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# Water Relations Characteristics of Competing Singleleaf Pinyon Seedlings and Sagebrush Nurse Plants

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## ABSTRACT

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Encroachment of singleleaf pinyon (*Pinus monophylla*) into adjacent low sagebrush (*Artemisia arbuscula*) and basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*) communities may be enhanced by the efficient use of limited water resources by tree seedlings. Seedlings and sagebrush nurse plants were monitored over two growing seasons to determine water-use patterns. Predawn xylem water potential of low sagebrush declined rapidly, reaching −3.5 to −5.5 MPa by late summer. Big sagebrush values dropped to −2.0 to −3.0 MPa during summer drought. The drop in sagebrush xylem water potential was related to the decline in soil water potential ($r = 0.68$ and 0.82). The change in pinyon predawn xylem water potential was moderate, declining to values of −1.5 to −2.5 MPa. An apparent diurnal threshold xylem water potential (−2.3 to −3.0 MPa) that results in stomatal closure enables pinyon seedlings to maintain a seasonally stable xylem water potential. Water use by pinyon seedlings declined by 50% from May to August in association with a reduction in stomatal conductance. Despite reduced stomatal conductance, sagebrush water use continued to increase during summer and reached levels up to five times greater (per unit leaf area) than associated pinyon. Pinyon seedlings appear to have greater drought avoidance than sagebrush nurse plants.

## INTRODUCTION

The conifer woodland subformation covers extensive areas in the western United States and Mexico. Singleleaf pinyon (*Pinus monophylla*) is a major component of the conifer woodland subformation in the Great Basin, U.S.A., and a closely associated species pinyon (*Pinus edulis*) is a major vegetation component of the Colorado Plateau. Conifer encroachment into adjacent plant communities has been documented in many forest types (Arno and Gruell, 1983) and has received much attention in the conifer woodland subformation because of associated losses in livestock forage and wildlife habitat (Blackburn and Tueller, 1970).

Pinyon seedlings are associated with understory species in encroachment areas because tree seedlings require nurse plants to survive (Phillips, 1909; Everett et al., 1986). Nurse plants provide shade and ameliorate microclimate stress for conifer seedlings (Youngberg, 1965) but also compete for water and nutrients (Wright and Mooney, 1965).

In the shrub steppe of the Great Basin two species of sagebrush, basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*) and low sagebrush (*Artemisia arbuscula*), can serve as nurse plants for singleleaf pinyon seedlings (Fig. 1). Basin big sagebrush tends to grow in the deep soils of drainage bottoms where soil moisture is available (Barker and McKell, 1983). Low sagebrush grows on shallow sideslope soils with lower water-holding capacity (Miles and Leonard, 1984).

A review of the literature on water potentials of conifers and sagebrush species shows water potentials of conifers to be relatively stable compared to sagebrush species. Dawn water potentials of red pine (*Pinus resinosa*) declined gradually during a drought before reaching a stable value of $-1.6$ bar (Sucoff, 1972). Lopushinsky (1969) reported a decline in transpiratory losses from conifer seedlings resulting from stomatal closure at twig moisture stresses ranging from 1.46 to 2.51 MPa.

A larger drop in basin big sagebrush water potential, to the range of $-2.0$ to $-7.0$ MPa, has been found during summer drought conditions (Branson et al., 1976; Campbell and Harris, 1977; Everett et al., 1977). Decreasing basin big sagebrush water potential results in reduced stomatal aperture and a concomitant control of water loss (DePuit and Caldwell, 1973).

Mooney et al. (1966) compared metabolic functions (transpiration, net photosynthesis, and dark respiration) of bristlecone pine (*Pinus longaeva* Bailey) and big sagebrush and found bristlecone pine much less sensitive to environmental conditions. Bristlecone pine dominance on harsh sites has been attributed in part to the tree's ability to maintain lower internal water stress than competing curlleaf mountain mahogany *Cercocarpus ledifolius* Nutt. (Beasley and Klemmedson, 1976).

Given the above differences in conifer and shrub response to environmental conditions and the linkage of water stress to species distribution patterns (Mooney et al., 1966), we suggest that differences in water relations of singleleaf pinyon seedlings and sagebrush nurse plants may partially explain pinyon encroachment into adjacent plant communities. Xylem water potentials of singleleaf pinyon seedlings, basin big sagebrush, and low sagebrush were measured over two growing seasons. Daily patterns of transpiration were used to document water use, determine the existence of threshold water potentials that result in stomatal closure, and investigate the effect of threshold values on seasonal changes in water potential. Our objective was to test the null hypoth-

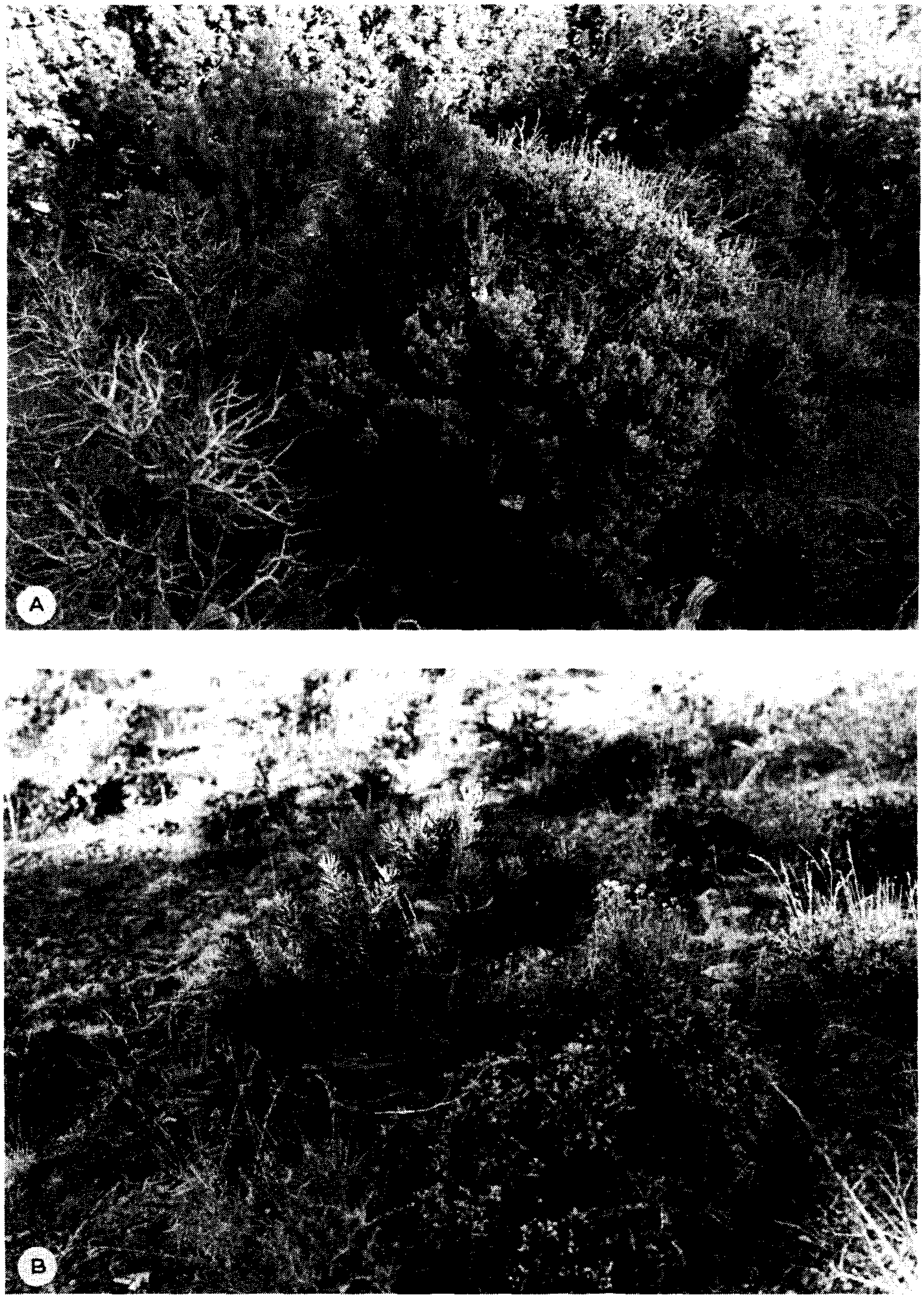

Fig. 1. Nurse plant and seedling in (A) basin big sagebrush (ARTR) and (B) low sagebrush (ARAR) ecotones.

esis of no difference in transpiration and plant water potential between singleleaf pinyon seedlings and sagebrush nurse plants.

## METHODS

### *Study area*

The study area, in the Virginia Range of western Nevada, receives 320 mm of precipitation annually. Six singleleaf pinyon-shrub ecotone areas served as study sites. Basin big sagebrush was the nurse plant on three sites and low sagebrush the nurse plant on the remaining sites. Elevation at the sites ranges from 1520 to 2080 m. Low sagebrush communities were found on side slopes of south (high elevation) and east (low elevation) aspects. Soils are a very stony clay loam of the Cagle Series. Basin big sagebrush communities occur in drainage bottoms on deeper sandy loam soils of the Indiano Series.

### *Water potentials*

Predawn xylem water potentials of sagebrush and seedlings were measured with a Soilmoisture[1] 300 pressure bomb (Scholander et al., 1965). Six nurse plant-seedling pairs (two pairs at each of three sites) from each community type were randomly selected and sampled on a weekly basis from April until September in 1985 and 1986. The sample size was increased to 24 shrub-seedling pairs at each site at the time of maximum and minimum xylem water potential ($\Psi_x$) for singleleaf pinyon seedlings. Diurnal sampling, every 2 h from predawn until sunset, was done four times during 1986. Soil water potential was measured on a two-weekly basis during the 1986 growing season. Soil samples were taken from a depth of approximately 20 cm and returned to the lab for analysis in a Decagon SC-10A thermocouple psychrometer.

### *Transpiration*

Transpiration was sampled during the spring, early summer, late summer, and fall of 1986. Three shrub-seedling pairs were sampled at one site for each of the two sagebrush community types. Transpiration and stomatal conductance were estimated with a LI-COR 1600 steady state porometer. Porometer readings were taken in conjunction with $\Psi_x$ measurements every 2 h from predawn to sunset. Sagebrush leaves and singleleaf pinyon needles did not completely cover the porometer chamber (area$=$4.0 cm$^2$), so transpiration and conductance values were adjusted for leaf area (LI-COR LI-3000 Portable

[1]The use of trade or firm names in this paper is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

TABLE 1

Predawn xylem water potentials ( −MPa) of singleleaf pinyon seedlings (PIMO) and basin big sagebrush (ARTR) or low sagebrush (ARAR) nurse plants at minimum (spring) and maximum (summer) periods of water stress

| Species | Spring | | Summer | |
|---|---|---|---|---|
| | 1985 | 1986 | 1985 | 1986 |
| ARTR | 0.95[b] | 0.97[d] | 2.10[b] | 2.27[b] |
| PIMO | 1.10[a] | 1.40[b] | 1.56[d] | 1.77[d] |
| ARAR | 0.96[b] | 1.20[c] | 3.85[a] | 3.73[a] |
| PIMO | 1.10[a] | 1.57[a] | 1.79[c] | 2.00[c] |

Values in each column with dissimilar letters are significantly ($P=0.05$) different.

Area Meter). Water use for shrubs and seedlings was calculated by integrating under diurnal transpiration curves. Daily water use is reported on a per-$cm^2$ basis. Therefore, direct comparisons can be made between seedlings and nurse plants.

### *Analysis*

Pinyon seedling and nurse plant $\Psi_x$ were compared using analysis of variance (Snedecor, 1956). We used 15 sampling dates (six replicates each) to compare seasonal changes in $\Psi_x$ of seedlings and shrubs. We used 72 replicates (three plots of 24 plants each) to test for differences between seedlings and sagebrush nurse plants in each community at spring minimum and summer maximum water stress periods.

## RESULTS AND DISCUSSION

### *Seasonal water potential*

Singleleaf pinyon seedlings (PIMO) had lower (more negative) predawn $\Psi_x$ than basin big sagebrush (ARTR) or low sagebrush (ARAR) nurse plants during the period of minimum water stress early in the 1985 and 1986 growing seasons (Table 1). Predawn $\Psi_x$ of seedlings and nurse plants changed similarly during the period of abundant soil moisture in spring (Fig. 2). Predawn $\Psi_x$ of ARTR in 1985 declined (became more negative) more rapidly than PIMO $\Psi_x$ during late June and remained about 0.5 MPa lower through the summer. At the time of maximum midsummer water stress, ARTR $\Psi_x$ was significantly more negative than PIMO $\Psi_x$ (Table 1). Predawn $\Psi_x$ of ARAR had decreased below associated PIMO $\Psi_x$ by early June and remained lower through September 1985. The rapid decline of ARAR $\Psi_x$ to the −4.5 to −5.5 MPa range contrasts the

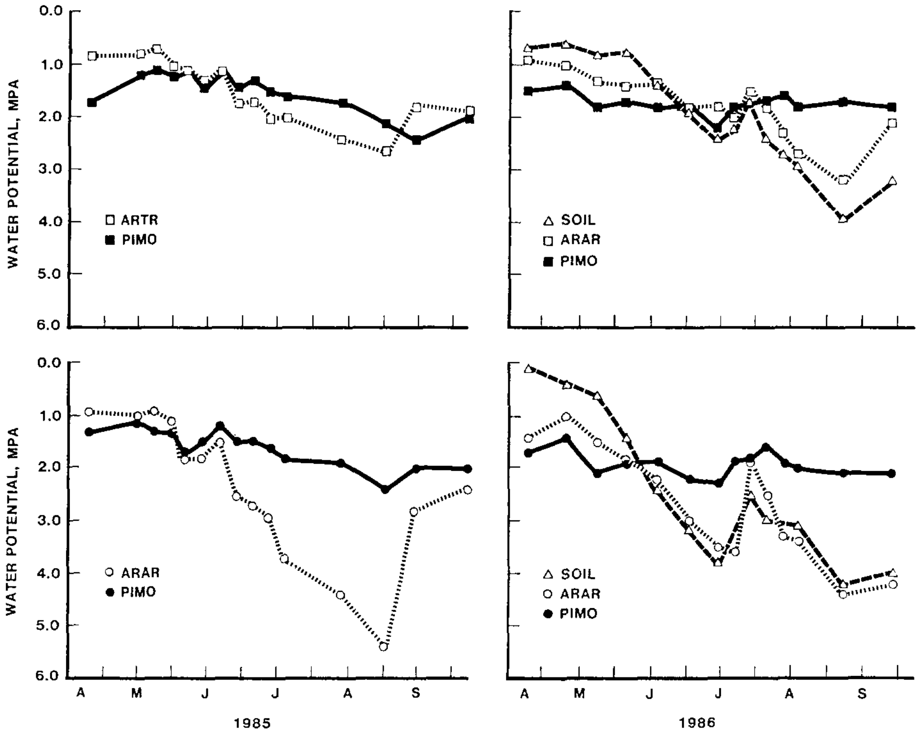


Fig. 2. Predawn xylem water potential (MPa) of basin big sagebrush (ARTR), low sagebrush (ARAR), and associated singleleaf pinyon seedlings (PIMO) during the 1985 and 1986 growing seasons. Predawn soil water potential (MPa) from the 1986 growing season.

moderate drop in PIMO $\Psi_x$ to about $-2.3$ bar. Shrub $\Psi_x$ again became less negative early in September, following late summer precipitation.

Spring PIMO $\Psi_x$ was again lower than sagebrush species in 1986 and remained so until early June in ARAR communities and mid July in ARTR communities (Fig. 2). The steady decline of plant $\Psi_x$ seen in 1985 was interrupted in 1986 by midsummer precipitation, which afforded an excellent opportunity to examine the effect of near-surface soil water potential on plant $\Psi_x$.

Sagebrush $\Psi_x$ increased in late July, apparently in response to higher soil water potential subsequent to the storms. Values for sagebrush rapidly declined as the soil dried, and then increased at the time of early September precipitation. A significant correlation was found for shrub $\Psi_x$ and soil water potential over the season: ARTR ($r=0.82$) and ARAR ($r=0.68$). The significant relationship between ARTR $\Psi_x$ and soil water potential has been previously reported by Branson and Shown (1975). PIMO $\Psi_x$ was not related to soil water potential ($r=0.38$ and 0.23) and showed little response to midsummer precipitation. Schott and Pieper (1987) found a similar lack of pinyon water potential response to precipitation.

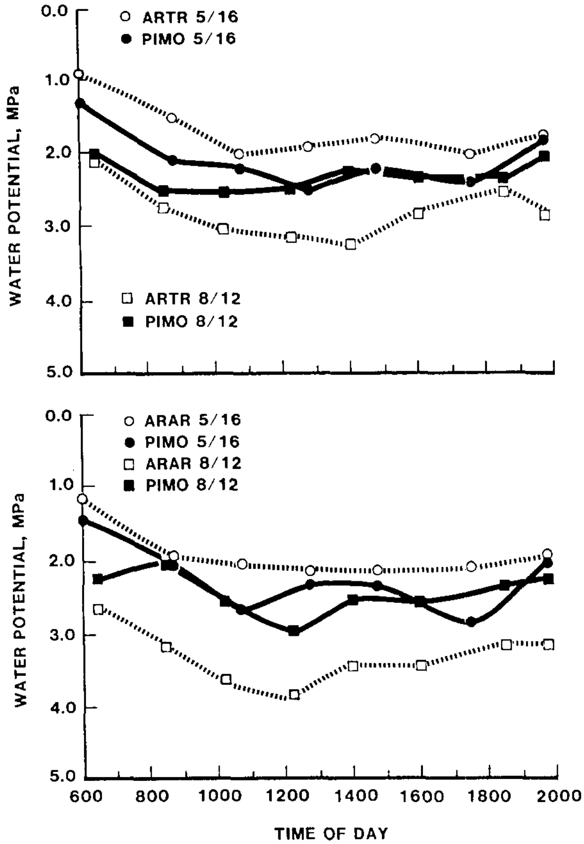


Fig. 3. Diurnal xylem water potential (MPa) patterns of basin big sagebrush (ARTR), low sagebrush (ARAR), and associated singleleaf pinyon seedlings from 16 May and 12 August 1986.

No overall seasonal difference in predawn $\Psi_x$ of PIMO and ARTR nurse plants was found during either year. ARAR values declined sufficiently over the summer to make the seasonal mean significantly less than associated PIMO $\Psi_x$ both years. During 1985, PIMO $\Psi_x$ did not differ between sagebrush ecotones. However, in 1986 PIMO on the ARAR sites had $\Psi_x$ 0.1 to 0.4 MPa more negative than PIMO in the ARTR community.

*Diurnal water potential and stomatal conductance*

PIMO $\Psi_x$ was lower than sagebrush nurse plants in spring, reaching midday values in the range of −2.3 to −2.6 MPa. Midday $\Psi_x$ of ARTR in summer was near −3.0 MPa, a decline of more than 1.0 MPa from spring (Fig. 3). Midday $\Psi_x$ for associated PIMO, near −2.5 MPa, was virtually the same as the spring value. Midday $\Psi_x$ for ARAR fell from about −2.1 MPa to −3.5 to −4.0 MPa.

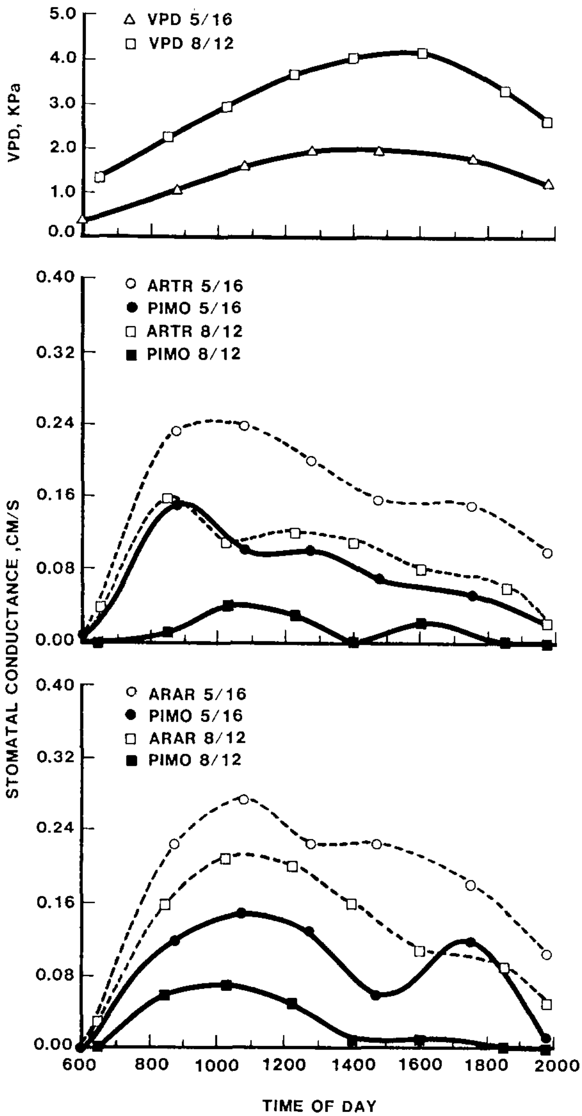


Fig. 4. Diurnal stomatal conductance (cm/s) patterns of basin big sagebrush (ARTR), low sagebrush (ARAR), and associated singleleaf pinyon seedlings (PIMO) from 16 May and 12 August 1986.

Values for PIMO in the ARAR ecotone declined by 0.4 MPa and reached a lower level ( −2.9 MPa) than PIMO associated with ARTR.

Diurnal stomatal conductance patterns show relatively higher values for nurse plants than for PIMO during spring and summer (Fig. 4). During summer we found PIMO stomata were closed by midafternoon in apparent response to

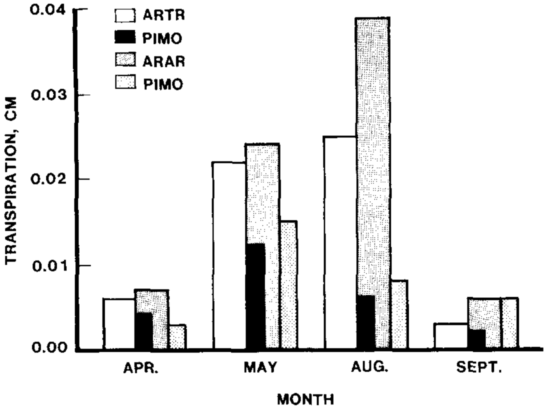


Fig. 5. Daytime water use (cm) per $cm^2$ of leaf area for basin big sagebrush (ARTR), low sagebrush (ARAR), and associated singleleaf pinyon seedlings (PIMO) from 13 April, 16 May, 12 August and 28 September 1986.

a threshold $\Psi_x$. Threshold values for stomatal closure appear to be in the range of −2.3 to −2.7 MPa for PIMO associated with ARTR and −2.5 to −3.0 for PIMO associated with ARAR. The slightly lower range of PIMO values in the drier ARAR community suggests threshold $\Psi_x$ may vary among community types. Threshold values for PIMO appear to be more negative than those reported for other conifers (−1.46 to −2.51 MPa; Lopushinsky, 1969; Running, 1976). Stomatal response to water stress for juvenile *P. edulis* resulted in net photosynthetic rates that declined linearly to zero at −1.8 MPa (Barnes and Cunningham, 1987). Figure 3 shows PIMO $\Psi_x$ stabilized in the ARTR community and increased in the ARAR community following stomatal closure. Larcher (1980) attributed the late-afternoon reopening of conifer stomata, seen for PIMO in spring and summer, to sufficient alleviation of the water deficit following stomatal closure.

A partial reduction in conductance by midday, rather than stomatal closure, was found for shrubs during summer. The continued reduction in stomatal aperture over the season in response to decreasing $\Psi_x$ agrees with previous work done with ARTR (DePuit and Caldwell, 1975).

*Transpiration*

Daily water use was less for PIMO seedlings (0.002–0.004 cm) than sagebrush nurse plants (0.006–0.007 cm) in early spring (Fig. 5). Water use by PIMO had risen to the range of 0.012–0.015 cm by May, which was 30–50% lower than nurse plant values. By August, conductance for PIMO had declined to the lowest rates seen for the year, with a corresponding reduction of about 50% in water use. Water use by nurse plants was higher in August, despite the increase in stomatal resistance. Therefore, PIMO appears to have a more efficient means for control of transpiratory losses during drought conditions. September water use by all species had returned to early-spring level.

## CONCLUSION

Nurse plant (in particular low sagebrush) $\Psi_x$ showed a greater response to summer drought than $\Psi_x$ of singleleaf pinyon seedlings. Seasonal changes in soil water potential showed a good correlation ($r=0.68$ and 0.82) with sagebrush predawn xylem water potentials but no relation to seedling values. Threshold $\Psi_x$, for pinyon, of $-2.3$ to $-2.7$ MPa in the big sagebrush community and $-2.5$ and $-3.0$ MPa in the low sagebrush community resulted in midafternon stomatal closure during summer drought. Stomatal closure in seedlings proved to be an efficient means for limiting transpiratory losses and resulted in a stable $\Psi_x$ the remainder of the day. The seasonally stable $\Psi_x$ of singleleaf pinyon seedlings can be attributed to threshold values that result in control of water loss by stomatal closure.

The partial reduction in stomatal conductance for nurse plants as $\Psi_x$ decreased appeared to be relatively ineffective at controlling water loss. Lack of an apparent $\Psi_x$ threshold that results in stomatal closure, and the good correlation of shrub and near-surface soil water potential, contributed to the relatively large changes in nurse plant $\Psi_x$ over the season.

Pinyon had its greatest water use in spring when soil moisture was available, while sagebrush water use peaked during midsummer when soil moisture was dwindling. Pinyon seedlings limit water loss via transpiration to a greater degree than sagebrush nurse plants during drought. Thus, pinyon seedlings appear to be more sensitive to water stress than sagebrush, and have a more efficient means for control of water use during drought conditions.

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