SEASONAL WATER RELATIONS OF JUVENILE AND MATURE *ARTEMISIA TRIDENTATA* (NUTT.) IN EASTERN WASHINGTON STATE

By

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To the Faculty of Washington State University:

The Members of the Committee appointed to examine the thesis of FENTON KHAN find it satisfactory and recommend that it be accepted.

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Chair

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SEASONAL WATER RELATIONS OF JUVENILE AND MATURE *ARTEMISIA TRIDENTATA* (NUTT.) IN EASTERN WASHINGTON STATE

Abstract

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Two studies were conducted to examine seasonal variations of plant water relations of *Artemisia tridentata* (big sagebrush). First, seasonal differences of plant water status were examined for juvenile and mature *A. tridentata* shrubs growing in a mixed-age stand. Monthly measurements of leaf xylem potentials at predawn and midday over a two-year period showed no significant differences in predawn leaf water potentials between juvenile and mature shrubs. However, midday xylem pressure potentials were significantly different between age classes: mature shrubs had lower midday xylem potentials in spring, summer, and fall and juveniles had lower xylem potentials in winter. Predawn xylem pressure potentials for juvenile and mature shrubs were highest in spring months (-0.59 MPa and -0.64 MPa, respectively) and and lowest in early fall (-2.32 MPa and -3.11 MPa, respectively). Midday xylem pressure potentials were also highest in spring months for juvenile and mature shrubs (-1.25 MPa and -1.31 MPa, respectively) and lowest in summer (-3.21 MPa and -3.97 MPa, respectively). Juveniles exhibited greater stomatal conductances than mature shrubs in April and September. Second,

seasonal plant water relations were examined for a contiguous population of *A. tridentata* shrubs on two adjacent soils of different textures. *Artemisia tridentata* in a loamy sand experienced greater predawn and midday water stress than shrubs in an adjacent stabilized sand dune in summer, fall, and winter. Predawn xylem pressure potentials were highest in spring, -0.64 MPa (sand dune) and -0.60 MPa (loamy sand), and lowest in early fall, -3.13 MPa (sand dune) and -3.94 MPa (loamy sand). Midday xylem pressure potentials for the two age classes of shrubs were also highest in spring, -1.31 MPa (sand dune) and -1.40 MPa (loamy sand); however, seasonal lows occurred in different months: shrubs on the sand dune were lowest in summer (-3.97 MPa), whereas shrubs in the loamy sand were lowest in October (-4.59 MPa). Concurrent measurements of soil water contents indicate that differences in plant water potentials between shrubs in the two soils were correlated with differences in total soil water storage for the two soils.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS iii

ABSTRACT iv

LIST OF TABLES viii

LIST OF FIGURES ix

GENERAL INTRODUCTION 1

REFERENCES 5

CHAPTER ONE: SEASONAL VARIATION IN PLANT WATER RELATIONS OF JUVENILE AND MATURE *ARTEMISIA TRIDENTATA* (NUTT.) WITHIN A STAND

1. ABSTRACT 8
2. INTRODUCTION 9
3. MATERIALS AND METHODS 11
4. RESULTS 16
5. DISCUSSION 32
6. CONCLUSION 38
7. REFERENCES 39

CHAPTER TWO: SEASONAL DIFFERENCES IN PLANT WATER RELATIONS OF A CONTIGUOUS POPULATION OF *ARTEMISIA TRIDENTATA* (NUTT.) GROWING ON TWO ADJACENT SOILS OF DIFFERENT TEXTURES

1. ABSTRACT 41
2. INTRODUCTION 42
3. MATERIALS AND METHODS 44

4. RESULTS 46

5. DISCUSSION 60

6. CONCLUSION 64

7. REFERENCES 65

LIST OF TABLES

CHAPTER ONE

Table 1. Annual temperatures for the study site 13

Table 2. Repeated measures ANOVA for predawn xylem pressure potentials of juvenile and mature *A. tridentata* 25

Table 3. Repeated measures ANOVA for midday xylem pressure potentials of juvenile and mature *A. tridentata* 27

Table 4. Repeated measures ANOVA for stomatal conductances for juvenile and mature *A. tridentata* 31

CHAPTER TWO

Table 5. Repeated measures ANOVA for predawn xylem pressure potentials of *A. tridentata* on two soil types 53

Table 6. Repeated measures ANOVA for midday xylem pressure potentials of *A. tridentata* on two soil types 56

Table 7. Repeated measures ANOVA for stomatal conductances for *A. tridentata* on two soil types 59

LIST OF FIGURES

CHAPTER ONE

Figure 1. Study site 12

Figure 2. Monthly precipitation of the study are 17

Figure 3. Monthly soil water storage (gravimetric) in the top 1.5 m of soil 18

Figure 4. Monthly soil water storage (neutron probe) in the upper and deeper layers of soil 19

Figure 5. Soil water content throughout the soil profile 20

Figure 6. Soil water content throughout the soil profile surrounding juvenile and mature *A. tridentata* 22

Figure 7. Monthly predawn xylem pressure potentials of juvenile and mature *A. tridentata* 24

Figure 8. Monthly midday xylem pressure potentials of juvenile and mature *A. tridentata* 26

Figure 9. Monthly stomatal conductances of juvenile and mature *A. tridentata* 30

CHAPTER TWO

Figure 10. Monthly precipitation of the study area 47

Figure 11. Monthly soil water storage (gravimetric) in the top 1.5 m of soil in two soil types 48

Figure 12. Monthly soil water storage (neutron probe) in the upper and deeper layers of soil of two soil types 49

Figure 13. Soil water content throughout the soil profiles of two soil types 50

Figure 14. Monthly predawn xylem pressure potentials for *A. tridentata* on two soil types 52

Figure 15. Monthly midday xylem pressure potentials for *A. tridentata* on two soil types 55

Figure 16. Monthly stomatal conductances for *A. tridentata* on two soil types 58

GENERAL INTRODUCTION

Artemisia tridentata Nutt. (big sagebrush) is a woody evergreen plant with an extensive distribution in the semi-arid intermountain region of the western United States (Miller and Shultz, 1987; Smith et al., 1997). It is a dominant rangeland shrub in the interior Columbia River Basin of eastern Washington State (Daubenmire, 1970). This plant species endures environmental extremes of summer drought and cold winters (Barker and McKell, 1983; Kolb and Sperry, 1999a) and tolerates the seasonal soil water stresses experienced in such climates (Matzner and Richards, 1996).

In eastern Washington, most of the annual precipitation and soil water recharge occur in the fall and winter, and drought conditions persist throughout the summer months (Rickard et al., 1988). Soil water is depleted throughout the spring and summer months by evaporation and transpiration processes (Campbell and Harris, 1977). Furthermore, Anderson and others (1987) indicate evapotranspirational demands generally exceed precipitation inputs in semi-arid regions suggesting that plants in this region may experience different levels of water stress in different seasons.

Because *A. tridentata* maintains leaves throughout the year (Kolb and Sperry, 1999a), measurements of leaf water potential can be used to monitor seasonal changes in plant water stress over time (Everett et al., 1977; Miller et. al., 1986). Studies of plant water relations of *A. tridentata* (e.g. Campbell and Harris, 1977; Barker and McKell, 1983; Black and Mack, 1986; Miller et al., 1986; Shumar and Anderson, 1986; Miller, 1988; Kremer and Running, 1996) describe a correlation between plant water stress and seasonal availability of soil moisture. Leaves of *A. tridentata* exhibit high plant water

potentials in the spring months when soil water is near field capacity, and low water potentials in summer months, when soil water is depleted.

Plants of same species and size growing in adjacent soils of different textures, but under the same environmental conditions, may display dissimilar plant water relations when measured concurrently. Barker and McKell (1983) found differences in plant water potentials between two subspecies of *A. tridentata* growing on two different types of soils within the same stand. Water infiltrates deeper in coarse-textured soils compared to fine-textured soils (Shumar and Anderson 1986; Brown and Archer 1990). Therefore, seasonal water stress of plants may be affected by variations in soil properties (Brown and Archer 1990).

Mature and juvenile plants generally differ greatly in size and have different proportions of above and belowground biomass (Frazer and Davis, 1988). Developmental constraints may cause juveniles to respond differently to microenvironments (e.g., water, nutrients, temperature, and light) than mature plants (Brown and Archer 1990; Donovan and Ehleringer 1992). In a mixed stand of juvenile and mature plants, juveniles with less extensive root systems are likely to be subjected to greater variations of water availability than mature plants (Campbell and Harris, 1977; Brown and Archer, 1990; Knapp and Fahnestock, 1990).

Mature *A. tridentata* is deep-rooted (Rupp, 1969; Reynolds and Fraley, 1989) therefore, it maintains water uptake from deep in the soil during dry summer months, when moisture in the upper layers has been exhausted (Cline et al., 1977; Daddy et al., 1988; Matzner and Richards, 1996). However, juvenile shrubs with shallow roots may experience greater water stress than mature shrubs after stored water in the upper layers

of soils has been depleted. Donovan and Ehleringer (1991,1992) found that juveniles exhibited lower plant water potentials and greater instantaneous water use efficiency and gas exchange rates than mature shrubs when soil water in the upper layers was depleted. Brown and Archer (1990) also suggest that differences in available soil water may relate to differences in plant water stress and photosynthesis between juvenile and mature woody plants.

The change from juvenile (non-reproductive) to mature (reproductive) status in woody plants is generally determined by plant size (Harper and White, 1974). Plant growth and size are influenced by the capability of individual plants to maximize water uptake while minimizing transpirational loss (Romo and Haferkamp, 1987). Therefore, growth, development, and survival of *A. tridentata* depend on effective water uptake for transpirational demands throughout all seasons. Numerous studies document plant water relations of *A. tridentata* (e.g., Campbell and Harris, 1977; Black and Mack, 1986; Richards and Caldwell, 1987; Donovan and Ehleringer, 1991, 1992; Kolb and Sperry, 1999a; Evans et al., 1991; Downs, 2000); however, most of these studies were conducted only in spring and summer months. Year-round studies are scarce if they exist at all. Furthermore, no studies have compared seasonal plant water relations for a year or more between juvenile and mature *A. tridentata* shrubs growing in the same stand.

The purpose of this study was to measure the year-round water relations of mature and juvenile *A. tridentata* shrubs growing in a mixed age stand. In addition, I examined the seasonal water relations of mature *A. tridentata* shrubs growing in a continuous stand across soils of different textures. Chapter one describes the seasonal differences found in plant water relations between juvenile and mature *A. tridentata* shrubs growing in the

same stand over a two-year period. I hypothesize that juveniles will experience greater water stress than mature shrubs for all seasons. Juvenile *A. tridentata* shrubs are expected to exhibit lower plant water potentials than mature shrubs as a result of differences in rooting depth and seasonal changes in plant available soil water. In addition, this study is one of the first to examine plant water relations of juvenile and mature *A. tridentata* shrubs throughout all the months of a year.

Chapter two describes the seasonal differences in plant water relations between mature *A. tridentata* shrubs in a contiguous stand growing on different textured soils. I hypothesize that there will be a difference in plant water stress between mature shrubs growing in different textured soils within the stand. Differences in plant water stress are expected between shrubs growing in the two soil types because soil water storage will differ in soils of different textures (Brown and Archer 1990). Coarse-textured soils will allow more drainage whereas, fine-textured soils will store water closer to the surface where the water will be subjected to evaporation and uptake by shallow rooted plants (Shumar and Anderson 1986; Brown and Archer 1990).

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CHAPTER 1

SEASONAL VARIATION IN PLANT WATER RELATIONS OF JUVENILE AND MATURE *ARTEMISIA TRIDENTATA* (NUTT.) WITHIN A STAND

Abstract: Seasonal differences of plant water status were examined for juvenile and mature *Artemisia tridentata* shrubs growing in a mixed-age stand. Monthly predawn and midday measurements of leaf xylem pressure potentials over a two-year period showed no significant differences in predawn leaf water potentials between juvenile and mature shrubs. However, midday xylem pressure potentials were significantly different between age classes: mature shrubs exhibited lower midday xylem potentials in the spring, summer, and fall months and juveniles displayed lower xylem potentials in winter. Predawn xylem pressure potentials for juvenile and mature shrubs were highest in spring months (-0.59 MPa and -0.64 MPa, respectively) and lowest in early fall (-2.32 MPa and -2.97 MPa, respectively). Midday xylem pressure potentials were also highest in spring months for juvenile and mature shrubs (-1.25 MPa and -1.31 MPa, respectively) and lowest in summer (-3.21 MPa and -3.97 MPa, respectively). Juveniles exhibited greater stomatal conductances than mature shrubs only in April and September. The results of this study indicate mature shrubs experienced greater midday plant water stress than juvenile shrubs for most of the year, except winter months when juveniles experienced greater plant water stress than mature shrubs.

INTRODUCTION

Water is often the factor most limiting to plant growth and survival in arid and semi-arid regions where precipitation is variable and temperatures can be extreme (Daubenmire, 1970; Richards and Caldwell, 1987). Under such conditions, shallow-rooted juvenile shrubs compete with neighboring plants for water stored in the upper layers of soil and may experience water stress earlier in the growing season than older shrubs with large and deep rooting systems (Campbell and Harris, 1977; Knapp and Fahnestock, 1990; Donovan and Ehleringer, 1991, 1992). Campbell and Harris (1977) and Donovan and Ehleringer (1991, 1992) found that juvenile plants of two common western shrub species, *Artemisia tridentata* and *Chrysothamnus nauseosus*, exhibited greater water stress than larger sized adult plants in spring and summer months.

A number of publications document the plant water status of *A. tridentata* (e.g., Campbell and Harris, 1977; Black and Mack, 1986; Richards and Caldwell,1987; Donovan and Ehleringer, 1991, 1992; Kolb and Sperry, 1999a; Evans et al., 1991; Downs, 2000), but most studies were conducted in the spring and summer months. Year-round studies are scarce if they exist at all. Furthermore, no studies have compared the seasonal plant water relations of a mixed stand of juvenile and mature *A. tridentata* shrubs.

The purpose of this study was to assess whether seasonal variations in plant water status exist between juvenile and mature *A. tridentata* shrubs within a stand. I hypothesize that juveniles will experience greater water stress than mature shrubs for all seasons. Juvenile *A. tridentata* shrubs are expected to exhibit lower plant water potentials than mature shrubs as a result of differences in rooting depth and seasonal

changes in plant available soil water. To evaluate plant water status, I measured plant water potentials and stomatal conductance of shrubs and soil water content on a monthly schedule for two years (February 1999 to January 2001).

MATERIALS AND METHODS

I evaluated seasonal variations in plant water relations for juvenile and mature *A. tridentata* shrubs witin a 2500-m^2 study plot established in the winter of 1998 on the Hanford Site in eastern Washington State (Figure 1). The site, which is at an elevation of 229 m, lies on a stabilized sand dune within the *Artemisia tridentata-Bromus tectorum* (sagebrush-cheatgrass) habitat type (Daubenmire, 1970) where the climate is considered to be semi-arid (Rickard et al., 1988). The soils of the sand dune are classed as Rupert Sand (Hajek 1966), which is brown to grayish brown coarse sand. According to Hajek (1966), "Rupert Soils developed under grass, sagebrush, and hopsage in coarse sandy alluvial deposits, which were mantled by wind-blown sand."

Fourteen *A. tridentata* plants were randomly selected within the study plot: seven non-reproductive, juvenile (< 50 cm tall) shrubs and seven reproductive mature (>100 cm tall) shrubs were chosen to represent the two age classes. The average height of mature shrubs was 1.41 m and average height of juvenile shrubs was 0.46 m.

Climatological data were obtained from the Hanford Meteorological Station (HMS) approximately two miles west of the study plot at the same elevation. Average annual precipitation for the Hanford Site, for years 1947 through 2000, was 17.25 cm; with lowest in 1976, which was 7.60 cm and the highest in 1995, which was 31.27 cm (Hoitink et al., 2000). Approximately 67% of the annual precipitation on the Hanford Site occurs in the winter and early spring months (between October and April) (Rickard et al., 1988). Average seasonal temperatures for the Hanford Site for

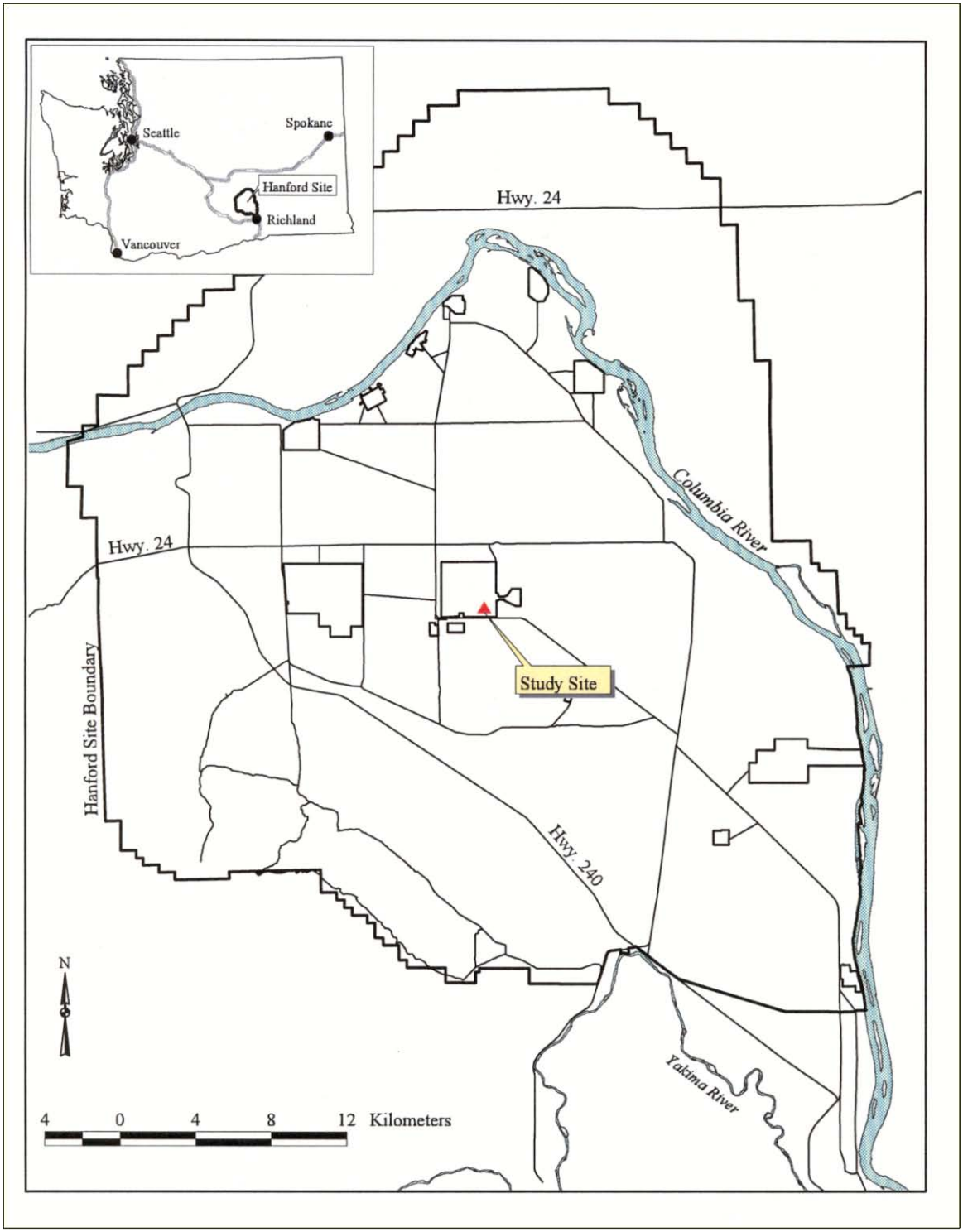

Figure 1. Location of the study area within the boundaries of the Hanford Site in eastern Washington State.

1947 through 2000 are portrayed in table 1. The average temperature of some summer days can reach as high as 39.1 °C while during the winter it can be as low as -2 °C.

Table 1. Minimum, maximum, and average temperatures measured at the Hanford Meteorological Station (1947 – 2000) (Hoitink et al., 2000).

Season	Avg. Minimum Temperature (°C)	Avg. Maximum Temperature (°C)	Average Temperature (°C)
Winter	-13.0	14.8	0.9
Spring	-2.0	27.4	11.8
Summer	8.4	39.1	23.1
Fall	-2.2	26.7	11.7

Plant water potential measurements

Xylem pressure potentials of *A. tridentata* were measured on the seven selected shrubs of each age class (juvenile and mature). For the first year (February 1999 – January 2000), measurements were conducted on a monthly schedule except in April and May when measurements were taken at two-week intervals. During the second year (February 2000 – January 2001), xylem pressure potentials were measured bi-weekly except in February, July, August, December, and January. Xylem pressure potentials were measured on terminal branches (approximately 5 cm long) selected from the top of each shrub at predawn (at least 30 minutes before first light) and midday (between 1200 hours and 1300 hours) of the same day, using the pressure chamber[a] technique as described by Koide and others (1989).

[a] Soil Moisture, Inc., Santa Barbara, CA.

Stomatal conductance measurements

Stomatal conductances were measured for five of the seven shrubs chosen for xylem pressure potential measurements of each size class (juvenile and mature) of *A. tridentata* shrubs. Measurements were conducted on a monthly basis from February through September 2000 with a LI-1600 porometer[b]. Stomatal conductances were measured on the same day as plant water potentials, approximately every two hours between 0700 hours and 1400 hours on terminal branches at the top of the shrub canopy. Leaves within the measurement cuvette were harvested and leaf areas were measured with a LI-3000 leaf area meter[c]. Peak stomatal conductances for both size classes were analyzed to detect differences between the juvenile and mature shrubs.

Soil water measurements

Soil cores were collected from two locations for water content in the morning on the same days that plant water potentials were measured. Soils were sampled within 50 cm of mature shrubs, to a maximum depth of 1.5 m at the following depths: 0-10 cm, 10-20 cm, 40-50 cm, 90-100 cm, and 140-150 cm. Soil moisture was determined gravimetrically for each sample. Water contents for all depth increments were pooled and the total soil water storage from the surface to 1.5 m deep was calculated using a measured dry bulk density of 1.675 g/cm^3.

Soil water content was also measured using a soil neutron probe[d] in measurement year 2000 (March – December). Access ports were installed to 3.4 m deep next to three each of the juvenile and mature *A. tridentata* shrubs selected for study. These ports were

[b] LI-COR Inc., Lincoln, NE.
[c] LI-COR Inc., Lincoln, NE
[d] CPN International, Inc., Martinez, CA.

installed within 30 cm of each shrub. A calibration equation for soils of the area was used to correct the neutron probe measurements.

Volumetric water content (%) = (neutron counts/mean standard neutron count) x 23.0 - 4.33

Readings were taken at 15 cm intervals from the surface on the same day or the day following xylem pressure potential measurements. Soil moisture content values were pooled for two depth layers: upper layer from the soil surface to 1.5 m deep, and the deeper layer from 1.5 to 3.4 m deep and total water storage was calculated for each layer.

Data analysis

Data were analyzed using repeated measures Analysis of Variance by The Mixed Procedure (SAS Ver. 8.1[e]) to test for significant differences in xylem pressure potentials between juvenile and mature *A. tridentata* shrubs on a monthly basis. Bi-weekly measurements were pooled to establish a single value for xylem pressure potentials for that month. Significant differences in stomatal conductances between the two size classes of shrubs were also tested using the same model and procedures. For soil water data, bi-weekly measurements were pooled to establish a single number for that month.

[e] SAS Institute, Cary, North Carolina

RESULTS

Precipitation and soil water storage

Data obtained from the Hanford Meteorological Station indicate 65% of the annual precipitation for 1999 and 2000 occurred between October and March, however, rainfall events also occurred in the summer months of both years (Figure 2). Annual precipitation for 1999 and 2000 was 10.03 and 18.49 cm, respectively. Monthly precipitation inputs were greatest in February of both years (1.78 cm in 1999; 2.85 cm in 2000).

During both years, the total water storage for the top 1.5 m of soil was highest in early spring (approximately 14.0 cm H_20), after recharge from fall-winter precipitation, and lowest in summer months (approximately 6.5 cm H_20) as reflected by both gravimetric measurements in 1999 and 2000 (Figure 3) and neutron probe measurements in 2000 (Figure 4). Soil water in the upper layer of soil declined throughout the growing season and recharge was evident again in the fall after commencement of the fall rains. Water content in the soil profile from the surface to 3.4 m deep (Figure 5) indicate recharge generally occurred in the upper layer of soil (0-1.5 m deep), however, there is an indication that recharge occured in the deeper layer of soil in the surrounding areas of mature shrubs.

No clear differences in water storage were seen for the upper layer of soil from neutron probe measurements of soil water in the vicinity of juvenile and mature shrubs. Neutron probe measurements for the deeper layer of soil indicated water storage generally remained the same throughout the year, except for October when a decline was

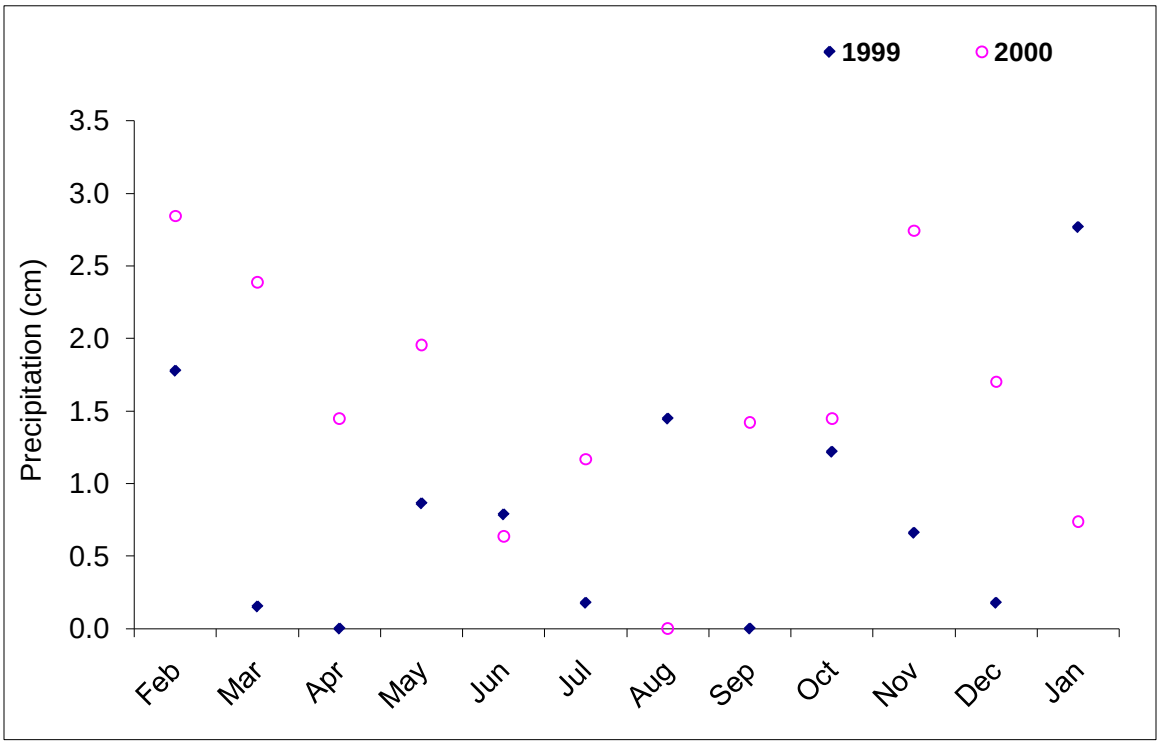

Figure 2. Total monthly precipitation on the Hanford Site as reported by HMS (Hoitink et al., 2000).

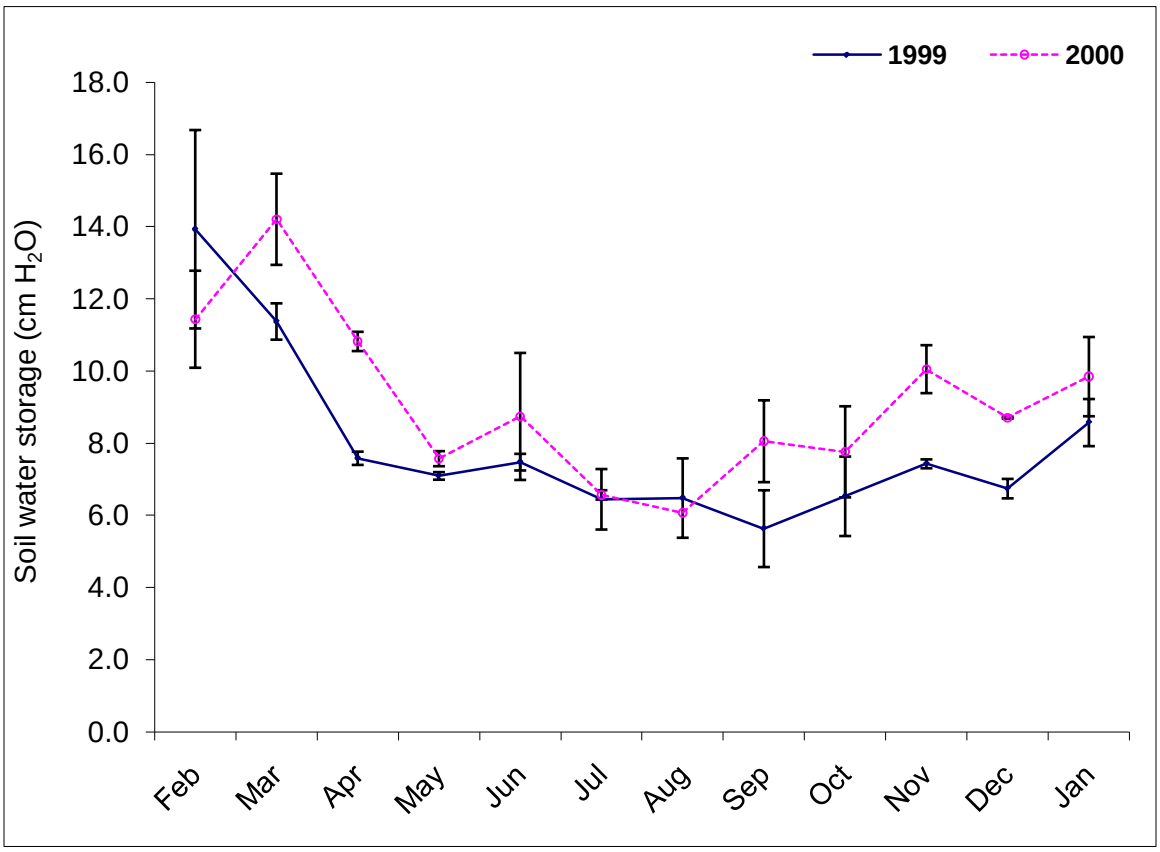

Figure 3. Total monthly soil water storage in the top 1.5 m of soil in the study area (calculated from gravimetric measurements). Data points are means of two replicates of sampling for each month ± 1 S.E.

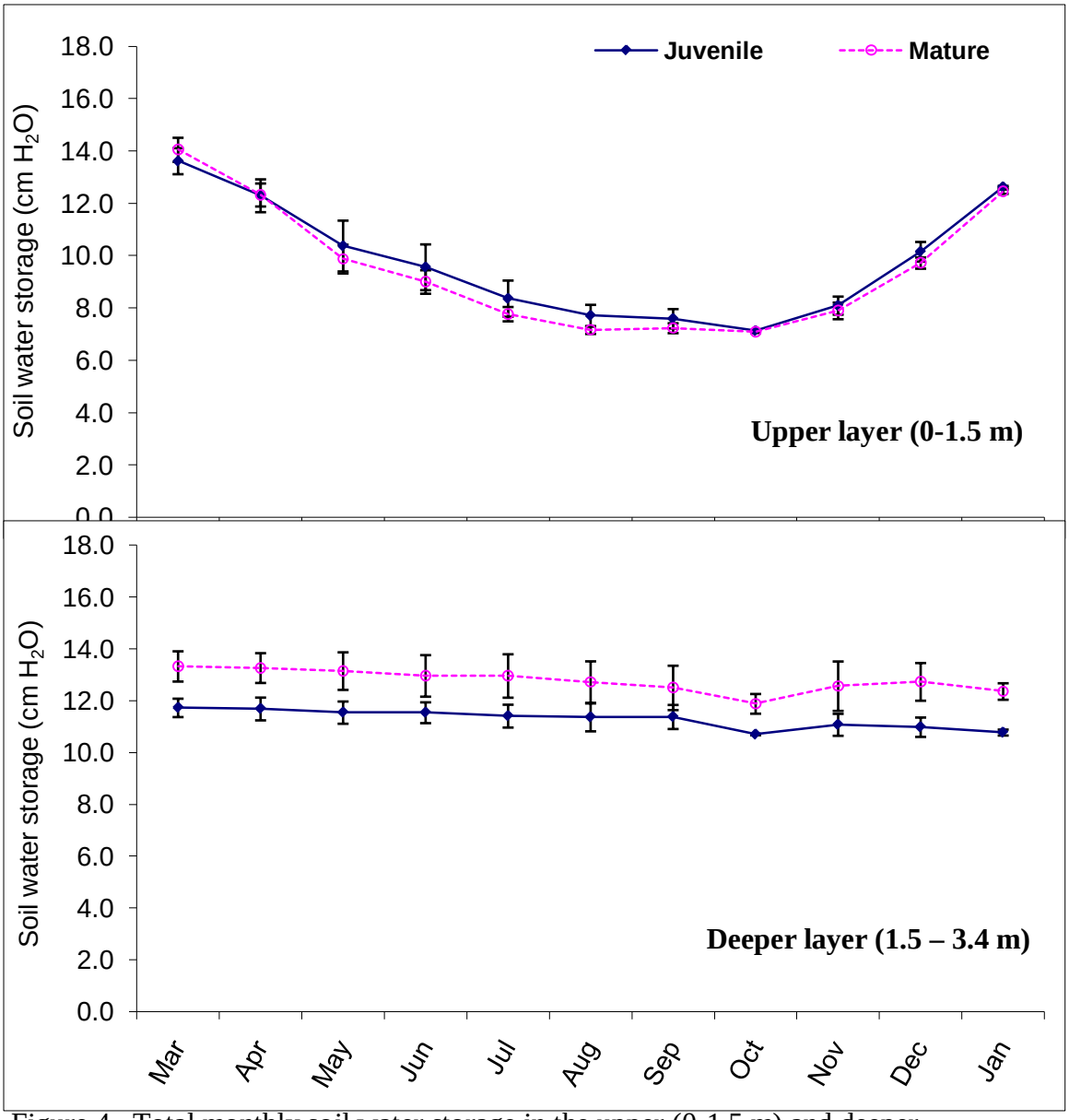

Figure 4. Total monthly soil water storage in the upper (0-1.5 m) and deeper (1.5 - 3.4 m) layers of soil in the study area (calculated from neutron probe measurements). Data points are means of three replicates of sampling adjacent to juvenile and mature *A. tridentata* shrubs for each month ± 1 S.E. (Mar. 2000-Jan. 2001).

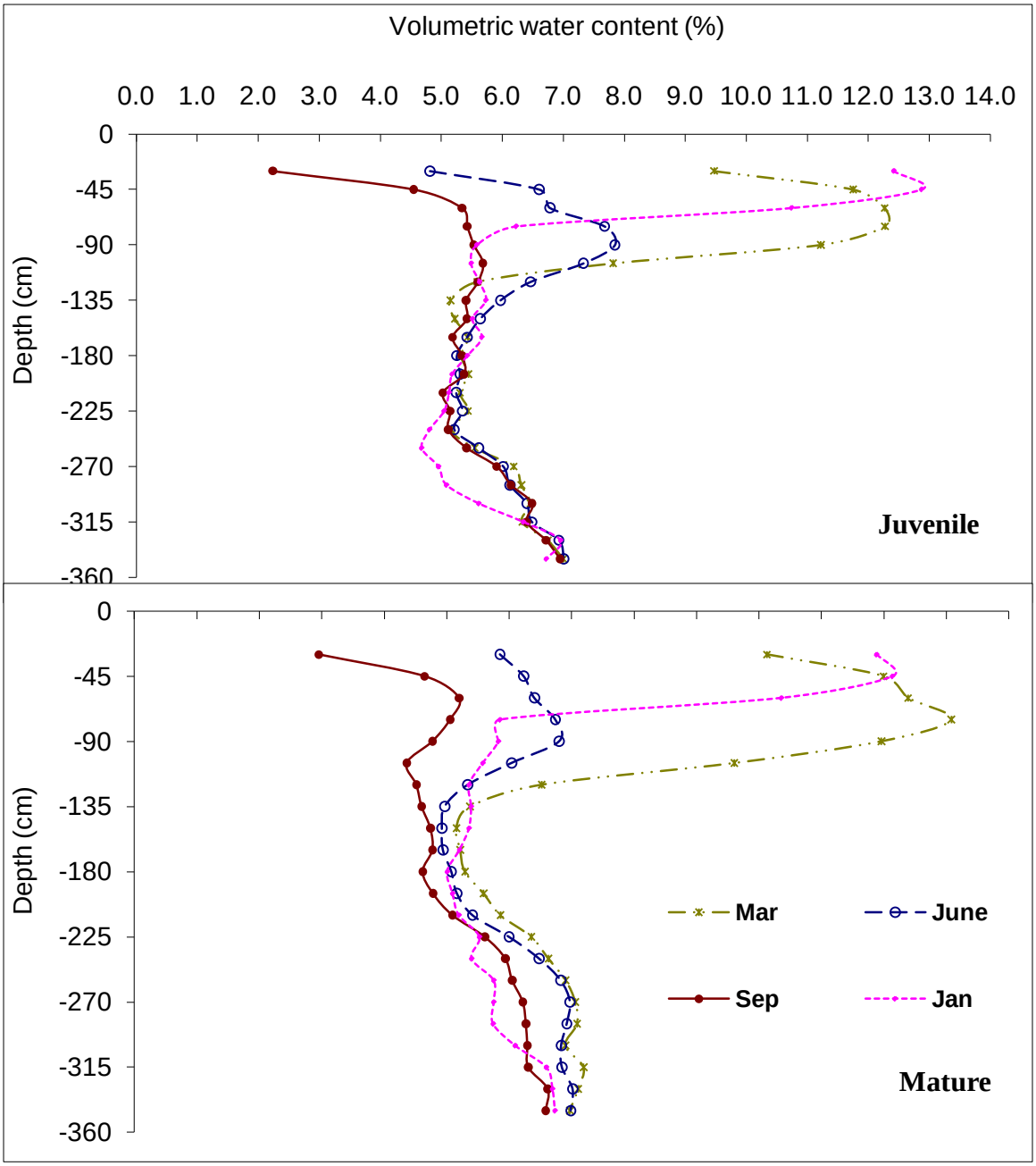

Figure 5. Volumetric soil water content (from neutron probe measurements) throughout the soil profile in the vicinity of juvenile (top) and mature (bottom) *A. tridentata* shrubs in the study area. Figure illustrates months with greatest recharge (Mar. 2000 and Jan. 2001) and months of least recharge (June and Sep. 2000).

observed. In the deeper layer of soil, soil water storage differed between mature and juvenile shrubs, where water storage in the surrounding area of the mature shrubs was consistently greater (by a mean of 1.48 cm H_2O for all months) than water storage in the vicinity of juveniles for the study period. In March, neutron probe measurements of the soil profile in the surrounding areas of juvenile and mature shrubs indicate greater water content in the neighborhood of mature shrubs deep in the soil profile, between 2.1-m and 3.3-m (mean of 0.85 % cm^3/cm^3), compared to juveniles (Figure 6). Neutron probe measurements in September indicate water content in the vicinity of juvenile shrubs was greater (by a mean of 0.80 % cm^3/cm^3) between 0.9-m and 2.1-m deep, compared to mature shrubs (Figure 6).

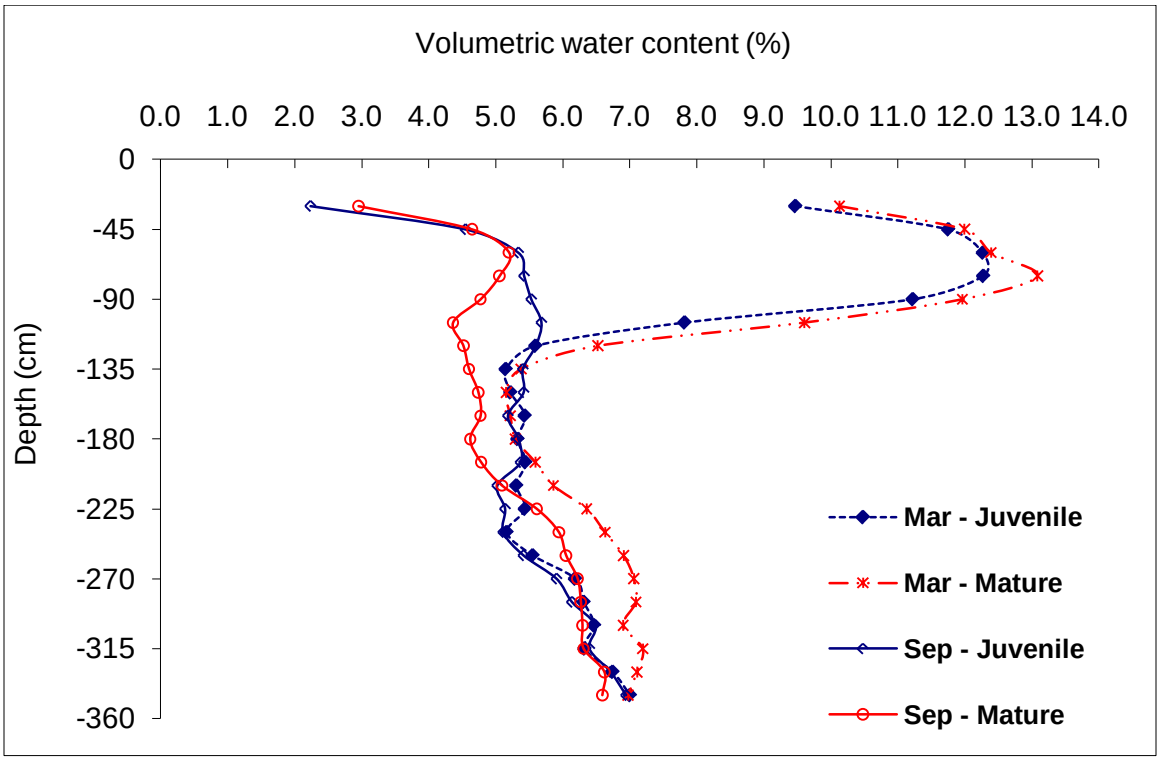

Figure 6. Volumetric soil water content (from neutron probe measurements) throughout the soil profile in the surrounding area of juvenile and mature *A. tridentata* shrubs in the study area. Figure illustrates the changes of water content throughout the soil profile in the vicinity of juvenile and mature shrubs during the month of greatest recharge and the month of least recharge.

Plant water potentials

Predawn xylem pressure potential measurements of *A. tridentata* exhibited no significant differences ($p < 0.05$) in plant water stress between juvenile and mature plants for 1999, except in September. However, predawn xylem pressure potentials of the two age classes were significantly different ($p < 0.05$) for most of the summer and early fall months of 2000 (Figure 7 and Table 2). Mean predawn xylem pressure potentials for juveniles were highest (least negative) in March and lowest (most negative) in October of both years (ranging from -0.79 MPa in March to -3.31 MPa in October of 1999, and -0.59 MPa in March to -2.32 MPa in October of 2000). Mean predawn xylem pressure potentials for mature plants were highest in February and March and lowest in September and October (from -0.83 MPa in February and March to -3.13 MPa in September of 1999, and -0.64 MPa in March and April to -2.97 in October of 2000).

For the two-year study period, predawn xylem pressure potentials for both juvenile and mature plants were highest in the spring months, declined through the growing season and summer drought months, and were lowest in October. Predawn xylem pressure potentials increased again in November after the seasonal low. In 1999, predawn xylem pressure potentials decreased once more through the winter months before increasing to the seasonal high in the spring. No such decline was observed in the winter of 2000.

Significant differences ($p < 0.05$) in midday xylem pressure potentials were observed between juvenile and mature plants for most of the two-year study period, except in March and December of both years and January 2001 (Figure 8 and Table 3). Mature plants exhibited consistently lower midday xylem pressure potentials than

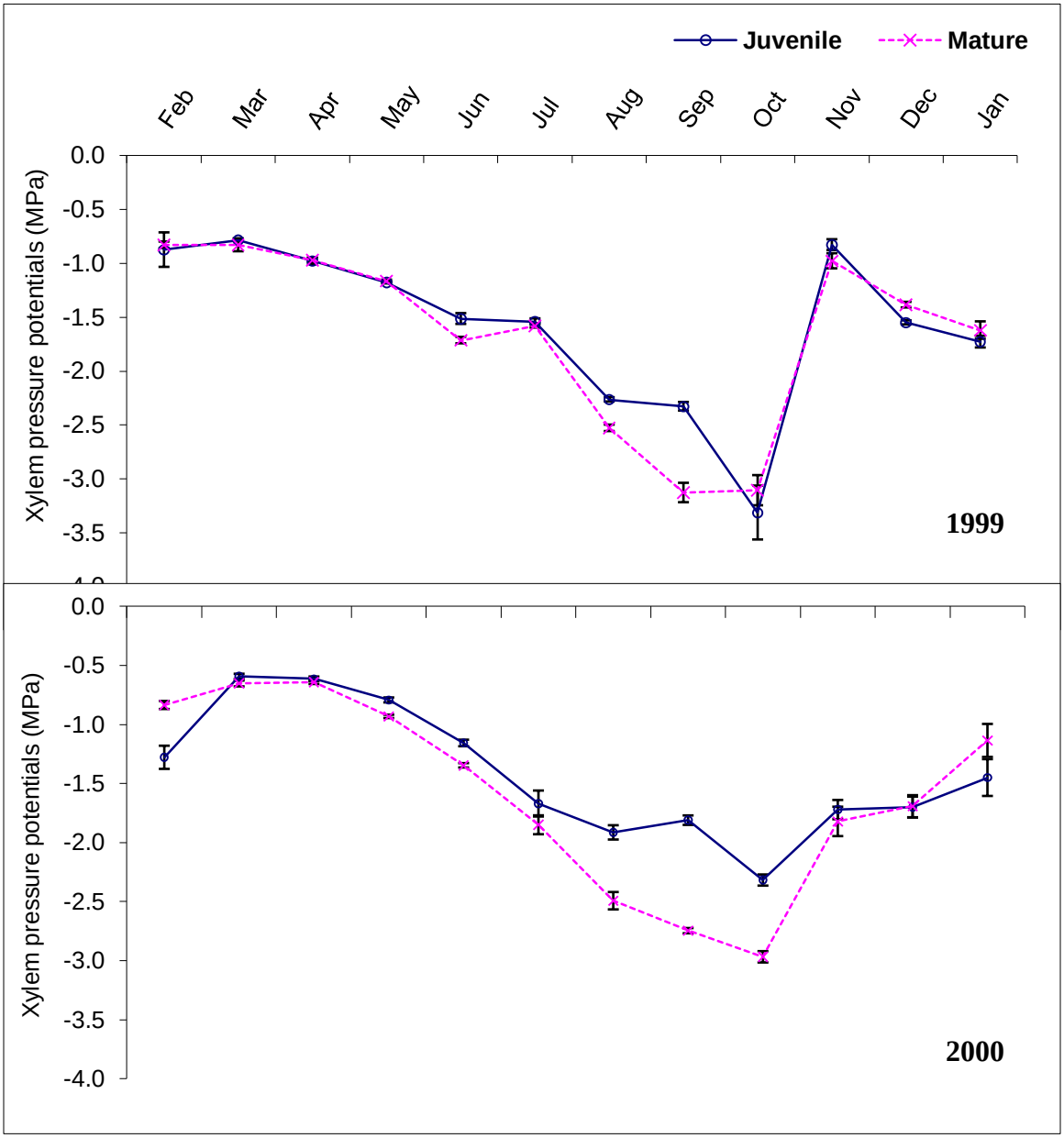

Figure 7. Mean monthly predawn xylem pressure potentials for juvenile and mature *A. tridentata* shrubs for 1999 (top) and 2000 (bottom). Data points are means of seven replicates of sampling for juvenile and mature shrubs for each month ± 1 S.E.

Table 2. Results of the repeated measures ANOVA for predawn xylem pressure potentials of seven replicates each of juvenile and mature *A. tridentata* shrubs.

Year	Effect	Month	df	t-value	P > |t|
1999	Ageclass*month*year	February	109	-0.05	0.9616
		March	109	0.49	0.6232
		April	109	-0.17	0.8684
		May	109	-0.24	0.8110
		June	109	1.52	0.1305
		July	109	0.28	0.7813
		August	109	1.32	0.1904
		September	109	3.51	0.0007
		October	109	-0.65	0.5179
		November	109	1.94	0.0545
		December	109	-1.35	0.1811
2000		January	109	-0.82	0.4130
		February	109	-4.89	<.0001
		March	109	1.68	0.0965
		April	109	1.11	0.2693
		May	109	2.64	0.0095
		June	109	2.62	0.0102
		July	109	1.32	0.1904
		August	109	3.15	0.0021
		September	109	7.15	<.0001
		October	109	4.20	<.0001
		November	109	0.78	0.4392
		December	109	-0.06	0.9527
2001		January	109	-3.01	0.0032

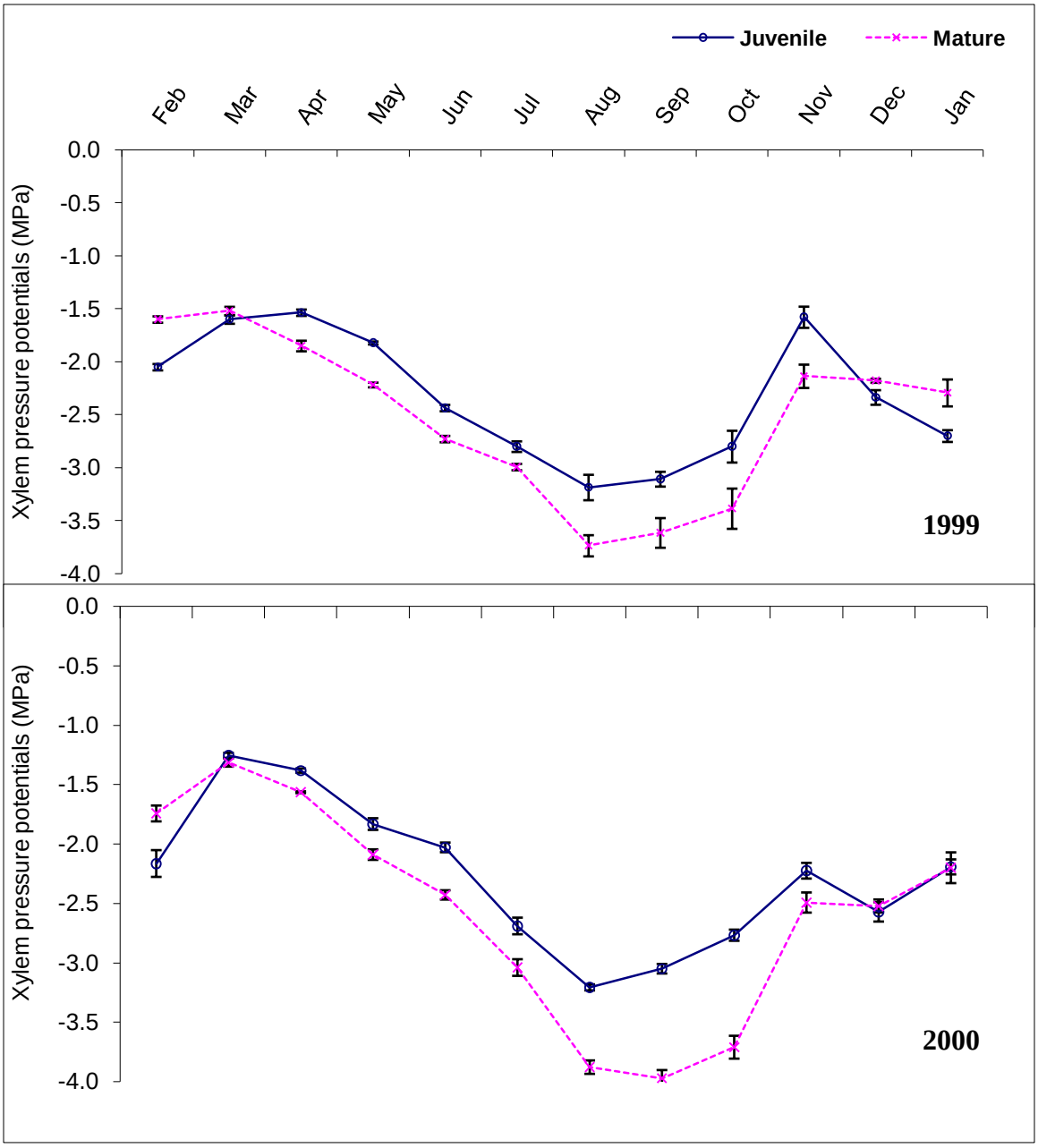

Figure 8. Mean monthly midday xylem pressure potentials for juvenile and mature *A. tridentata* shrubs for 1999 (top) and 2000 (bottom). Data points are means of seven replicates of sampling for juvenile and mature shrubs for each month ± 1 S.E.

Table 3. Results of the repeated measures ANOVA for midday xylem pressure potentials of seven replicates each of juvenile and mature *A. tridentata* shrubs.

Year	Effect	Month	df	t-value	P > |t|
1999	Ageclass*month*year	February	109	-2.81	0.0059
		March	109	-0.65	0.5144
		April	109	3.20	0.0018
		May	109	4.61	<.0001
		June	109	1.86	0.0656
		July	109	1.10	0.2721
		August	109	2.64	0.0096
		September	109	2.43	0.0169
		October	109	3.10	0.0025
		November	109	5.04	<.0001
		December	109	-1.10	0.2745
2000		January	109	-2.80	0.0061
		February	109	-3.49	0.0007
		March	109	1.37	0.1748
		April	109	2.89	0.0046
		May	109	3.12	0.0023
		June	109	4.19	<.0001
		July	109	2.01	0.0464
		August	109	3.11	0.0024
		September	109	6.14	<.0001
		October	109	6.68	<.0001
		November	109	2.02	0.0456
		December	109	-0.30	0.7684
2001		January	109	-0.06	0.9518

juveniles for the spring, summer, and fall months, while juveniles displayed lower xylem pressure potentials than mature shrubs only in the winter months. Mean midday xylem pressure potentials for juvenile shrubs ranged from -1.54 MPa in April to -3.19 MPa in August of 1999, and -1.25 MPa in March to -3.21MPa in August of 2000. For mature shrubs, midday xylem pressure potentials ranged from -1.52 MPa in March to -3.74 MPa in August of 1999, and -1.31 MPa in March to -3.97 in September of 2000.

Midday xylem pressure potentials for both juvenile and mature shrubs were highest in the spring months and lowest in the summer drought months for the two years of study. In 1999, midday xylem pressure potentials for the two age classes of shrubs increased again in September after the seasonal low, but decreased once more in December, before increasing to the seasonal high in the spring. For 2000, midday xylem pressure potentials increased again in September and October after the seasonal low for juvenile and mature shrubs, respectively.

Both predawn and midday xylem pressure potential measurements indicate a consistent trend in plant water relations for juvenile and mature shrubs throughout the seasons of both years of study. Mature shrubs displayed lower xylem pressure potentials than juveniles during the late spring, summer, and fall seasons, while in the winter and early spring months (December through March) juveniles exhibited lower xylem pressure potentials than mature shrubs.

Stomatal conductance

Peak stomatal conductances occurred late morning in the early spring months (1100 in February) and occurred earlier as daylight hours increased (0900 in April and 0700 in the summer months, May-August). Significant differences ($p < 0.05$) in stomatal

conductances between juvenile and mature shrubs occurred only in April and September when juveniles exhibited greater conductances than mature shrubs (Figure 9 and Table 4). No measurements were made in the fall and winter months. Stomatal conductances for juvenile shrubs were lowest in February (78.20 mmol m^{-2} s^{-1}) and highest in April (586.13 mmol m^{-2} s^{-1}). For mature shrubs, stomatal conductances were lowest in February (71.00 mmol m^{-2} s^{-1}) and September (67.53 mmol m^{-2} s^{-1}) and highest in April (414.27 mmol m^{-2} s^{-1}).

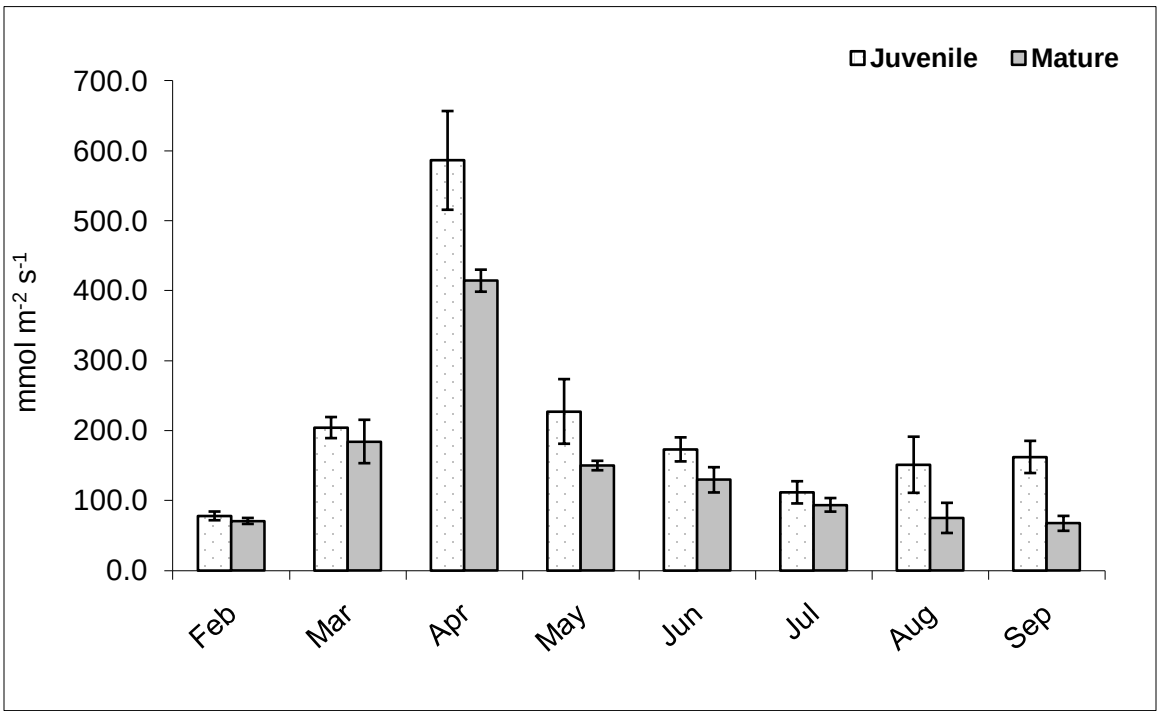

Figure 9. Mean monthly stomatal conductances between juvenile and mature *A. tridentata* shrubs in 2000. Data points are means of five replicates of sampling for juvenile and mature shrubs for each month ± 1 S.E.

Table 4. Results of the repeated measures ANOVA for stomatal conductances for five replicates of juvenile and mature *A. tridentata* shrubs in 2000.

Year	Effect	Month	df	t-value	P > |t|
2000	Ageclass*month	February	56	-0.36	0.7189
		March	56	-0.50	0.6217
		April	56	-4.29	<.0001
		May	56	-1.93	0.0586
		June	56	-2.00	0.0500
		July	56	-0.45	0.6572
		August	56	-1.90	0.0630
		September	56	-2.37	0.0213

DISCUSSION

Midday xylem pressure potential measurements indicate mature *Artemisia tridentata* shrubs experienced greater plant water stress than juvenile shrubs in the same stand for most of the year, except winter and early spring months when juveniles exhibited greater plant water stress than mature shrubs. My results are not consistent with other studies of the water relations of perennial plants conducted in spring and summer seasons (Campbell and Harris, 1977; Knapp and Fahnestock, 1990; Donovan and Ehleringer, 1991, 1992). In those studies, juveniles were found to have lower (more negative) xylem pressure potentials than mature plants, but I found the opposite. Mature *A. tridentata* shrubs exhibited lower xylem pressure potentials than juveniles for most of the year, at predawn in the summer months and at midday in the spring, summer, and fall seasons whereas, juveniles experienced greater midday water stress than mature shrubs only in the winter months.

Predawn xylem pressure potentials did not differ for juvenile and mature shrubs for most of the two years except for September 1999 and late summer 2000, when mature shrubs exhibited significantly ($p < 0.05$) lower xylem pressure potentials than juveniles. Romo and Haferkamp (1989) and Shumar and Anderson (1986) suggest predawn xylem pressure potentials may be used as an indicator of available soil water in the rooting zones. The similar predawn xylem pressure potentials of the two age classes for most of the study period, except late summer months, and the consistently lower midday xylem pressure potentials of mature shrubs compared to juveniles suggest that the mature shrubs are experiencing greater demand for water during the day while the shrubs are transpiring. Klepper (1968) found roots of 12 year-old woody plants were not able to

adequately maintain water uptake to replace what was lost through transpiration. The lower predawn xylem pressure potentials exhibited by mature shrubs compared to juveniles suggest the mature shrubs may not be able to recover overnight as well as juveniles from the previous day's water loss.

Predawn and midday xylem pressure potentials for both juvenile and mature *A. tridentata* shrubs declined throughout the spring months, as stored soil water decreased, and did not increase again until fall, after soil water recharge occurred. This seasonal decline of xylem pressure potentials throughout the spring months is comparable to other studies conducted on *A. tridentata* (DePuit and Caldwell, 1973; Campbell and Harris, 1977; Black and Mack, 1986). Black and Mack (1986) found *A. tridentata* responded to summer rains by displaying higher xylem pressure potentials just five days after the rainfall. However, neither age class of shrubs I measured showed a clear response to summer rains when measured seven to ten days after the precipitation events.

During the two-year study, the total soil water storage for the top 1.5 m of soil in the stand was highest in early spring after recharge from the fall-winter precipitation inputs, declined throughout the growing season, and recharge was evident again in the fall after commencement of the fall rains. Neutron probe measurements for the deeper layer of soil indicated water storage generally remained the same throughout the year, suggesting the shrubs may not be using water deep in the soil profile. No clear differences were seen in soil water storage for the upper layer of soil in the vicinity of juvenile and mature shrubs indicating both age classes of shrubs may be using similar amounts of available soil water. However, in the deeper layer of soil, differences in water storage adjacent to mature and juvenile shrubs were observed. Soil water storage

in the vicinity of the mature shrubs was consistently greater (by a mean of 1.5 cm H_2O for all months) than that in the area of juveniles for the study period. Soil water contents throughout the soil profile show a similar trend.

The greater amount of total water stored in the deeper layer of soil in the surrounding area of mature shrubs indicate these shrubs were able to access water at depths of 1.5 – 3.4 meters. The difference in soil water storage in the deeper layer of soil in the surrounding areas of juvenile and mature shrubs may be related hydraulic lift. Richards and Caldwell (1987) found the roots *A. tridentata* shrubs have the ability to relocate water from deep in the soil to shallower layers during the night so that water is available for uptake by shallow roots during the day. However, we did not see a clear difference in water storage in the upper layer of soil in the vicinity of the two age classes.

Previous studies have shown *A. tridentata* uses available soil water in the shallow layer of soil during the spring months and maintains water uptake from deeper depths during the summer and early fall months, when water in the upper layers of the soil has been lost to transpiration and evaporation (Campbell and Harris, 1977; Cline et al. 1977; Daddy et al., 1988; Matzner and Richards, 1996). Differences in plant water stress between seedlings and adults can be related to rooting depth (Frazer and Davis, 1988). Even though mature *A. tridentata* shrubs are considered to have deep roots and had access to more soil water at deeper depths than juveniles as reflected in my soil water storage results, I found the mature shrubs exhibited considerably lower midday xylem pressure potentials than juveniles for most of the year except for winter months. The trend of mature shrubs displaying greater midday water stress than juveniles suggest

rooting depth may not be a factor in differences of plant water stress between the two age classes of shrubs as I thought.

Juvenile shrubs were able to maintain higher midday xylem pressure potentials than mature shrubs in the summer months indicating that the juveniles were less water stressed. This suggests that juvenile shrubs are able to access enough water in the rooting zone. This is in contrast to studies by Campbell and Harris (1977) and Donovan and Ehleringer (1991,1992) where they suggested that limited root system of juvenile *A. tridentata* and *C. nauseosus* shrubs were a possible reason juveniles exhibited greater midday water stress than mature shrubs in the spring and summer months.

The reproductive phenology of mature *A. tridentata* shrubs may be one reason these shrubs experienced greater midday water stress than juvenile shrubs. Evans et al., (1991) found the reproductive growth of sagebrush was photosynthetically active throughout development of the inflorescence in the spring and summer months. Gas exchange, which supports photosynthetic activity, corresponds to some level of transpirational water loss that juvenile shrubs may avoid in the spring and summer months.

Another explanation for the greater midday water stress seen in mature shrubs may be the difference in total leaf area between juvenile and mature shrubs. The total leaf area of mature *A. tridentata* shrubs is greater than that of juveniles in the stand on a per plant basis (Downs and Khan[1]). According to Donovan and Ehleringer (1992), mature shrubs transpire more water than juveniles because they have a greater total leaf area than the smaller shrubs, thus I believe transpirational demands coupled with the development of inflorescences may have caused the mature shrubs to experience greater midday water stress than juveniles in the spring, summer and fall months.

[1] Unpublished data, J. L. Downs and F. Khan, Pacific Northwest National Laboratory, Richland, WA.

Differences in age is a third explanation for the greater water stress displayed by mature shrubs compared to juveniles in the stand. Based on the history of the Hanford Site, mature *A. tridentata* shrubs in the study site are likely to be between 40 to 50 years old (Rickard[2]). Because the mature shrubs are considerably older than juveniles, the xylem vessels in these shrubs may not be able to transport water to the terminal branches as efficiently as those in juvenile shrubs (Anderson[3]). Furthermore, Kolb and Sperry (1999b) suggest older water transport vessels in plants may stop functioning or become plugged with age, thus the hydraulic resistance of the mature *A. tridentata* shrubs I measured may be affected by the age of the xylem vessels, especially during periods of growth and water and heat stress.

Soil water status affects water potentials and transpiration resistance of plants (Kramer and Boyer, 1995) and plants generally adjust water use and stomatal conductance as a response to available soil water (Toft et al., 1989). I saw a correlation of stomatal conductance of both juvenile and mature *A. tridentata* shrubs to the seasonal decline of xylem pressure potentials and available soil water. This is consistent with studies conducted by Brown and Archer (1990) on woody plants and Toft et al. (1989) on cold desert plants. No significant differences ($p < 0.05$) in stomatal conductance were seen between juvenile and mature shrubs for most of the study period (year 2000) except for April and September when juveniles exhibited greater conductances. Although the conductances displayed by the juveniles in April and September were significantly greater ($p < 0.05$) than mature shrubs, midday xylem pressure potentials were higher than

[2] Personal communication, W. H. Rickard, Pacific Northwest National Laboratory, Richland, WA.
[3] Personal communication, J. E. Anderson, Dept. of Biological Sciences, Idaho State University, ID.

mature shrubs for these two months. In contrast, Brown and Archer (1990) found lower gas exchange rates complemented lower xylem pressure potentials.

The lack of differences found in predawn xylem pressure potentials between juvenile and mature *Artemisia tridentata* shrubs growing in the same stand suggest both juvenile and mature shrubs are able to access adequate soil water at all depths throughout the year and rooting depth may not be a factor for greater water stress as suggested in other literature (Campbell and Harris, 1977; Knapp and Fahnestock, 1990; Donovan and Ehleringer, 1991, 1992). Mature shrubs exhibited greater midday water stress than juveniles during spring, summer, and fall months, however, no differences of predawn xylem potentials were found between the two age classes, except for late summer months when mature shrubs displayed lower xylem pressure potentials than juveniles shrubs.

CONCLUSION

My work seems to suggest that plant age, especially xylem age, and reproductive phenology may play a large role in determining plant water stress of mature *A. tridentata* shrubs compared to juveniles. The results of this study also suggests that juvenile *A. tridentata* shrubs have sufficient rooting depth and extent to access stored soil water deep in the profile. The differences found in plant water relations and stomatal conductances between juvenile and mature *A. tridentata* shrubs may be used as a validation data set to which model simulations of plant responses to seasonal environmental changes in semi-arid regions can be compared and allow for a better understanding of how shrubs use available soil moisture throughout the year.

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CHAPTER 2

SEASONAL DIFFERENCES IN PLANT WATER RELATIONS OF A CONTIGUOUS POPULATION OF *ARTEMISIA TRIDENTATA* (NUTT.) GROWING ON TWO ADJACENT SOILS OF DIFFERENT TEXTURES

Abstract: Seasonal plant water relations were examined for a contiguous population of *A. tridentata* shrubs on two adjacent soils of different textures. *Artemisia tridentata* in a loamy sand experienced greater predawn and midday water stress than shrubs in an adjacent stabilized sand dune in summer, fall, and winter. No differences in plant water potentials of shrubs in both soil types were seen during spring months. Predawn xylem pressure potentials for shrubs in both soil types were highest in spring, -0.64 MPa (sand dune) and -0.60 MPa (loamy sand), and lowest in early fall, -3.13 MPa (sand dune) and -3.94 MPa (loamy sand). Midday xylem pressure potentials of shrubs in both soil types were also highest in spring, -1.31 MPa (sand dune) and -1.40 MPa (loamy sand); however, seasonal lows occurred in different months: shrubs on the sand dune exhibited lowest water potentials in summer (-3.97 MPa), whereas shrubs in the loamy sand displayed lowest water potentials in October (-4.59 MPa). Concurrent measurements of soil water contents indicate that differences in plant water potentials between shrubs in the two soils were correlated with differences in total soil water storage for the two soils.

INTRODUCTION

Water is often the factor most limiting to plant growth and survival in arid and semi-arid regions where precipitation is variable and temperatures can be extreme (Daubenmire, 1970; Richards and Caldwell, 1987). In the semi-arid eastern Washington State, most of the annual precipitation (approximately 67%) occurs from October through April (Daubenmire, 1970; Rickard et al., 1988). Furthermore, soil water recharge occurs in the winter and early spring months and stored soil water is depleted by evaporation and transpiration during the spring and summer months (Rickard et al., 1988). Under these conditions, soils of different textures may store different amounts of plant available soil water because of the physical characteristics of each soil type (Barker and McKell, 1983; Brown and Archer, 1990).

Coarse-textured soils do not retain water in the upper layers of the soil profile as well as fine textured soils (Shumar and Anderson, 1986; Brown and Archer, 1990). As a result, a contiguous population of plants growing in adjacent soils of different textures may display dissimilar water stress due to differences in available soil water. Brown and Archer (1990) suggest that water stress and rooting patterns of plants can be determined by variations in soil characteristics. In addition, Barker and McKell (1983) found differences in plant water potentials between two subspecies of *Artemisia tridentata* growing on two different types of soils within the same stand.

Plants water stres is generally affected by available soil water as described by several studies (e.g., Campbell and Harris, 1977; Barker and McKell, 1983; Black and Mack, 1986; Miller et al., 1986; Shumar and Anderson, 1986; Richards and Caldwell, 1987; Brown and Archer, 1990; Knapp and Fahnestock, 1990; Donovan and Ehleringer,

1991, 1992). In semi-arid regions, plant water potentials are usually highest in the spring, when plant available soil water is near field capacity, and lowest in the summer when available soil water is exhausted (Black and Mack, 1986; Miller et al., 1986; Shumar and Anderson, 1986). Therefore, *A. tridentata*, a dominant shrub in semi-arid regions, is least water stressed in the spring months and experiences greatest water stress in dry summer and fall months (Miller, 1988).

This purpose of this study was to examine whether seasonal differences exist in plant water relations within a stand of mature *A. tridentata* shrubs growing on two adjacent soils of different textures. I hypothesize that there will be a difference in water status between mature shrubs growing on different textured, but adjacent, soils. It is expected that differences will exist between shrubs growing on the two types of soils because soil water storage will differ in soils of different textures (Brown and Archer 1990). Coarse-textured soils will allow more drainage whereas, fine-textured soils will store water closer to the surface where the water will be subjected to evaporation and uptake by shallow rooted plants (Shumar and Anderson 1986; Brown and Archer 1990). To adequately examine plant water status, I measured xylem pressure potentials and stomatal conductance of *A. tridentata* shrubs and soil water contents in two study plots on soils of different textures.

MATERIALS AND METHODS

My investigations focused on defining seasonal water relations for a stand of mature *A. tridentata* shrubs growing on two different soils adjacent to each other. This study was conducted over a two-year period, from February 1999 to January 2001. Two study plots (2500 m^2) were established in the winter of 1998 on the Hanford Site in eastern Washington State where the climate is considered to be semi-arid (Rickard et al., 1988) (Figure 1 in Chapter 1).

Both plots lie within the *Artemisia tridentata-Bromus tectorum* (sagebrush-cheatgrass) habitat type as described by Daubenmire (1970). One study plot, located on a stabilized sand dune (elevation 229 m) in Rupert Sand (Hajek 1966), was used for the previous study (Chapter 1). The second study plot was located approximately 325 m north of the first plot at 220 m in elevation. The soil type of the second plot is Burbank Loamy Sand (Hajek, 1966), which is coarse-textured soil underlain by gravel. According to Hajek (1966), the upper layer of soil is between 40.6 cm and 76.2 cm thick and is dark grayish brown in color. To distinguish between the two plots, the plot in the Rupert Sand soil type was labeled RS and the plot in the Burbank Loamy Sand soil type was labeled BLS.

Fourteen mature *A. tridentata* shrubs were selected for this study. Seven shrubs were randomly chosen in each plot to represent the shrubs growing in each soil type. The seven mature shrubs on the sand dune (RS) used for the previous study were also used for this study. Average height of shrubs in the RS plot was 1.41 m and average height of shrubs in the BLS plot was 1.51 m. All measurements performed for plant water relations, stomatal conductance, and soil water contents of mature shrubs in the previous

study were replicated concurrently for shrubs in the BLS plot. Because the two plots are located in the vicinity of each other, see chapter one for climatological data.

Soil water measurements

Gravimetric and neutron probe[a] measurements of soil water contents from the previous study (Chapter 1) were replicated for the BLS plot. Total water storage for the BLS plot was calculated using a measured dry bulk density of 1.668 g/cm^3. The calibration used to convert neutron probe measurements to volumetric soil water for the RS plot was also used for the BLS plot and total soil water storage for both soil types were calculated.

Volumetric water content (%) = (neutron counts/mean standard neutron count) x 23.0 - 4.33

Although the calibration was not developed for BLS soil, it is adequate for determining differences in total soil water storage between the RS and BLS plots. Soil water values were pooled for two depths: the upper layer from the surface to 1.5 m deep, and the deeper layer from 1.5 to 3.4 m deep.

Data analysis

Data were analyzed using Repeated Measures Analysis of Variance by The Mixed Procedure (SAS Ver. 8.1[b]) to test for significant differences in xylem pressure potentials between *A. tridentata* shrubs of each study site. Significant differences in stomatal conductances between the two size classes of shrubs were also tested using the same model and procedures. For soil water data, bi-weekly measurements were pooled to establish a single number for that month.

[a] CPN International, Inc., Martinez, CA.
[b] SAS Institute, Cary, North Carolina

RESULTS

Precipitation and soil water storage

Data obtained from the Hanford Meteorological Station indicate 65% of the annual precipitation for 1999 and 2000 occurred between October and March, however rainfall events also occurred in the summer months of both years (Figure 10). Annual precipitation for 1999 and 2000 was 10.03 and 18.49 cm, respectively. Monthly precipitation inputs were greatest in February of both years (1.78 cm in 1999; 2.85 cm in 2000).

For both years, the total water storage for the top 1.5 m of soil at the two study sites was highest in early spring after recharge from the fall-winter precipitation, and lowest in the summer drought months as reflected by both gravimetric (1999 and 2000) and neutron probe (2000) measurements of soil water storage (Figures 11 and 12). Soil water declined throughout the spring months as expected, during the growing season, and recharge was evident again in the fall after commencement of the fall rains. Water content in the soil profile from the surface to 3.4 m deep (Figure 13) indicate recharge generally occurred in the upper layer of soil (0-1.5 m deep) for both soil types, however, there is an indication that recharge occured deeper in the soil profile on the sand dune, but no recharged was seen for the deeper layers of the loamy sand.

Gravimetric measurements indicate soil water storage was considerably greater in the RS plot than it was in the BLS plot for both years. In 1999, soil water storage in the RS plot was greater by an overall mean of 3.1 cm H_2O; seasonally 3.7 cm H_2O in the spring, 3.2 cm H_2O in the summer, and 2.5 cm H_2O in the fall-winter months. Soil water storage in the RS plot for 2000 was greater by an overall mean of 3.2 cm H_2O; seasonally

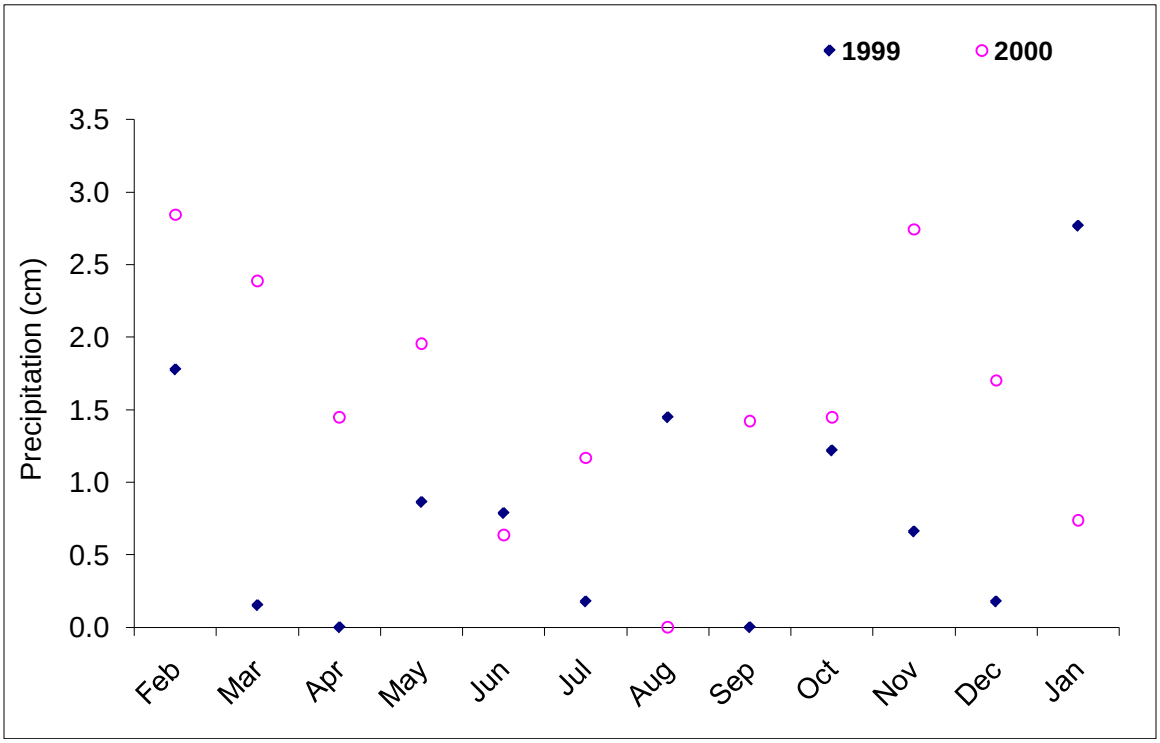

Figure 10. Total monthly precipitation on the Hanford Site as reported by HMS (Hoitink et al., 2000).

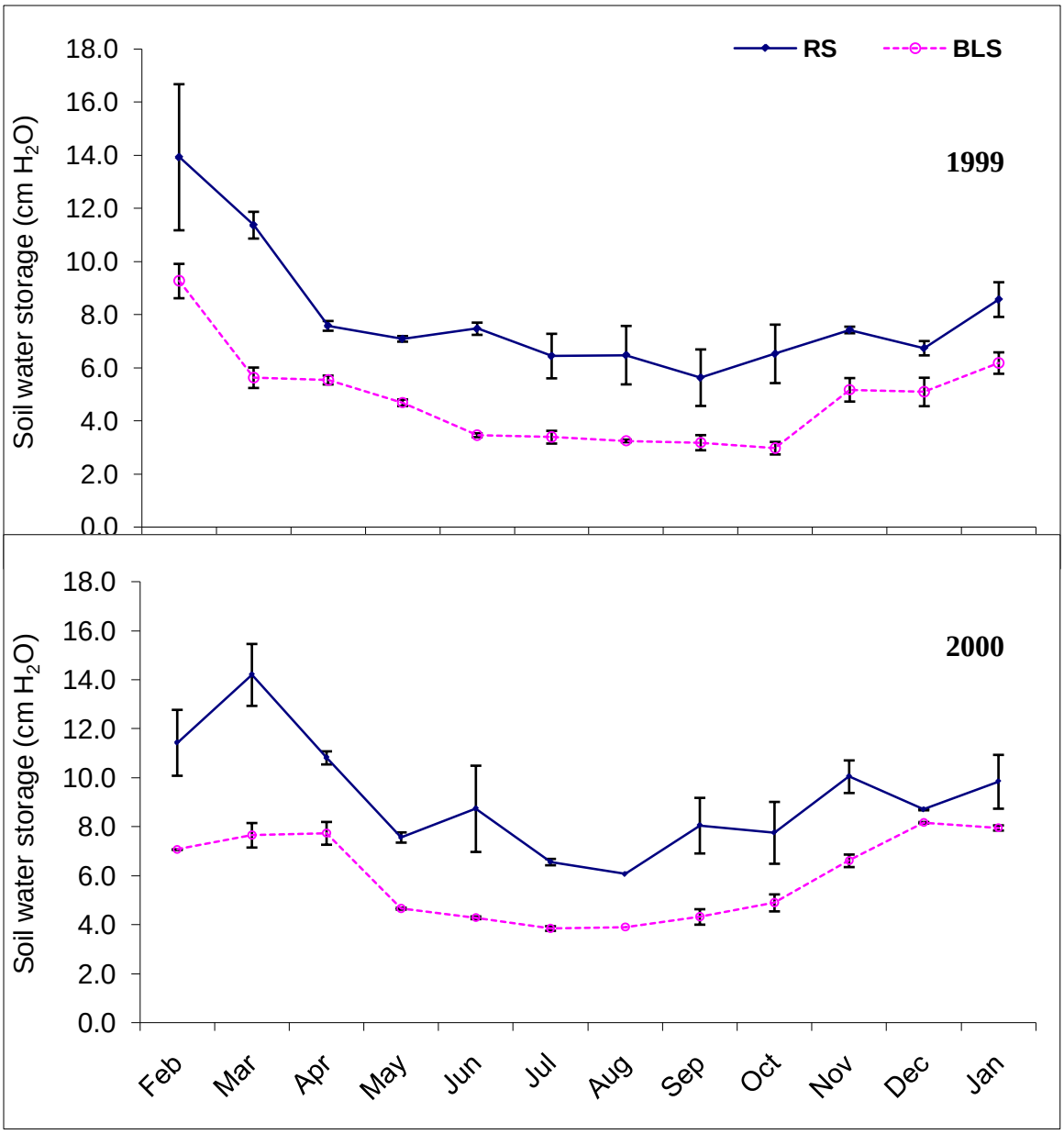

Figure 11. Total monthly soil water storage in the top 1.5 m of soil for the two soil types (calculated from gravimetric measurements). Data points are means of two replicates of sampling for each month ± 1 S.E.

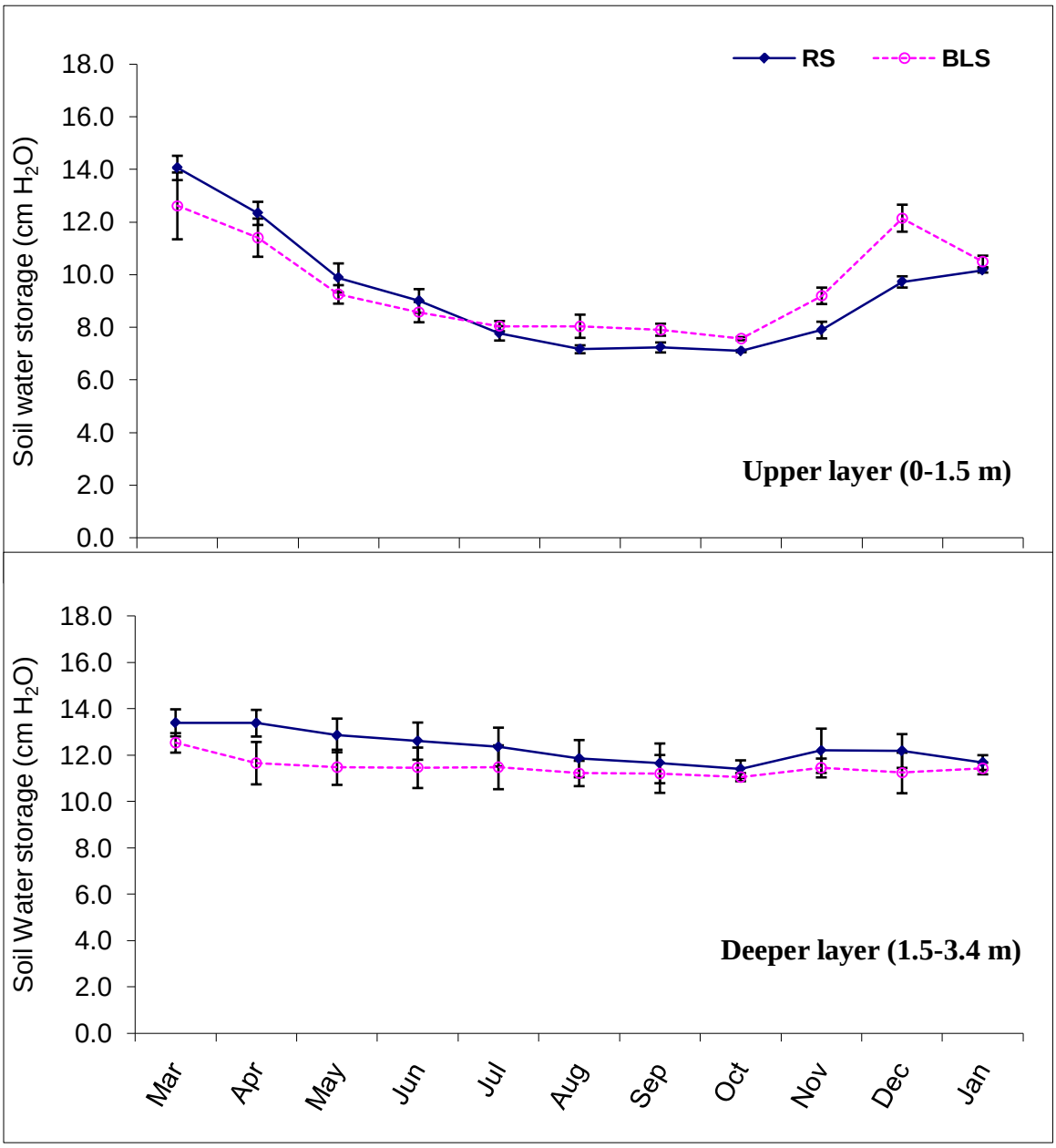

Figure 12. Total monthly soil water storage in the upper (0-1.5 m) and deeper layer (1.5 - 3.4 m) of soil for the two soil types (calculated from neutron probe measurements). Data points are means of three replicates of sampling adjacent to *A. tridentata* shrubs in the two soil types for each month ± 1 S.E. (Mar. 2000-Jan. 2001).

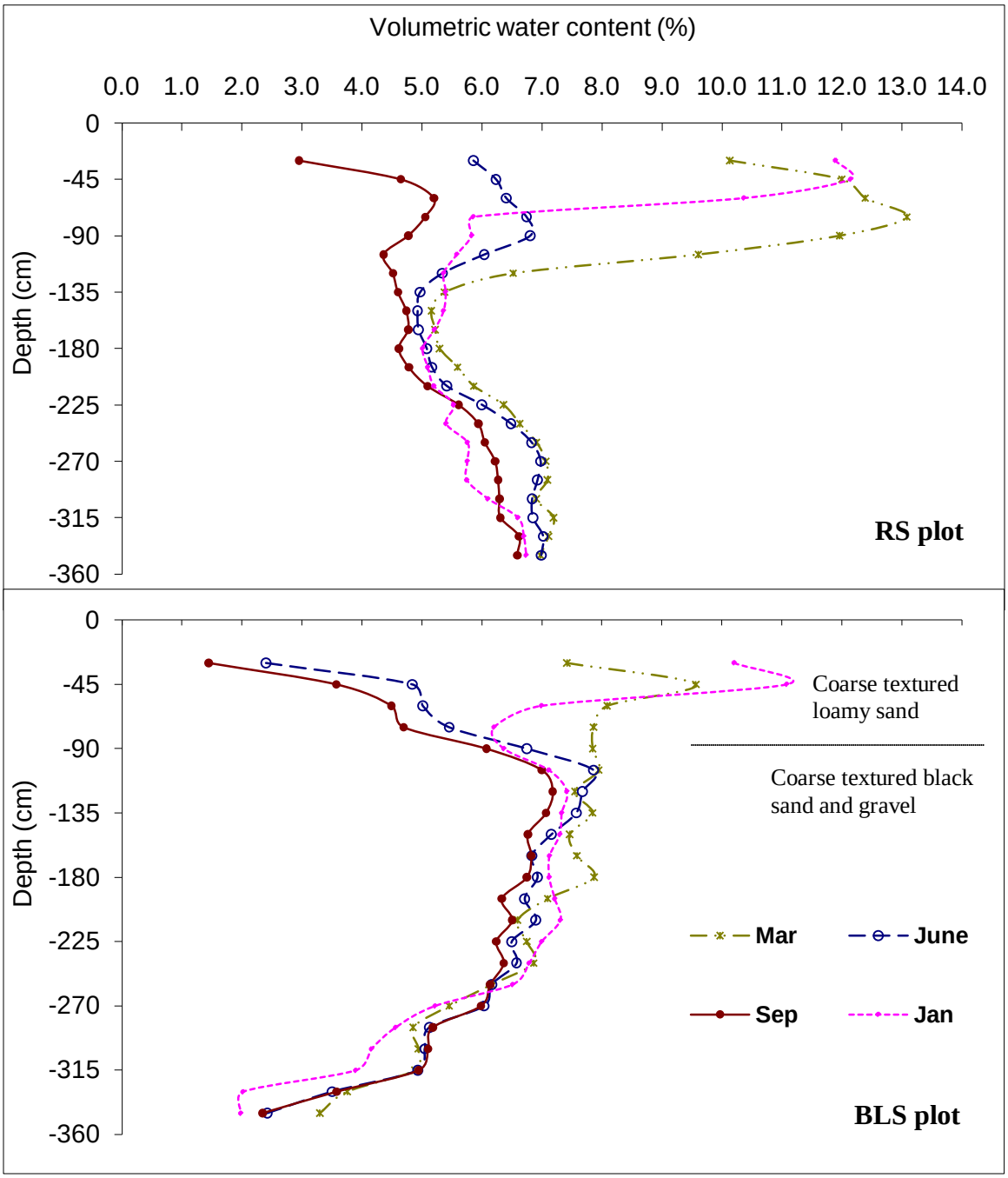

Figure 13. Volumetric soil water content (from neutron probe measurements) throughout the soil profile in the surrounding areas of *A. tridentata* shrubs in the RS plot (top) and BLS plot (bottom). Figure illustrates months with greatest recharge (Mar. 2000 and Jan. 2001) and months of least recharge (June and Sep. 2000).

4.2 cm H_2O in the spring, 3.3 cm H_2O in the summer, and 2.2 cm H_2O in the fall-winter months.

Neutron probe measurements for the upper layer of soil indicate no clear differences in soil water storage between the two soil types in the spring and summer months, however, soil water storage was greater in the BLS plot in November and December (by a mean of 1.9 cm H_2O). For the deeper layer of soil, neutron probe measurements indicate no considerable change of soil water storage in the two plots throughout the year and no clear differences in water storage between the two soil types were seen. Soil water storage in the RS and BLS plots averaged 12.8 cm H_2O and 11.9, respectively, for the year.

Plant water potentials

Predawn xylem pressure potential measurements of *A. tridentata* for 1999 exhibited significant differences ($p < 0.05$) in plant water status between shrubs in the two plots in February, the summer months (June through August) and winter months (November and December); however, in 2000 predawn xylem pressure potentials were significantly different ($p < 0.05$) for most of the year, except for March, April, and December (Figure 14 and Table 5). For both years, when significant differences in predawn xylem pressure potentials were observed, shrubs in the BLS plot exhibited lower xylem pressure potentials than shrubs in the RS plot.

Mean predawn xylem pressure potentials for shrubs in the RS plot were highest in February and March (-0.83 MPa for both months) and lowest in September (-3.13 MPa) of 1999, while in 2000 mean predawn xylem pressure potentials for same shrubs were

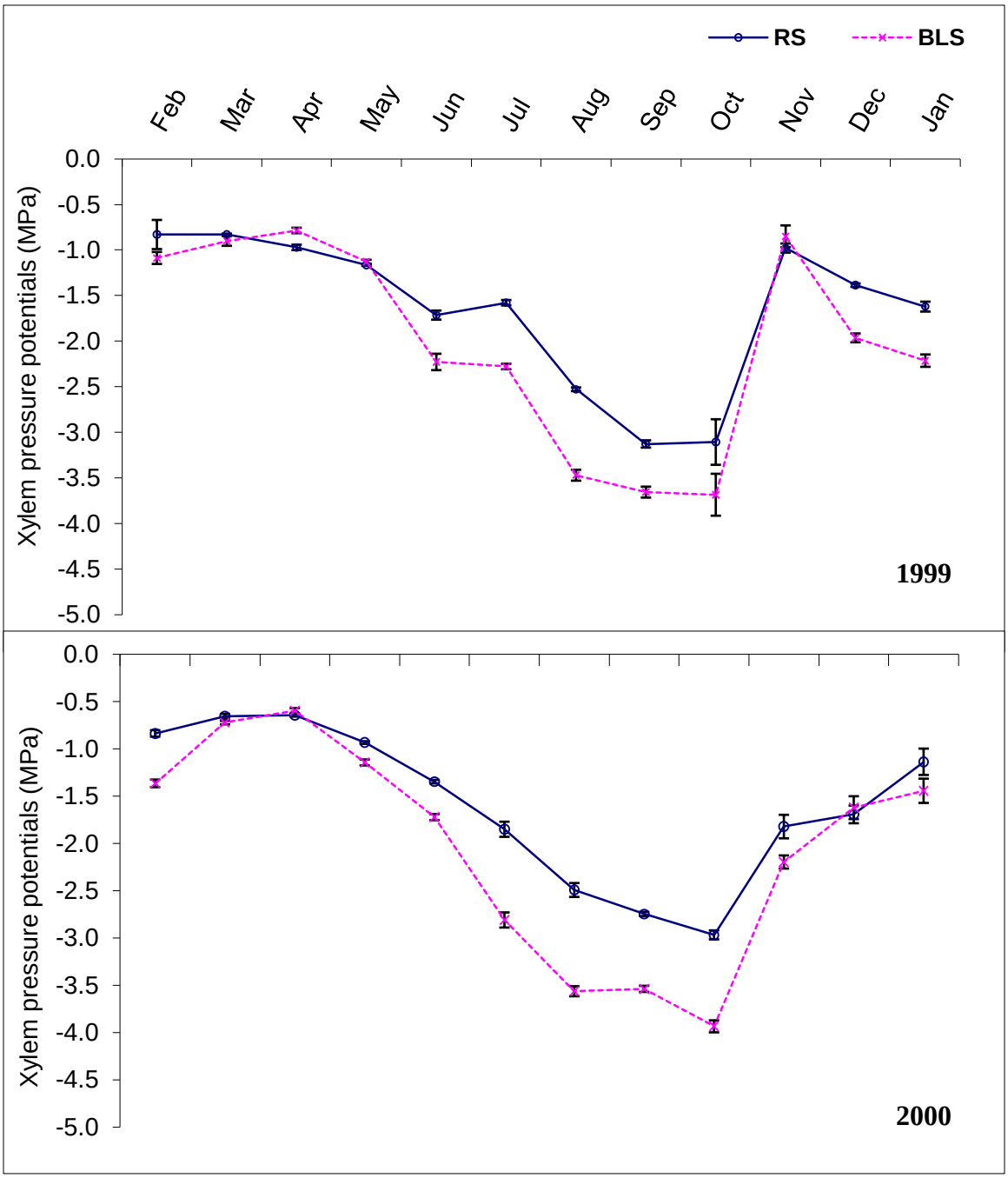

Figure 14. Mean monthly predawn xylem pressure potentials for *A. tridentata* shrubs in the two study plots for 1999 (top) and 2000 (bottom). Data points are means of seven replicates of sampling for juvenile and mature shrubs for each month ± 1 S.E.

Table 5. Results of the Repeated Measures ANOVA for predawn xylem pressure potentials of seven replicates of *A. tridentata* shrubs in each of the two study sites.

Year	Effect	Month	df	t-value	P > |t|
1999	Site*month*year	February	106	-0.02	0.0371
		March	106	-0.64	0.5259
		April	106	1.65	0.1021
		May	106	0.79	0.4333
		June	106	-2.92	0.0042
		July	106	-4.16	<.0001
		August	106	-3.59	0.0005
		September	106	-1.79	0.0759
		October	106	-1.88	0.0630
		November	106	1.99	0.0494
		December	106	-3.95	0.0001
2000		January	106	-3.59	0.0005
		February	106	-5.58	<.0001
		March	106	-1.62	0.1085
		April	106	1.31	0.1945
		May	106	-2.69	0.0082
		June	106	-4.16	<.0001
		July	106	-4.79	<.0001
		August	106	-4.08	<.0001
		September	106	-4.08	<.0001
		October	106	-4.58	<.0001
		November	106	-2.74	0.0072
		December	106	0.58	0.5647
2001		January	106	-3.02	0.0032

highest in April (-0.64 MPa) and lowest in October (-2.97 MPa). For shrubs in the BLS plot, mean predawn xylem pressure potentials were highest in April and lowest in October of both years (ranging from -0.79 MPa in April to -3.69 MPa in October of 1999, and -0.60 MPa in April to -3.94 MPa in October of 2000).

For the two-year study period, predawn xylem pressure potentials for shrubs in both study plots were highest (least negative) in the spring months, declined through the growing season and summer months, and were lowest (most negative) in October. Xylem pressure potentials increased again in November after the seasonal low. In 1999, xylem pressure potentials decreased through the winter months before increasing to the seasonal high in the spring, but no such decline was observed in the winter of 2000.

Xylem pressure potential measurements at midday were significantly different ($p < 0.05$) between plants at the two study sites in June, July, and September through December 1999, and January through March, June, October, November 2000, and January 2001. When significant differences in midday xylem pressure potentials were observed, plants in the BLS plot exhibited lower xylem pressure potentials than plants in the RS plot for both study years (Figure 15 and Table 6). Mean midday xylem pressure potential values for plants in the RS plot range from -1.52 MPa in March to -3.74 MPa in August of 1999, and -1.31 MPa in March to -3.97 MPa in September of 2000. For plants in the BLS plot, mean midday xylem pressure potentials were highest in March and lowest in October of both years (ranging from -1.40 MPa in March to - 4.31 MPa in October of 1999, and -1.51 MPa in March to -4.59 in October of 2000).

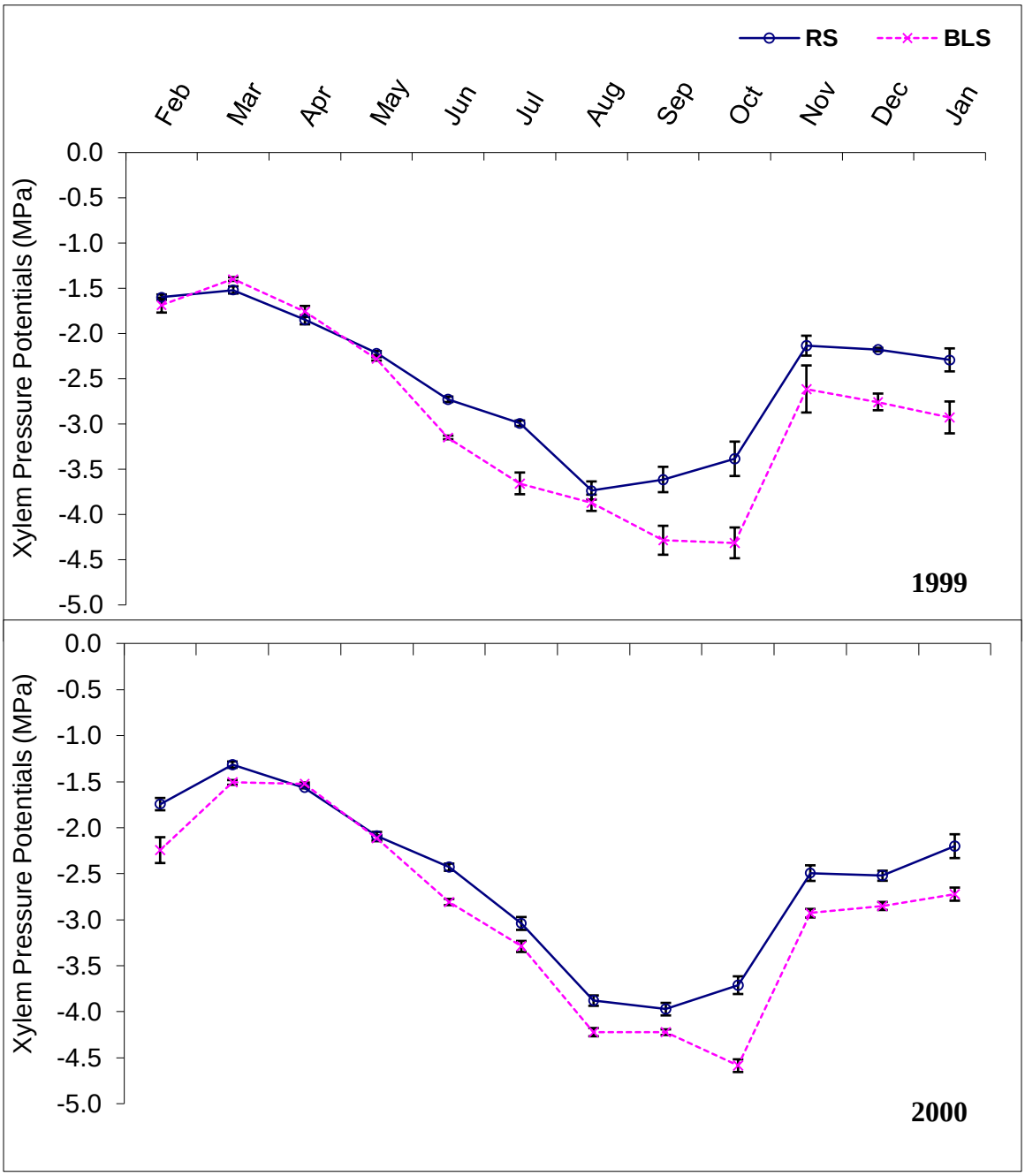

Figure 15. Mean monthly midday xylem pressure potentials for *A. tridentata* shrubs in the two study plots for 1999 (top) and 2000 (bottom). Data points are means of seven replicates of sampling for juvenile and mature shrubs for each month ± 1 S.E.

Table 6. Results of the Repeated Measures ANOVA for midday xylem pressure potentials of seven replicates of *A. tridentata* shrubs in each of the two study sites.

Year	Effect	Month	df	t-value	P > |t|
1999	Site*month*year	February	106	-0.51	0.6119
		March	106	0.88	0.3829
		April	106	1.83	0.0701
		May	106	-0.47	0.6390
		June	106	-2.20	0.0303
		July	106	-3.01	0.0032
		August	106	-0.56	0.6797
		September	106	-2.61	0.0104
		October	106	-3.77	0.0003
		November	106	-2.82	0.0057
		December	106	-3.55	0.0006
2000		January	106	-3.69	0.0005
		February	106	-3.73	0.0003
		March	106	-2.74	0.0073
		April	106	0.56	0.5771
		May	106	-0.25	0.8042
		June	106	-3.14	0.0022
		July	106	-1.25	0.2123
		August	106	-1.30	0.1974
		September	106	-1.29	0.2000
		October	106	-4.75	<.0001
		November	106	-3.74	0.0003
		December	106	-1.88	0.0628
2001		January	106	-3.36	0.0011

Midday xylem pressure potentials for plants at both study sites were highest in the spring months, declined through the growing season and were lowest in the late summer and fall months. Xylem pressure potentials increased again in fall after the seasonal low. In 1999, xylem pressure potentials decreased through the winter months before increasing to the seasonal high in the spring, but no such decline was observed in the winter of 2000.

Stomatal conductance

Peak stomatal conductances occurred late morning in the early spring months (1100 in February) and occurred earlier as daylight hours increased (0900 in April and 0700 in the summer months, May-August). Significant differences ($p < 0.05$) in stomatal conductances between shrubs in the two plots occurred only in March, April and August (Figure 16 and Table 7). Plants in the RS plot exhibited greater conductances in March and April, while plants in the BLS plot displayed greater conductances in August. No measurements were made in the fall and winter months. Stomatal conductances for plants at both sites were lowest in February (56.73 mmol m^{-2} s^{-1} at the BLS site; 71.00 mmol m^{-2} s^{-1} at the RS site), highest in April (270.68 mmol m^{-2} s^{-1} at the BLS site; 414.27 mmol m^{-2} s^{-1} at the RS site), and decreased through the summer months.

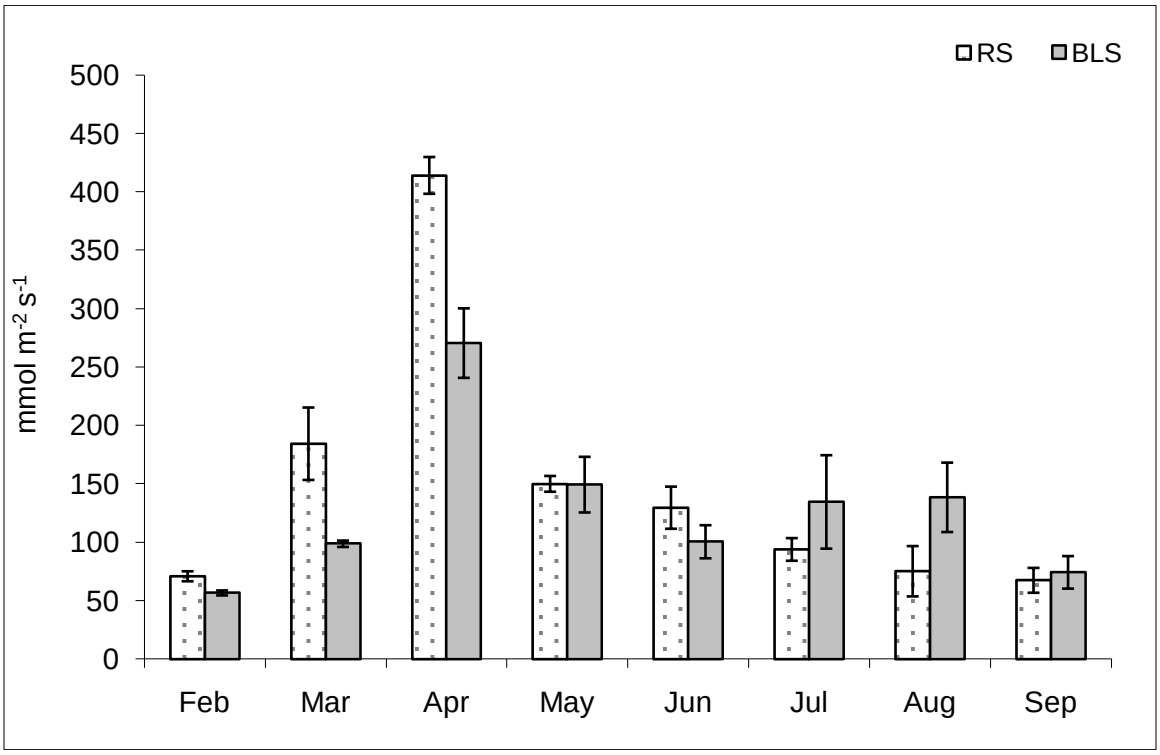

Figure 16. Mean monthly stomatal conductances for *A. tridentata* shrubs in the two soil types in 2000. Data points are means of five replicates of sampling for shrubs in each of the two soil types for each month ± 1 S.E.

Table 7. Results of the repeated measures ANOVA for stomatal conductances for five replicates of *A. tridentata* shrubs in each of the two soil types in 2000.

Year	Effect	Month	df	t-value	P > |t|
2000	Site*month	February	56	0.35	0.7255
		March	56	2.94	0.0048
		April	56	4.93	<.0001
		May	56	0.02	0.9813
		June	56	0.69	0.4962
		July	56	-1.40	0.1683
		August	56	-2.17	0.0341
		September	56	-0.23	0.8158

DISCUSSION

Plant water status measurements indicate *Artemisia tridentata* shrubs in the Burbank Loamy Sand (BLS) (Hajek 1966) experienced greater predawn and midday water stress than shrubs in the stabilized Rupert Sand dune (RS) (Hajek,1966) for summer, fall, and winter months. Barnes and Harrison (1982) reported similar results, where deep-rooted plants on sand dunes were less water stressed than plants on adjacent soils. In the spring months when soil water storage was near field capacity, no differences were seen in plant water potentials, both at predawn and midday, between shrubs in the two soil types, however shrubs in the RS plot exhibited greater stomatal conductances than shrubs in the BLS plot in March and April.

Plant water potentials for shrubs on both soil types exhibited similar seasonal patterns of increases and decreases reflecting increases and decreases in soil water storage. Several studies of plant water status of *A. tridentata* (e.g. Shumar and Anderson, 1986; Miller, 1988; Black and Mack, 1996; Kolb and Sperry, 1999) describe a similar correlation between plant water potentials and plant available soil water. Plant water potentials for shrubs we studied were highest in the spring months (-0.64 MPa for the RS plot and -0.60 MPa for the BLS plot) and lowest in the summer (-3.13 MPa for the RS plot and -3.94 MPa for the BLS plot). Black and Mack (1986) found that *A. tridentata* responded to summer rains by displaying higher xylem pressure potentials just 5 days after the rainfall. However, shrubs in the two soil types I measured did not show a clear response to summer rains when measured seven to ten days after the precipitation events.

Because *A. tridentata* maintains leaves in the winter months (Kolb and Sperry,1999), it may use available soil water for transpiration during these months. I saw

differences in predawn and midday plant water potentials between shrubs in the two soil types during the winter months of both years. Shrubs in the RS plot exhibited xylem pressure potentials of -1.62 MPa at predawn and -2.52 MPa at midday, while shrubs in the BLS plot exhibited xylem pressure potentials of -2.21 MPa at predawn and -2.93 MPa at midday. These differences in plant water potentials indicate the shrubs may be using available soil water and actively transpire in winter months when temperatures are mild.

According to Anderson and others (1987), plants in an *A. tridentata* community may deplete all available stored soil water throughout the growing season. During the two-year study, I found total water storage for the top 1.5 m of soil in both plots was highest in early spring, after recharge from the fall-winter precipitation inputs, declined throughout the growing season, and recharge was evident again in the fall after commencement of the fall rains. Romo and Haferkamp (1989) show a similar pattern in soil water storage for an *A. tridentata*/*S. vermiculatus* community. Calculated soil water storage below 1.5 m for both soil types did not appear to follow seasonal decline. However, soil water content indicate recharge was evident deep in the soil profile on the sand dune, but no recharge was seen for the deep profile of the loamy sand soil.

The greater predawn and midday water stress experienced by shrubs in the BLS plot compared to shrubs in the RS plot for most of the year is correlated to the differences in soil water storage between plots. Because soil water storage was lower in the BLS plot compared to the RS plot, shrubs in the BLS plot experienced greater water stress than shrubs in the RS plot. This is comparable to the results of Shumar and Anderson (1986), where differences in plant water potentials of two populations of *A. tridentata* were related to different amounts of stored water in associated soils. In addition, the results of

Barker and McKell (1993) show that differences in soil water potential in two substrates will result in differences in plant water potentials for a population of *A. tridentata*.

Stomatal conductance of *A. tridentata* shrubs declined in both study plots during the late spring months concurrently with the seasonal decline of xylem pressure potentials and available soil water. The results of studies by Brown and Archer (1990) on woody plants and Toft et al. (1989) on cold desert plants describe similar relationships between plant water potentials, stomatal conductances, and soil water storage. Significant differences ($p < 0.05$) in stomatal conductance were seen between shrubs in the two plots only in March, April, and August. However, these differences were not consistent. Shrubs in the RS plot exhibited greater conductances in March and April whereas, shrubs in the BLS plots displayed greater conductances in August. Although the conductances displayed by shrubs in the RS plot in March and April were significantly greater ($p < 0.05$) than shrubs in the BLS plot, midday xylem pressure potentials were lower for shrubs in the RS plot in March, while no differences in xylem pressure potentials were observed in April. In contrast, Brown and Archer (1990) found lower gas exchange rates for woody plants corresponded to lower xylem pressure potentials. The greater conductances exhibited by shrubs in the BLS plot in August were accompanied by lower xylem pressure potentials as expected.

Neutron probe data for water storage in the top layer of soil in the RS plot was analogous to gravimetric data, however neutron probe and gravimetric data were dissimilar in amounts of water storage in the top layer of soil in the BLS plot. This may be a consequence of the calibration equation used for that soil. I was unable to calibrate the neutron probe to the soil in the BLS plot; therefore, I used the calibration developed

for the RS soil which is similar to the BLS soil. The measurements were not intended to fully describe the soil water storage parameters, but to aid in better understanding plant water uptake throughout the year. The neutron probe data for the BLS plot appear to overestimate the amount of stored soil water with respect to concurrent gravimetric measurements.

CONCLUSION

I found differences in plant water potentials of *A. tridentata* shrubs growing in two adjacent, but different textured soils that may be related to differences in soil water storage. Soil water storage in the loamy sand was considerably lower than water storage in the RS plot; therefore, shrubs in the BLS plot experienced greater predawn and midday water stress than shrubs in the RS plot. Shrubs growing on BLS soils with less available soil water may control stomatal conductances to minimize transpirational water loss compared to shrubs on coarser RS soils. The results of this study may be used as a validation data set to which model simulations of plant responses to seasonal environmental changes in semi-arid regions can be compared. The results may also aid in better understanding of how shrubs use stored soil water in different textured soils throughout the year.

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