.99	18	0.44								
5	8/22/78	1845	30.32	30	0.73								
	8/22/78	2130	23.43	47	1.15								
	8/23/78	0630	19.30	50	1.32	0.88	66.52	7.73	14.22	1.00	6.00	28.95	11.89
	8/23/78	0945	27.57	30	0.73								
	8/23/78	1415	38.94	17	0.41								
	8/23/78	1830	33.77	31	0.76								
	8/24/78	0700	21.71	35	0.85			4.54	10.05	1.65	3.45	19.69	9.11
	8/24/78	0945	29.98	17	0.41								
	8/24/78	1330	38.59	16	0.39	0.35	88.85	1.75	4.30	0.87	1.32	8.24	3.04
	8/24/78	1800	35.84	17	0.41	0.27	65.20	0.95	3.96	0.39	0.82	6.12	2.66
	8/25/78	0700	21.02	38	0.93			5.99	11.25	0.35	4.93	22.52	9.87

a: π using an osmometer; b: π using electrical conductivity.

Fig. 36: Major cation concentrations of expressed xylem sap.


K⁺
Ca⁺⁺
Mg⁺⁺
Na⁺
me L⁻¹
14
12
10
8
6
4
2
5
15
25
35
45
55
65
π (mosM)

DISCUSSION

The desert environment, with a large portion of unvegetated soil, provides a unique setting for studying the ecology of a single species. The presence of *Atriplex canescens* was found to have significant influences on the ecology of its immediate environment. These influences were manifested through the physical and chemical alterations of the above- and below-ground space beneath the plant canopy. The return of nutrients to a restricted soil space and rhizosphere via the decomposition of plant litter, facilitates the acquisition from an otherwise impoverished soil nutrient pool. Profile trends of major cations leached from plant litter generally followed the trends in electrical conductivity. Differences in the soil chemistry between vegetated and unvegetated soils were most prominent in the top 15 cm, because the bulk of returned nutrients are rapidly diluted in the soil and/or taken up by plant roots. The slightly higher E.C. of vegetated surface soils at Bluff is attributable to higher values for K, Mg, and Cl. In most instances, the extent to which an element influenced the soil bore a direct relation to the content of that element in plant tissue. Potassium, for example, was the most prominent cation in the plant tissue and also was found in high concentrations in the soil. Highest sodium concentrations in both leaf tissue and in vegetated soils were found at Cedar Mtn. where prominent intersite differences in soil chemistry were found due to the occurrence of calcium and magnesium sulfate at the site. Vegetated surface samples from Cedar Mtn. and Bluff contained significantly more chloride than either Tipton or Kyle Canyon ($p < .01$). Chloride contents of plants from the former sites were 2.14 and 2.35%, while plants from Tipton and Kyle Canyon had 1.96 and 0.36% chloride, respectively. Because of the importance of chloride in maintaining the intracellular ionic balance, chloride may also be retained more by plants.

Vegetated soils had lower total carbonates than did unvegetated soils. The higher soil moisture of vegetated soils and the presence of plant roots are no doubt contributing factors in the dissolution and subsequent leaching of carbonates. Percolation rates beneath the shrubs and thus the upward movement of salts, are perhaps lower than those in unvegetated areas. Soils at all sites were calcareous, typical of most soils in the Great Basin (Suek and Knaup 1979). Alkaline earth carbonates are known to affect the absorption of micronutrients by plants and limit production, especially at concentrations like those measured at Kyle Canyon. Although carbonates may affect the productivity of other species at the site, *Atriplex canescens* does not appear to be limited by high carbonate concentrations.

Sparse distribution of perennial desert shrubs results in unique physical-chemical soil patterns. Most desert shrubs have high root/shoot ratios. As the shrub matures, nutrients are drawn from a large soil volume which extends both vertically and horizontally while litter is returned to a localized area. This process results in a soil enriched by nutrients and organic matter beneath the canopy and a continual depletion of nutrients from the surrounding bare soil (Charley and West 1975). Due to the longevity of most desert perennials, fertile islands are created in an otherwise nutrient deficient environment. An important aspect is, therefore, the rate at which islands of mineral accumulations develop and whether these reach an equilibrium within the lifespan of the individual or continue intensifying up to the time of death.

The windbreak created by the canopy helps maintain a mat of litter protected from removal by leaching and runoff. Reduced radiation, soil and air temperature, and evapotranspiration, provide a more favorable habitat under the shrub canopy for the establishment and growth of ephemeral annuals. Significantly higher nutrient concentrations under mesquite for example, resulted in a greater abundance and palatability of perennial grasses under mesquite than in adjacent open areas (Tiedemann and Klemmedson 1973a, b). The cation content of cheatgrass was shown to be differentially increased when growing beneath the canopy of two desert shrubs in eastern Washington (Richard and Keough 1968). Nutrition of perennial saltbush communities in New South Wales was closely related to the presence of nutrients in the top 5 to 10 cm of the profile as soil below this supported little plant growth (Charley and Cowling 1968). However, benefits that may accrue from nutrient-enrichment beneath the canopy could well be partially offset by harmful accumulations of some elements. For example, Sharma (1973) found that *Atriplex nummularia* induced significant changes in soil physical and physico-chemical properties on two soil types in southwest New South Wales. The accumulation of significantly greater amounts of exchangeable sodium resulted in the deterioration of soil structural stability under plant canopies.

Soil temperatures are determined by the amount of incoming radiation reaching the surface, the material overlying the soil, and the physical nature and aspect of the soil surface itself. Soil moisture content also affects the soil temperature by increasing the specific heat and thus decreasing the rate of temperature change. The surface temperatures of desert soils can be extreme during times of maximum incoming radiation and cool rapidly with re-radiation into chilling night time air.

Soil temperature is one of the dominant factors controlling the distribution of plants and behavior of animals in warm and cold deserts. The diel fluctuations in soil and ambient temperatures at Tipton were recorded (Figs. 27 and 28). Organisms active above ground during the day seek the shade provided by *Atriplex* and other plant species. Reduced temperatures of sub-surface ground soils provide temperature refugiums for fossorial and other below ground organisms.

The mean temperature of unvegetated soils at Tipton was 27.5° with extremes reaching 40.3°C. Although maximum growth of *Atriplex canescens* under laboratory conditions was shown to be 21°, the species grew well under both hot (28°), and cold (16°), desert soil conditions (Wallace et al. 1970). High temperature optimum for the species may partially explain its wider distribution than other *Atriplex* species, especially into southern hot deserts.

In normal soils of arid regions, calcium and magnesium are the principal cations in the soil solution. However, sodium frequently becomes the dominant cation in solution and may influence the soil structure and availability of other ions (Van der Merwe and Burger 1969). The electrical conductivity (E.C.) and exchangeable-sodium-percentage (E.S.P.) have been the diagnostic indicators of saline soils (Richards 1954). However, the highest sodium-absorption ratios of nearly all soils in this study were near 10 in lower profile depths where sodium tended to accumulate. This equates to an E.S.P. of 12, or always below 15, the lowest value to be considered alkali. Although the E.C. of some of the vegetated soils were near moderately saline (1 to 3 mmho cm^{-2}), as influenced by ions leached from plant litter, no unvegetated soils studied may be considered saline. Although *Atriplex canescens* has been widely reported as a dominant species in saline soils, none of the four sites could be classified as saline, saline-alkali, or nonsaline-alkali, but simply nonsaline-nonalkali.

Relative proportions of sand, silt and clay affect the aeration, compaction, and water percolation and retention qualities of the soil, all of which have important affects on plant growth. Soils with a course texture, like those in the present study, result in high permeability and good aeration but low water holding capacity as indicated by reduced saturation percentage. However, any available moisture in the rhizosphere is probably readily available to halophytic species, which are capable of extracting water under total water stress. It is estimated that 80% of stored moisture is used in the transpiration of plants (Kovda et al. 1979). Saturation percentages of soils at the four study sites were slightly higher for vegetated than unvegetated soils. Since there were no particle size differences between the two soils, saturation characteristics must be attributable to the presence of organic matter in the vegetated soils. Certain organic moieties have hydrophyllic properties and can act as colloids very similar to the behavior of montmorillonitic clays (Chen and Schnitzer 1976).

The overall saturation values for the soils in this study were approximately 30%. The relation of saturation percentage (S.P.) to

15-atmosphere percentage (F.A.P.), wilting percentage as influenced by soil texture has been reported by Richards (1954). The S.P. was found to be approximately equal to four times the F.A.P. over a large textural range. The F.A.P. of coursely textured soils such as these would therefore be close to 7%. Moisture content that would impose restrictions upon species establishment.

Plants inhabiting saline environments are subjected to three main types of stresses: (1) Water stress; (2) Toxicity of specific ions, and (3) Nutrient deficiencies and imbalances (Safaya 1980). Low osmotic potential of the soil solution forces plants to maintain still lower intracellular osmotic potentials through osmotic adjustment. Levels of sodium, however have been shown to stimulate the growth of many species including *Atriplex canescens* (Wallace, Mueller, and Romney 1973). Although not a contributing factor to salt tolerance in all species of *Atriplex* (Mozafar and Goodin 1970, Chatterton and McKell 1969), an important response stimulated by soil salinity in some species is an increase in leaf succulence. In many plants, an increase in intracellular salt content is brought about by chloride uptake accompanied by potassium or sodium. The maintenance of succulence in *Atriplex* species, however, appears to be different from many other genera. Increase in salt content is brought about primarily by active uptake of sodium, followed by an anion balance of chloride and/or oxalate (Jennings 1976). The control of succulence in *Atriplex canescens* has not been unequivocably determined. It can be speculated that potassium would assume a greater role since sodium is practically absent from leaves of the species. Potassium has been shown to be as affective as sodium in initially stimulating succulence in *Atriplex hortensis* (Jennings 1976).

Halophytes vary in mechanisms responsible for maintaining osmotic adjustment under saline conditions. In many species of *Atriplex*, this is accomplished by transporting sodium to leaves whereby it is partitioned into specialized cells or tissues. *Atriplex canescens* is unique among other species in the genera because sodium is found in low concentrations in the leaves compared to relatively high concentrations in the roots (Wallace, Mueller and Romney 1973). Sodium concentrations in leaves and expressed xylem sap were found to be up to fifty times less than potassium in the present investigation. It has been suggested therefore that regulation of sodium uptake takes place at the level of the rhizosphere, and thus is transported to leaves in low concentrations.

It is known that calcium modifies the sodium-potassium uptake mechanisms in that high potassium uptake is stimulated and sodium uptake decreases (Rickard and Keough 1968, Walter 1973). It has been suggested that calcium alters the chemical properties of membranes beyond changing their permeability or perhaps influencing the carrier system of sodium and potassium. This additional function of calcium emphasizes its importance in the influence it has on minimizing the diffusive permeability of membranes to ions as well as affecting the selectivity of ion transport mechanisms (Epstein 1972). The importance of high calcium/sodium ratios in maintaining this mechanism has been documented (Hyder and Greenway 1965). Calcium was the dominant cation in all soils in the present study; certainly adequate levels for sustaining a mechanism in natural populations of *Atriplex canescens*. The completely reversed potassium/sodium ratios of soil and plant tissue as seen here suggest that some selectivity mechanism for potassium is operating which is maintained by relatively high calcium concentrations. Cannon

(1971) provides interesting and contrasting patterns of ion concentrations between *A. canescens* which excludes salts at the level of the rhizosphere and *A. confertifolia*, a co-dominant with *A. canescens* at most sites, that sheds salts through vesicular hairs.

Sum of major cations in leaf tissue of *Atriplex canescens* ranged between 264 me/100 g and 369 me/100 g (Table 34). Higher concentrations of potassium, up to 8.59% dry weight, account for higher total cation levels for the species, 427, growing in the Mojave Desert (Wallace, Romney and Hale 1973). In all cases, cations greatly exceeded the anions in the present study, resulting in cation/anion ratios of between 2.19-3.97. However, these results do not include, among others, sulfur as SO_4^{-2}, silicon as SiO_2^{-2}, and bicarbonate. All are known to be important accompanying anions, bicarbonate the more important (Bear 1950, Wallace et al. 1974).

The modeling of nitrogen in desert systems has been given considerable attention because soil organic matter and total nitrogen in desert ecosystems as a whole are considered low (West and Skujins 1977, 1978). Consequently, the localized nutrient inputs near or under the scattered plant canopies assume great importance. The rate of litter decomposition in arid regions is dependent directly upon available moisture. Precipitation or dew insufficient in amount for plant use can be readily utilized by microorganisms for the oxidation of organic nitrogen. Soil microorganisms responsible for mineralization of nitrogen are more tolerant of moisture stress than are plants. Their activity is enhanced by increasing the temperature and length of drying of the soil prior to remoistening. Heat treated soils have been shown to exhibit a dramatic increase in respiration within minutes of remoistening

(Funke and Harris 1968). Such activity in the absence of uptake by plants thus results in the accumulation of mineral nitrogen in the soil. Systematic relationships between precipitation, mineralization of organic nitrogen, and subsequent uptake by plants have been useful in understanding such processes (Charley 1972).

The major input of nitrogen in desert ecosystems is probably attributable to cryptogamic crusts (blue-green algae and/or blue-green algae-lichen) rather than heterotrophic fixation or plant-microbial symbiotic fixation (Rychert et al. 1978, Farnsworth et al. 1978, Loftis and Kurtz 1980). Legumes are rare in most cold-winter and many warm deserts thus reducing the contribution made by symbiotic microbial associations. However, non-leguminous shrubs such as *Atriplex canescens*, have been implicated in microbial associations and to input small amounts of nitrogen (Wallace and Romney 1972). However, many of these biological pathways in the breakdwon of organic material and cycling of nitrogen have been shown to be inhibited by substances leached from plant litter (Skujins 1975). Both biological and nonbiological mechanisms of gaseous losses of nitrogen as well as ammonia volitilization have been observed in field studies in native desert ecosystems and may be significant enough to offset gains from biological fixation (West and Skujins 1977). Desert plants have long been expected to make greater use of ammonium nitrogen since soil nitrate nitrogen is generally low in desert ecosystems. However, desert species such as *Atriplex canescens* have been shown not only to be able to utilize nitrate nitrogen, but also respond to increased available nitrate nitrogen by an increase in nitrate reductase. Furthermore, high ratios of nitrate nitrogen to ammonium nitrogen uptake resulted when the species was grown in ammonium nitrate solutions (Wallace et al. 1978).

The carbon/nitrogen ratio of plant materials has been conveniently used as an estimate of the rate of mineralization. The higher the percent nitrogen of plant tissue the faster the rate of decomposition (Alexander 1977). Therefore, a wide carbon/nitrogen ratio is associated usually with slow decay. Nevertheless, the rate of decay is underscored by inherent properties of the material; for example, freshness and size of the tissue as well as the quantity of lignified organic material. The difficulty with understanding the meaning of soil carbon/nitrogen ratio at any given time in the community is the fact that during the processes of mineralization, the ratio is greatly reduced because of the utilization of carbon by microorganisms. Thus the carbon/nitrogen ratio tends to decrease with time.

Carbon/nitrogen ratio in arid soils is narrow. Skujins reported ratios in Great Basin soils ranging between 6 and 12 (Skujins 1972). Ratios less than 10 have been reported for other desert soils (Rixon 1970, Tiedemann and Klemmedson 1973, Charley and West 1975). Charley and West (1975) found significant differences in nitrogen, organic matter and carbon/nitrogen ratios between vegetated and unvegetated surface soils in *Atriplex confertifolia* communities. Soil nitrogen and organic matter were lower and higher respectively in the present study as compared to these reports. Wide carbon/nitrogen ratios for vegetated and unvegetated soils were found ranging from 12 to 27 at Tipton, 15 to 40 at Bluff and Cedar Mtn., and 22 to 81 at Kyle Canyon. No significant difference exists in nitrogen content between *A. canescens* and *A. confertifolia.*

Rapid decrease in both nitrogen and carbon with depth is a common occurence in arid soils. However, in many instances, carbon/nitrogen ratios increase at lower depths due to the presence of dead or decaying roots or other below ground plant parts high in carbon but low in nitrogen. This potentially explains the dramatic increase in carbon/nitrogen ratios at Kyle Canyon.

As mentioned above, nitrogen is one of the important nutrients redistributed to shoots and other plant parts from leaves prior to abscission. Withdrawal of the majority of nitrogen results in litter inherently low in nitrogen with characteristically slower decay processes resulting in wide carbon/nitrogen ratios. If in fact nitrogen is translocated back to stems prior to abscission, the return of nitrogen to the soil would not balance uptake and a net loss of nitrogen to perennial tissue would ensue.

Even though mineralization is supposed to be highest during moist times of the year, annual fluctuations in organic matter and/or nitrogen content of soils could go undetected despite seasonal variations in litter fall. The major portion of litter accumulation at Tipton occurs during the late fall and winter months through the action of wind. A part of this litter could be mineralized during the winter months. Since sub-zero temperatures are not continuous and moisture is adequate, short but frequent conditions may be present for favorable microbial activity. Decomposition of litter at just above freezing temperatures has been shown to occur under snow cover (Bleak 1970).

Nitrogen content of the top 15 cm was greater in September than June for all plants at all four sites. Like other shrubs, litter fall at the warm winter sites of *Atriplex canescens* would probably be greatest during summer months (West 1972). Coupled with the nitrogen mobilization from litter over the summer, surface and subsurface soil under plant canopies would therefore be expected to have higher nitrogen concentrations.

Oxalic acid plays an important role in the balance of cations in leaves of semiarid species. Oxalate levels among *Atriplex* species generally range from 50 to 400 me/100 g dry weight (Flowers et al. 1977). It has been suggested that both mono- and divalent ion supply control in plants and soil is the result of the chelating qualities of oxalate (Graustein et al. 1977). Although the biosynthesis of oxalate has not been established unequivocably, some lines of evidence lead to a relationship between oxalic acid synthesis and photosynthetic pathway (Zindler-Frank 1976). A study of $^{13}C/^{12}C$ ratios in crystalline oxalate from cacti suggest the synthesis of oxalate to be an enzymatic cleavage of oxaloacetate (Rivera and Smith 1979). Leaves of *Atriplex spongiosa* seedlings have been shown to increase in oxalate concentrations when grown in solutions with increasing sodium. Oxalate was found to balance up to 75% of the cation excess (Osmond 1967).

The poisonous properties of the free acid and its salts in rangeland species are well documented (Mathams and Sutherland 1952, Jones et al. 1970, and others). Ostensibly, concentrations of oxalate in *Atriplex canescens* remain sufficiently lower than those levels inducing toxicity in animals.

The total leaf oxalate content of *Atriplex canescens* in this study was found to be correlated positively with total cation and negatively with leaf chloride concentrations. Oxalate contributed up to 54% of the anion balance, while the combined effects of chloride and oxalic acid accounted for between 65% and 77% of the four anions measured. Despite intersite differences in leaf chloride concentrations, no differences in chloride values for unvegetated soils were found between sites (mean chloride content of the top 15 cm of unvegetated soil from all sites ranged from 7.3 ppm and 15 ppm). Plants with highest chloride and highest oxalate content were found at Bluff and Kyle Canyon, respectively. Since the phenologies of plants at these two sites were not appreciably different, site specific differences in leaf age, productivity, and climate would probably not be sufficient to account for the variations in chloride. It can be concluded therefore that plants at the four sites vary in the rate of chloride uptake.

Studies on the growth of plants in desert regions have recently been reviewed (Fisher and Turner 1978) and, as should be expected, water availability and efficient use are key areas of investigation. Energy production requires moist surfaces in plants. Species whose physiology requires gas exchange during peak heat loads would be at an advantage if moments of reduced external or environmental vapor pressure deficits could quickly be used for photosynthesis. This would result in decreased water loss thus ensuring energy production and greater water use efficiency.

The chemical potential of a substance is the free energy per gram molecular weight of that substance. The chemical potential of water depends upon ionic species concentration, system pressure, electrical potential, and gravitational influences. Water potential (ψ) refers to the difference in chemical potential of pure water and that in a reference state, divided by the partial molar volume of water. Such a difference indicates that water is not in equilibrium and that there is a tendency for water to flow toward a region of lower water potential. This reflects the capacity of water at some point in the system to perform work with respect to pure water. Water potential (ψ) in plants is composed of several independent components, $\psi = \psi_\rho + \psi_\pi + \psi_\tau + \psi_g$, of pressure potential (ρ), osmotic potential (π), matric potential (τ) and of gravitational effects (g) (Nobel 1974). An increase in pressure raises the free energy and this increases the water potential, while osmotic and matric components lower the activity of water and thus decrease the water potential. Since concentrations of osmotically active substances in the xylem sap are very small in most cases and matric components are at times absent, the difference between total water potential and xylem pressure potential is usually negligible. Pressure chamber determinations are commonly accepted as reasonable estimates of water potential, since pressure potential is generally by far the most important component of water potential. Water potential reflects not only the stress a plant is under but also its ability to draw water from the soil system.

The advances in the understanding of water relations in the soil-plant-atmosphere continuum (Slatyer 1967, Kramer 1968, Baver et al. 1972) notwithstanding, the adaptations by which plants can cope with tremendous temperature and water fluctuations and the concomitant internal osmotic changes, remain a fascinating field of study. It is, therefore, not surprising that the work of Scholander et al. (1965) on water potential should have paved the way for pursuing such studies vigorously (Waring and Cleary 1967, Boyer 1969, Wambolt 1970, Ritchie and Hinckley 1975, Branson et al. 1976). Poole and Miller (1975) and Tromp (1979) did not consider diurnal variation in the salt concentration of xylem sap. Striking diel variations both in ψ and ionic concentrations of expressed sap were found in the present study and, are considered of significant importance in the adaptations of cold desert shrubs to their environment.

A. canescens defoliates during winter months at the Tipton site, hence, productivity is limited to a relatively short growing season. Several species elsewhere limit their production to cool seasons, if possible, when atmospheric evaporative demands are reduced. In many such cases, ψ values are extremely low during summer months and the fluctuations are slight. However, cold desert shrubs thrive during ephemerally favorable, but otherwise highly stressful conditions. The unique phenology of these species may be one mechanism utilized for the conservation of water and the most efficient partitioning of assimilates (DePuit and Caldwell 1975).

Atriplex shows large diel ψ fluctuations and the rapid response rates serve to reduce water loss; such responses have been shown to occur in other species (Halvorson and Patten 1974, Haas and Dodd 1972). Immediate responses are governed, in most part, by changes in atmospheric conditions and may not be indicative of the true water regime at the root surface due to the great depth from which the water is taken up. In addition to being a phreatophyte, *Atriplex* has a large proportion of shallow roots at a depth of 30 cm. But the little precipitation that falls penetrates the soil only slightly. Although soil water integrates several environmental factors thus dictating water availability, it does not fluctuate sufficiently to account for rapid changes in ψ. Rainfall intensity and local features, however, are sufficient to cause runoff on to this site which perhaps determine the density and distribution of the species. Throughout the day, this plant is most probably responding to a constant supply of water which determines the baseline ψ. Therefore, fluctuations in ψ are hydrostatic pressure gradients established between this unchanging water supply and the fluctuating atmospheric evaporative demand.

Because this species is dioecious, one would expect the energy demands to be sex-related. Fertilization occurs early in the growing season after which staminate flowers senesce. Pistillate plants, on the other hand, produce a large seed crop which is not mature until late September. Although the percentage of annual growth attributable to twigs for the staminate plants is greater than for the pistillate individuals, it appears that the ratio of annual twig to leaf production is similar in both sexes. Since the overall mass and size of male and female plants does not differ significantly, and the % contribution of current biomass to the pistillate plant mass is almost twice as much as that of the staminate plants, then fruit production in pistillate plants would therefore be an expenditure of energy for reproduction at a stressful time. However, no differences in ψ behavior were found in male and female plants.

It has been shown that interspecific competition for water exists in desert ecosystems (Fonteyn and Mahall 1978); however, these workers did not find this competition effect to be significant enough to cause changes in the aboveground biomass. They also reported that intraspecific competition may be minimized by species-specific spacing distributions. Noting the distribution of *Atriplex canescens* and *Artemisia* *tridentata* at the Tipton site, it would be difficult to say that no belowground competition for water occurs. However, when solitary plants were compared with those surrounded by the same or other species, no differences in ψ were observed. Therefore, it is probable that individual range differences in diel ψ at the Tipton site are caused by differences in rooting depths and the spatial distribution of belowground biomass (Burk 1978).

Species unable to control stomates effectively and/or tolerate low ψ shed their leaves during stressful conditions. Stomatal closure in arid zone plants in response to low ψ decreases transpirational water loss. Since a decline in assimilation rates usually accompanies such a low ψ, the ability of the non-deciduous species to respond rapidly to favorable environmental conditions is highly adaptive. Stomates of *Atriplex* are presumably responding to a combination of high leaf temperatures and low ψ. The increases in water flux during midday in order to satisfy transpirational demands prevents the desiccation of leaves.

Observations show that the concentrations of solutes in the expressed sap are not varying selectively (Fig. 36), and that the linear changes in concentrations are accountable strictly on the basis of dilution effects. It has been stated that only the earliest effluxes of sap represent intracellular osmotic potentials (Barrs 1968). The fact that even excessively applied pressures yield relatively dilute sap concentrations indicates that few, if any, cells are ruptured in the process and that, in actuality the sap is water that has moved through the cell membranes by ultrafiltration (Scholander et al. 1966, Tyree and Hammel 1972). Certainly other components contribute to the osmotic balance than those listed in Table 39. For example, the synthesis of organic acids such as oxalic acid (usually in crystalline form as calcium oxalate) for the purpose of osmotic regulation has been given considerable attention (see above). However, oxalate would not be expected to be found in expressed sap due to the limitations mentioned regarding the origin of sap.

Although the true intracellular osmotic potentials may not directly estimated from those of the expressed sap, the rate of water movement, and thus dilution of solute species at low ψ, suggests several features regarding water balance. As the atmospheric evaporative demands progressively increase as midday approaches, a greater flux of water at the roots is required in order to satisfy increasing transpirational demands. Although the volume of sap was difficult to quantify, it was observed that the flow rate was greater at lower ψ than at high potentials. The increase in water movement accounts for the dilution of the baseline concentration of sap solutes. It would be easy to conclude that such an increase in ψ is merely an effect of the higher external pressures applied in obtaining the sap. However, similar pressures used when tissue water potentials were higher did not yield concomitant quantities of expressed water. It may be assumed, therefore, that even though the plant is under low ψ during midday, the rate of water movement through the xylem at this time is greater. Such a system supports the concept that stomatal closure is not merely a direct response to loss of water from the tissues but a regulatory function responding to low pressure potential values (Cowan 1977, Ehret and Boyer 1979).

Phenological measurements have been shown to expeditiously provide reliable indicators of shrub productivity (Rutherford 1979). Total above ground and leaf weight have been adequately predicted using basal diameter of several Rocky Mountain shrub species (Brown 1976). Dry weight of *Artemisia tridentata* was predicted using plant height and circumference as independent variables (Harniss and Murray 1976). Springfield (1974) estimated total mass of *Atriplex canescens* using the number of background grid squares obscured by the plant. Even though site-specific relationships are in no way new (Pechanec and Pickford 1937), the validity of these estimates of biomass of a species over a large range encompassing large variations has remained untested. In the present study, standing biomass and net annual productivity of *Atriplex canescens* from distinctively separate sites was predicted from species-specific equations using total crown volume as the independent variable. Although a combination of phenological and/or morphological factors may prove more reliable in predicting biomass, a single variable may be a more practical sampling method.

From the limited data used, it appears that the linear model is the closest approximation of the relationship between total crown volume and biomass, power curve fit equations indicate that the relationship is close to linearity (Table 26). However, such predictive models should be examined more closely. Total crown volume was not always a good predictor of plant age. Old plants with rotten or spintery wood had ostensibly fallen victim to a variety of damaging factors such as those of climate, disease, time, and/or trampling. The remains of old and decaying plants in many instances have the ability to sprout new growth from old stock above or below ground level. Several "juvenile" plants when excavated were observed to have arisen from below ground "dead stock". It appears that the old wood determines the basic framework and thus the space occupied by a plant. Given volumes of mature plants can therefore represent a wide range of component biomass age classes. Old wood seems to determine the skeletal size of the plant at the Tipton site, hence, it would be expected to yield the best relationship with total crown volume. This has been shown in Table 23. Indeed, the B_m would be free to vary and not dramatically alter the total plant volume, thus the lowest r^2 values. The intra-site comparisons of biomass components are interesting (Table 30); the large percentage of total above ground biomass at Cedar Mtn. composed of old wood indicates there is perhaps better survival of plants at Cedar Mtn. than at Tipton.

The limitations of equations such as these, based on a single harvest center on underestimations of productivity due to continuous shedding and regrowth of leaves. Errors of this nature are probably most important at Bluff and Kyle Canyon, where plants are not deciduous. However, since the regression approach predicts standing productivity as an estimation of available browse, standing biomass is adequate, if it is combined with information on phenological patterns (see West and Wein 1971) and grazing influences. Equations for predicting production of *Atriplex canescens* in this study are preliminary and must include a larger number of populations and plant ages. However, given similar equations for other range species, the quantity of wild and/or domestic livestock a particular stand can support could be estimated easily. The regression approach might also be useful in browse utilization studies, i.e., prebrowse and postbrowse inventory. Equations predicting old biomass or standing dead biomass of species could be used for efficient management in areas such as chaparral communities where the timing of fire plays an important role in community succession. This approach would be a worthwhile, rapid and undestructive method for assessing shrub rangeland productivity just as the cover has been used to estimate biomass in other ecosystems (Levy and Madden 1933). Land reclamation practices are required to comply with stringent plant community stipulations, one of which is productivity. Publications listing general productivity estimates for species under a variety of environmental conditions may prove useful to meet this end.

Calculations of mineral return based on concentrations only in the new litter underestimate total mineral return for several reasons. Unless leaves are collected immediately following abscission, the degree of nutrient mobilization from leaves as litter is essentially neglected. Fresh leaf litter from *Artemisia tridentata* has been shown to lose up to 16% of initial concentrations of K, Mg, Ca and P within the first three weeks (Mack 1977). Speculation regarding the degree of such mobilization is difficult and relies on accurate estimations of nutrient translocation from leaves prior to abscission. Potassium, sodium, nitrogen, and phosphorus are known to be mobile in phloem and capable of being redistributed from older leaves (Epstein 1972). However, the immobility of calcium in the phloem has been well documented (Loneragen 1968 and others). Thus, any dramatic reduction of calcium from fresh leaf tissue is unaccountable by retranslocation and must be attributable partially to leaching processes.

Pools of nutrients represented by new litter include only the leaf component of annual productivity. However, reproductive structures, stems, and twigs of present and past years of growth also contribute to litter. Of the plants chosen for litter analysis, standing leaf biomass accounted from only 26±10% of net annual production. Although twigs and stems accounted for only 4% of annual litter production of *Atriplex vesicaria*, fruit production (361 kg ha^{-1} or 33% of annual litter production) was significantly greater (Charley and Cowling 1968). Mack (1971) found *Artemisia tridentata* to produce 34 kg ha^{-1} of leaves and 28 kg ha^{-1} inflorescences annually. Fruit production in *Atriplex canescens* ranged from 21.42 kg ha^{-1} to 738.72 kg ha^{-1} in this study contributing to nutrient return substantially. It is particularly true at Kyle Canyon where utricles constituted 67% of net annual productivity.

Data from shrubs in both warm and cool deserts indicate that senescence and shedding of old leaves and regrowth of new leaves are concomitant processes. The total annual leaf litter fall would be greater therefore than the standing leaves at any time. Annual litter from *Artemisia tridentata* weighed, on an average, 26% more than standing leaf biomass (Mack 1977). Therefore, a single harvest method for productivity assessment, even in stands where vegetation is deciduous, could greatly underestimate net annual production and litter return.

Nutrient contents of new leaf litter represent the contribution of leaf production to the total litter mineral pool (Table 37). However, speculation regarding the amount and rate of mobilization of these nutrients is difficult. Obviously, the decomposition and mineralization of annual litter fall is not completed within a year's time, since a heavy mat of litter, representing various stages of decomposition, lies beneath each canopy. Data in the present study are partially conclusive only for potassium. Comparisons of new and old litter from Tipton and Cedar Mtn., and from Bluff and Kyle Canyon suggest that up to 55.5±2.1% and 33.0±1.4% of potassium has been mobilized respectively. Old litter at the former sites is at least a year old since *Atriplex canescens* is deciduous at these locations. However, not only is it quite possible for old litter to be less than a year old at the latter sites, but also subjected to fewer periods of adequate moisture for decomposition and mineralization. In any case, the minimum amount of potassium mobilized for example at Bluff was 13.92 g plant^{-1} yr^{-1}, or 51% of the 27.30 g initially contained in the new litter. However, from other studies, it can be speculated that over 90% of leaf potassium would be leached within a year. Mack (1977) reported less than 5% initial potassium in leaf litter remaining after one year. Given the magnitude of potassium levels in leaf tissue and the extent to which it is mobilized from litter, potassium would therefore be the fastest cycled element (with the exception of carbon, hydrogen and oxygen) through the plant-soil system. Nutrient content of new leaf litter beneath *Atriplex canescens* at Tipton, Cedar Mtn., and Kyle Canyon was 60%, 60% and 51% less than the fresh leaf concentrations, respectively. Nitrogen in new litter from individual plants at these sites ranged from 1.18 to 4.71 g. However, the nitrogen content of new litter from Bluff was less, and represented an 11% reduction from standing leaf concentrations. Levels of other elements are similar to those measured in new litter at other sites.

Nitrogen is one of the important nutrients redistributed to shoots and new plant parts from leaves prior to abscission. Up to 60% of the leaf nitrogen from senescing leaves has been shown to return to plant stems in desert species (Dina and Klikoff 1973, Wallace et al. 1978). Such a mechanism is thought to help conserve nutrients and thus obviate an otherwise paucity of nitrogen in semiarid systems. Standing leaf biomass from the individual plant at Bluff would therefore represent

16.19 g N in the mineral pool of new litter. Rapid mobilization of this element therefore leads to plant uptake commensurate to plant size and thus mineral return. Dioecious plants are relatively advanced in sexual dimorphism not only insuring obligate outcrossing (xenogamy), but also in resultant differential resource utilization and reduced inter-sexual competition. They are relatively rare among the angiosperms. World wide, 4% of the species of dicotyledons and 3% of the species of monocotyledons are dioecious (Yampolsky and Yampolsky 1922). The frequency commonly increases in tropical habitats (Grant 1975). All native species of *Atriplex* in Utah and northern deserts are dioecious (Hanson 1962). Even though *Atriplex canescens* is predominantly dioecious, monoecious and gynodioecious plants appear to be alternative breeding systems and were found in low percentages at Tipton, Wyoming.

The reproductive investment by females is greater than that of males per unit offspring, since ovule production and maturation require more energy than pollen grain production. Additionally, seed development occurs at a time of greater environmental stress than does pollen production. Because of these differential requirements, males are locally found on more xeric sites than females. For example, the predominance of male and female jojoba plants on south and north facing slopes respectively has been related to moisture stress (Cole 1979). Just as staminate individuals acquire a tolerance for xeric sites, females could develop competitive superiority on mesic sites. Differential success of males and females on xeric and moist sites has been documented for five wind-pollinated species (Freeman et al. 1976). Given the nature of a desert habitat, a distinct advantage would be conferred to those shrubs which are dioecious. It is thought that the longer life span of shrubs insures against the risk of fertilization failing and seeds not germinating, that separation of sexes prevents in plants with a shorter life span. Herein lies one of the reasons annual plants are rarely dioecious (Dzhaparidze 1967). Individuals unable to successfully reproduce as pistillate plants because of intense environmental stress but capable of responding by changing sex, would be at a distinct fitness advantage. Unusually harsh winters have been shown to shift sex ratio of *Atriplex canescens* in favor of staminate plants (McArthur 1977).

With this brief background, two questions regarding the breeding system of *Atriplex canescens* remains. First, what accounts for the imbalanced sex ratios? And secondly, why do pistillate plants grow larger than staminate plants?

Selection for a sex ratio other than one is operating at the level of production, germination and/or survival of either staminate or pistillate plants. However, in view of the plasticity of sex determination in *Atriplex canescens,* sex ratios would more realistically be regulated by the success of pollen donation and/or ovule maturation. Pollen-ovule ratios have been correlated with habitat, successional stage, and breeding systems in a number of species (Cruden 1977). Varying sex ratios in dioecious anemophilous species would be a mechanism for regulating pollen/ovule ratio and would be expected to change in relation to stand density, and wind direction and intensity (Wilson 1979). When a species is growing in a stand where the success of pollen donation is low, investment in male flowers would be disadvantageous, and thus favor female plants. The sex ratio of *Atriplex confertifolia* was influenced by localized moisture gradients and pistillate plants were always more abundant (Freeman et al. 1976); such a selective advantage for the pistillate plants of *Atriplex canescens* also seems to prevail.

Imbalanced sex ratios once established within a population would result in intrasexual competition for mates of the sex in least supply. An effective means of intrasexual competition among female plants would be an increase in pollen reception by the enlargement of plant size. A larger plant would therefore be a larger target and acquire not only more pollen, but pollen from a greater number of donors.

SUMMARY AND CONCLUSIONS

1. *Atriplex canescens* is a facultatively evergreen dioecious shrub inhabiting sandy calcareous soils of moderate alkalinity throughout cold and warm winter deserts of western United States.

2. It is commonly a co-dominant in many communities throughout its distribution and frequently found with members of the Compositae and Chenopodiaceae.

3. *Atriplex canescens* has the ability to resprout vigorously from underground stock and once established, can live well over 100 years. Experiments indicate that seeds from all sites germinate easily in wetted, well aerated soil. Moisture is probably the limiting factor regulating germination and survival of seedlings in the field.

4. The mean plant size ranged from 0.62±0.48 to 7.05±2.19 m^3. Density and cover ranged from 400 to 1.022×10^3 plants ha^{-1}, and from 5.7 to 38.4% of the ground space, respectively.

5. *Atriplex canescens* had a significant influence on the chemical and physical properties of the soil. Vegetated soils had significantly higher moisture content, organic matter, electrical conductivity, alkaline earth carbonates, nitrogen, potassium, sodium, calcium, magnesium and manganese than unvegetated soils.

6. Both organic matter and nitrogen of unvegetated soils from the four study sites were typical of semiarid environments, generally below 0.7 and 0.03% respectively. In addition to moisture, nitrogen may be a limiting factor for the growth of other species on unvegetated soils.

7. Fertile islands beneath the shrub canopies provided microclimates favorable to the growth of ephemeral grass species.

8. Major cations in plant parts were in the order K > Ca > Mg > Na. Concentrations of these cations in plant parts decreased thus: leaves, fruits, twigs, middle and old growth. The mean sum of major cations in leaf tissue was 317.96±42.78 me 100 g^{-1} dry weight.

9. Major anions in leaf tissue followed the order Cl > C_2O_4 > N > P. The mean sum of major anions in leaf tissue was 116.15±15.54 me 100 g^{-1} dry weight.

10. High K/Na ratios were found in plant tissue, in contrast to low K/Na ratios in unvegetated soils.

11. Leaf chloride content of *Atriplex canescens* was negatively correlated with total oxalate but positively correlated with the sum of major cations in the leaf.

12. Water potential (ψ) measurements of *Atriplex canescens* at Tipton revealed a range of -15.5 to -45.1 bars. Minimum values coincided with the lowest air and soil temperatures, maximum with the greatest atmospheric evaporative demand.

13. Change in ψ exceeded 12 bars hr^{-1} during the periods of rapidly moving storm systems. Changes in ψ appeared to be independent of plant size, age, sex and the spatial location of plants.

14. Chemical analyses revealed that expressed sap was up to three times more concentrated at high than at low ψ. The flow rate of sap was greater at lower than at higher ψ. The increase in water movement accounted for the dilution of the concentration of sap solutes.

15. Together, Ca, Mg, K and Na contributed 58% of the mean osmolality of the expressed sap; the dominant ions, however, were K and Cl.

16. Productivity of *Atriplex canescens* at southern warm desert sites was significantly greater than that at the cold-desert locations.

17. Net annual productivity estimated from species-specific prediction equations, ranged from 0.203×10^3 kg ha^{-1} yr^{-1} at Cedar Mtn., to 2.482×10^3 kg ha^{-1} yr^{-1} at Bluff.

18. Potassium had the highest rate of return of any single element in plant litter. Rates of potassium mobilization from leaf litter at Tipton ranged from 3.94 to 11.12 g K yr^{-1}. It was also found in the largest concentration.

19. Data suggest that K and N, and possibly other elements are redistributed to plant parts from leaves prior to leaf senescence.

APPENDIX A

COMBINED WATER POTENTIAL DATA FOR *Atriplex canescens*, AUGUST 1977, TIPTON, WYOMING

Table 40. Combined water potential data for *Atriplex canescens*, August 1977, Tipton, Wyoming.

Plant No.	Date	Time	$-\psi$(bars)	light (cal cm^{-2} min^{-1})	Temp. (^{o}F)	Relative Humidity (%)	Vapor Pressure Deficit
4	5 Aug	0913	26.19	0.72	68	45	9.65
		0915	24.81	0.72	68	45	9.65
		1202	28.26	0.40	68	39	10.70
		1207	27.91	0.40	68	39	10.70
		1502	25.50	0.60	68	49	8.95
		1506	25.16	0.60	68	49	8.95
		1816	22.05	0.40	65	58	6.82
		1821	22.05	0.40	65	58	6.82
		2213	25.50	0	51	82	1.73
		2217	17.92	0	51	82	1.73
	6 Aug	0710	18.26	0.1	51	82	1.73
		0713	15.85	0.1	51	82	1.73
		0716	17.57	0.1	51	82	1.73
		1003	26.19	0.89	66	46	8.79
		1008	24.12	0.89	66	46	8.79
		1308	32.39	1.50	76	21	18.11
		1313	33.77	1.50	76	21	18.11
		1607	34.11	1.30	77	13	20.67
		1612	34.11	1.30	77	13	20.67
		2016	18.95	0	58	80	2.46
		2018	20.68	0	58	80	2.46
	7 Aug	0135	18.95	0	52	77	2.30
		0139	17.23	0	52	77	2.30
		0624	16.54	<0.1	47	86	1.16
		0626	16.20	<0.1	47	86	1.16
		0938	27.22	0.85	69	34	12.01
		0942	27.57	0.85	69	34	12.01

Table 40. (Continued)

Plant No.	Date	Time	$-\psi$(bars)	light (cal cm^{-2} min^{-1})	Temp. (^{o}F)	Relative Humidity (%)	Vapor Pressure Deficit
4	7 Aug	1205	36.87	1.40	87	8	30.30
		1216	34.80	1.45	87	8	30.30
		1219	35.84	1.45	87	8	30.30
		1452	37.90	1.40	94	1	40.39
		1456	39.97	1.40	94	1	40.39
		2038	23.43	0	78	15	20.93
	8 Aug	0525	18.95	0	66	79	3.42
		0528	18.26	0	66	79	3.42
		0840	21.36	0.5	75	48	11.50
		0842	21.36	0.5	75	48	11.50
5	5 Aug	0921	25.50	0.75	68	44	9.82
		0926	24.12	0.75	68	44	9.82
		1216	27.22	0.44	68	39	10.70
		1221	26.53	0.44	68	39	10.70
		1225	25.50	0.40	68	39	10.70
		1512	26.19	1.10	68	47	9.30
		1518	25.84	0.90	68	47	9.30
		1827	22.74	0.28	66	58	6.83
		1832	23.09	0.28	66	58	6.83
		2220	17.57	0	51	82	1.73
		2224	17.23	0	51	82	1.73
	6 Aug	0718	16.20	0.2	51	82	1.73
		0721	15.51	0.2	51	82	1.73
		1013	23.43	0.94	67	43	9.63
		1017	24.12	0.94	67	43	9.63
		1317	34.46	1.40	77	19	19.25
		1322	34.46	1.40	77	19	19.25

Table 40. (Continued).

Plant No.	Date	Time	$-\psi$(bars)	light (cal cm^{-2} min^{-1})	Temp. (^{o}F)	Relative Humidity (%)	Vapor Pressure Deficit
5	6 Aug	1616	38.59	1.30	79	12	22.45
		1620	36.18	0.80	79	12	22.45
		1625	36.87	0.65	79	12	22.45
		2000	19.30	0	58	74	3.20
		2003	19.64	0	58	74	3.20
	7 Aug	0142	17.23	0	51	80	1.92
		0147	17.92	0	51	80	1.92
		0555	16.54	0	47	88	0.99
		0558	16.54	0	47	88	0.99
		0913	22.74	0.80	69	38	11.28
		0920	22.74	0.80	69	38	11.28
		1221	38.94	1.45	87	8	30.30
		1227	38.59	1.45	87	8	30.30
		1422	39.28	1.49	92	1	38.19
		1426	39.97	1.49	92	1	38.19
		1429	40.32	1.49	92	1	38.19
		1617	41.01	≃1.40	96	0	43.60
		1620	41.35	≃1.40	96	0	43.60
		2011	24.47	0	80	15	22.20
		2016	22.74	0	80	15	22.20
		2018	23.78	0	80	15	22.20
	8 Aug	0500	19.64	0	68	76	4.21
		0504	19.99	0	68	76	4.21
		0811	21.36	0.5	77	49	12.12
		0814	21.36	0.5	77	49	12.12

Table 40. (Continued)

Plant No.	Date	Time	-ψ(bars)	light (cal cm^{-2} min^{-1})	Temp. (^{o}F)	Relative Humidity (%)	Vapor Pressure Deficit
6	5 Aug	0932	24.12	0.8	69	44	10.19
		0937	24.47	0.8	69	44	10.19
		1232	29.29	1.12	68	39	10.70
		1237	30.32	1.12	68	39	10.70
		1525	26.53	0.6	72	42	11.64
		1531	25.50	0.4	72	42	11.64
		1840	23.09	0.25	65	57	6.82
		1845	22.74	0.25	65	57	6.82
		2228	18.61	0	51	82	1.73
		2232	18.61	0	51	82	1.73
	6 Aug	0724	16.54	0.18	51	82	1.73
		0727	16.54	0.18	51	82	1.73
		1022	24.81	0.95	67	43	9.63
		1028	24.12	0.95	67	43	9.63
		1327	37.90	1.48	77	19	19.25
		1332	34.46	1.48	77	19	19.25
		1337	35.49	1.48	77	19	19.25
		1631	34.11	1.07	79	11	22.70
		1635	35.15	1.07	79	11	22.70
		2025	20.68	0	57	80	2.37
		2027	21.71	0	57	80	2.37
	7 Aug	0151	19.64	0	52	80	2.00
		0155	19.30	0	52	80	2.00
		0629	18.61	0.1	47	86	1.16
		0632	16.88	0.1	47	86	1.16
		0635	17.23	0.1	47	86	1.16

Table 40. (Continued)

Plant No.	Date	Time	$-\psi$(bars)	light (cal cm^{-2} min^{-1})	Temp. (^{o}F)	Relative Humidity (%)	Vapor Pressure Deficit
7	5 Aug	0942	28.26	0.80	71	43	11.03
		0947	28.95	0.96	71	43	11.03
		1242	32.39	1.24	73	37	13.12
		1251	31.01	0.55	73	37	13.12
		1537	27.57	0.40	72	41	11.84
		1850	24.12	0.24	64	58	6.42
		1855	25.16	0.24	64	58	6.42
		2235	20.68	0	51	82	1.73
		2238	20.33	0	51	82	1.73
	6 Aug	0730	18.95	0.18	51	82	1.73
		0734	18.61	0.18	51	82	1.73
		1032	26.88	0.95	67	43	9.63
		1039	28.26	0.95	67	43	9.63
		1044	28.26	0.95	67	43	9.63
		1339	38.59	1.42	77	19	19.25
		1344	38.59	1.42	77	19	19.25
		1639	35.84	0.60	81	11	24.08
		1643	35.84	0.60	81	11	24.08
		2007	21.71	0	59	79	2.69
		2011	21.71	0	59	79	2.69
	7 Aug	0159	19.30	0	51	80	1.92
		0203	19.64	0	51	80	1.92
		0603	18.61	0	47	86	1.16
		0610	18.26	0	47	86	1.16
		0923	27.57	0.85	73	35	13.53
		0928	27.57	0.85	73	35	13.53

Table 40. (Continued)

Plant No.	Date	Time	$-\psi$(bars)	light (cal cm^{-2} min^{-1})	Temp. (^{o}F)	Relative Humidity (%)	Vapor Pressure Deficit
7	7 Aug	1230	37.90	1.50	87	8	30.30
		1235	37.90	1.50	87	8	30.30
		1432	38.59	1.49	92	1	38.19
		1437	40.66	1.30	92	1	38.19
		1441	41.01	1.35	92	1	38.19
		1624	39.28	≃1.30	95	0	42.18
		1627	37.56	≃1.30	93	0	39.90
		1631	37.90	≃1.30	91	0	37.31
		1707	38.94	≃<1.0	94	0	40.80
		2021	26.19	0	78	15	20.93
		2025	26.19	0	78	15	20.93
	8 Aug	0508	21.71	0	68	77	4.03
		0512	22.05	0	68	77	4.03
		0818	24.12	0.4	75	49	11.41
		0823	24.12	0.4	75	49	11.41
	9 Aug	1132	39.97	1.2	85	16	25.83
8	6 Aug	2034	20.33	0	57	79	2.48
		2039	18.26	0	57	79	2.48
		2041	20.68	0	57	79	2.48
	7 Aug	0207	17.57	0	51	80	1.92
		0211	17.23	0	51	80	1.92
		0214	17.57	0	51	80	1.92
		0614	16.54	0.05	47	86	1.16
		0617	16.54	0.05	47	86	1.16

Table 40. (Continued)

Plant No.	Date	Time	$-\psi$(bars)	light (cal cm^{-2} min^{-1})	Temp. (^oF)	Relative Humidity (%)	Vapor Pressure Deficit
8	7 Aug	0932	24.81	0.85	69	34	12.01
		0936	25.16	0.85	69	34	12.01
		1238	36.18	1.50	87	7	30.62
		1242	34.11	1.50	87	7	30.62
		1245	36.18	1.50	87	7	30.62
		1446	39.28	1.41	94	1	40.39
		1449	39.63	1.41	94	1	40.39
		1648	37.90	≃1.4	93	0	39.90
		1650	36.87	≃1.4	93	0	39.90
		1703	36.87	≃1.4	93	0	39.90
		2029	24.81	0	78	15	20.93
		2034	24.81	0	78	15	20.93
	8 Aug	0517	20.68	0	67	79	3.55
		0520	20.68	0	67	79	3.55
		0828	22.05	0.4	74	49	11.01
		0829	25.50	0.4	74	49	11.01
		0837	21.71	0.4	74	49	11.01
9	9 Aug	1051	40.66	1.15	80	17	21.68
		1054	38.59	1.15	80	17	21.68
		1056	40.32	1.15	80	17	21.68
		1058	38.59	1.15	80	17	21.68
		1310	43.07	1.45	88	13	29.65
		1312	43.07	1.45	88	13	29.65
		1506	44.45	1.35	87	9	19.97
		1508	42.73	1.35	87	9	29.97

Table 40. (Continued)

Plant No.	Date	Time	$-\psi$(bars)	light (cal cm^{-2} min^{-1})	Temp. (^{o}F)	Relative Humidity (%)	Vapor Pressure Deficit
9	9 Aug	1511	43.07	1.35	87	9	29.97
		1717	39.97	0.97	86	7	29.59
		1719	39.97	0.97	86	7	29.59
		1903	37.22	0.35	82	7	26.06
		1906	35.84	0.35	82	7	26.06
		2102	27.22	0	65	24	12.06
		2105	27.57	0	65	24	12.06
	10 Aug	0302	24.12	0	50	78	2.03
		0305	23.09	0	50	78	2.03
		0500	23.09	0	48	83	1.44
		0502	24.12	0	48	83	1.44
		0808	26.88	0.25	60	59	5.24
		0812	27.22	0.25	60	59	5.24
		1137	36.18	1.25	77	34	15.68
		1140	35.84	1.25	77	34	15.68
		1143	34.11	1.25	77	34	15.68
		1302	39.28	1.43	83	25	21.77
		1307	38.59	1.43	83	25	21.77
		1500	38.94	1.27	89	13	30.33
		1502	42.04	1.27	89	13	30.33
		1505	41.01	1.27	89	13	30.33
		1706	38.59	0.95	84	11	26.43
		1708	38.59	0.95	84	11	26.43
		1938	27.57	0.1	65	68	5.08
		1941	26.19	0.1	65	68	5.08

Table 40. (Continued)

Plant No.	Date	Time	$-\psi$(bars)	light (cal cm^{-2} min^{-1})	Temp. (^oF)	Relative Humidity (%)	Vapor Pressure Deficit
10	9 Aug	1105	44.80	1.15	80	17	21.68
		1108	42.38	1.15	80	17	21.68
		1115	43.07	1.15	80	17	21.68
		1315	45.14	1.45	87	13	28.65
		1317	45.49	1.45	87	13	28.65
		1513	45.49	1.3	88	10	30.67
		1517	44.80	1.3	88	10	30.67
		1720	40.66	1.0	86	6	29.91
		1722	39.63	1.0	86	6	29.91
		1908	36.53	0.3	83	7	26.99
		1911	36.53	0.3	83	7	26.99
		2108	29.98	0	64	25	11.46
		2110	29.29	0	64	25	11.46
	10 Aug	0307	25.50	0	50	78	2.03
		0310	25.84	0	50	78	2.03
		0505	24.47	0	48	83	1.44
		0507	24.47	0	48	83	1.44
		0815	26.88	0.38	61	57	5.94
		0819	26.88	0.38	61	57	5.94
		1146	36.87	1.3	78	33	16.50
		1149	36.53	1.3	78	33	16.50
		1310	38.25	1.44	83	24	22.06
		1316	38.25	1.44	83	24	22.06
		1507	41.35	1.27	89	13	30.33
		1510	40.66	1.27	89	13	30.33

Table 40. (Continued)

Plant No.	Date	Time	-ψ(bars)	light (cal cm^{-2} min^{-1})	Temp. (^oF)	Relative Humidity (%)	Vapor Pressure Deficit
10	10 Aug	1711	37.22	0.9	83	11	25.83
		1714	38.59	0.9	83	11	25.83
		1945	26.88	0.05	64	68	4.89
		1949	26.88	0.05	64	68	4.89
11	9 Aug	1118	33.77	1.20	82	16	23.54
		1122	34.11	1.20	82	16	23.54
		1323	36.87	1.45	88	12	30.00
		1326	39.28	1.45	88	12	30.00
		1329	38.94	1.45	88	12	30.00
		1521	39.28	1.30	86	8	29.27
		1524	38.25	1.30	86	8	29.27
		1725	37.90	0.97	86	6	29.91
		1728	37.56	0.97	86	6	29.91
		1914	32.39	0.3	82	8	25.78
		1916	32.05	0.3	82	8	25.78
		2113	21.02	0	64	26	11.31
		2115	21.71	0	64	26	11.31
	10 Aug	0315	18.95	0	50	78	2.03
		0317	17.92	0	50	78	2.03
		0510	16.54	0	48	83	1.44
		0514	16.88	0	48	83	1.44
		0826	19.30	0.43	62	55	6.38
		0829	18.61	0.43	62	55	6.38
		1153	29.63	1.32	78	33	16.50
		1156	28.95	1.32	78	33	16.50

Table 40. (Continued)

Plant No.	Date	Time	$-\psi$(bars)	light (cal cm^{-2} min^{-1})	Temp. (^{o}F)	Relative Humidity (%)	Vapor Pressure Deficit
11	10 Aug	1322	34.11	1.42	85	22	23.99
		1327	33.08	1.42	85	22	23.99
		1513	33.43	1.26	89	13	30.33
		1515	33.77	1.26	89	13	30.33
		1716	33.08	0.90	83	11	25.83
		1719	34.46	0.90	83	11	25.83
		1721	33.77	0.90	83	11	25.83
		1952	20.68	0.05	60	68	4.25
		1956	18.95	0.05	60	68	4.25
12	9 Aug	1125	37.90	1.2	82	16	23.54
		1127	38.25	1.2	82	16	23.54
		1332	40.32	1.42	88	11	30.33
		1339	40.32	1.42	88	11	30.33
		1527	42.38	1.3	90	8	33.18
		1529	41.01	1.3	90	8	33.18
		1532	40.32	1.3	90	8	33.18
		1731	38.25	0.95	86	6	29.91
		1734	37.90	0.95	86	6	29.91
		1918	35.84	0.3	80	9	23.77
		1921	34.46	0.3	80	9	23.77
		1923	34.11	0.3	80	9	23.77
		1925	34.46	0.3	80	9	23.77
		2119	28.26	0	62	28	10.20
		2122	27.57	0	62	28	10.20

Table 40. (Continued)

Plant No.	Date	Time	$-\psi$(Bars)	light (cal cm^{-2} min^{-1})	Temp. (^{o}F)	Relative Humidity (%)	Vapor Pressure Deficit
12	10 Aug	0319	25.50	0	50	78	2.03
		0321	24.47	0	50	78	2.03
		0517	23.43	0	48	84	1.36
		0519	23.43	0	48	84	1.36
		0833	26.19	0.44	62	55	6.38
		0838	26.19	0.44	62	55	6.38
		1159	34.46	1.32	78	33	16.50
		1202	34.11	1.32	78	33	16.50
		1332	38.94	1.42	85	22	23.99
		1337	38.59	1.42	85	22	23.99
		1517	38.59	1.25	89	13	30.33
		1520	38.59	1.25	89	13	30.33
		1724	37.90	0.85	81	11	24.08
		1727	37.22	0.85	81	11	24.08
		2000	25.16	0	60	68	4.25
		2003	25.50	0	60	68	4.25

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