

Water Relations and Leaf Morphology of *Juniperus occidentalis* in the Northern Great Basin

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ABSTRACT. Relationships between seasonal and diurnal leaf conductance, xylem sap potential, transpiration rates, osmotic potential, vapor pressure deficit, soil and air temperatures, soil water potential, and photosynthetic active radiation are quantified for *Juniperus occidentalis* Hook. Additionally, xeromorphic aspects of leaf morphology were examined with electron microscopy. Xylem sap potentials and leaf conductance ranged from -0.5 to -2.7 MPa and 0.02 to 0.13 cm s^{-1} , respectively, during the two-year study. Leaf conductance is not clearly related to any single environmental variable, but is primarily influenced by vapor pressure deficit, photosynthetically active radiation, and factors such as soil and air temperatures, and soil water, which influence the resistance of water flow through the plant. Stomates usually closed when xylem sap potentials reached -2.0 MPa. Stomates on mature leaves are distributed unequally on adaxial and abaxial surfaces, with none occurring on exposed surfaces. Drought avoidance mechanisms displayed by the plant were leaf morphological characteristics, low maximum leaf conductance, and reduced maximum leaf conductance under high evaporative conditions. Cold soil temperatures increased resistance of water flow through the soil-plant-atmosphere continuum. Xeromorphic leaf structure as well as seasonal osmotic adjustment provide primary mechanisms in the tolerance of *Juniperus occidentalis* to drought stress. FOR. SCI. 33(3):690-706.

ADDITIONAL KEY WORDS. Leaf conductance, transpiration, xylem sap potential, western juniper, stomata.

Juniperus occidentalis is one of nine tree-sized junipers occupying semiarid portions of the western United States (Figure 1) and is often the only tree species in much of the northwestern portion of the Great Basin. Since the late 1800s, this species has been actively invading adjacent sagebrush grass communities (Burkhardt and Tisdale 1976, Caraher 1978) and the present distribution may be double that of the late 1800s (Eddleman 1983). It is suspected that, as dominance of *Juniperus occidentalis* increases on a site, understory plant cover and net annual primary productivity, and water infiltration rates, are reduced, with consequent increases in sediment yields (Buckhouse and Mattison 1980, Eddleman 1983). As *Juniperus occidentalis* stands expand in the Great Basin, it becomes more important to address questions relating to this species' competitive abilities and impacts on the site. Of particular interest is its use of limited water resources.

A few studies have evaluated water relations of desert trees (Slayter 1961,

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Adams and Strain 1968, Nilsen et al. 1983), but essentially no work exists in the literature concerning water relations for any of the *Juniperus* species growing in the Great Basin. Also, few studies have described leaf morphological structure of cold desert woody plants and related these characteristics to water use. We know of no other studies on stomatal distribution in *Juniperus* that relate to leaf conductance. In a study of Arizona junipers, Johnson (1963) describes the leaf anatomy of *J. deppeana*, *J. scopulorum*, *J. monosperma*, and *J. osteosperma*. Quantitative data are limited to stomatal frequency for *J. monosperma*, providing our only reference for comparison in this study.

This study addresses questions of how environmental parameters influence water relations of *Juniperus occidentalis* throughout the year, and how leaf morphology and plant-water-related responses may serve as mechanisms allowing the species to survive and successfully compete in semiarid conditions.

MATERIALS AND METHODS

STUDY AREA

Data were gathered from September 1982 through September 1984 on the Squaw Butte Experimental Range located on the northern fringe of the Great Basin in southeastern Oregon (Figure 1). The 40-year mean annual precipitation for this area is approximately 300 mm. The Squaw Butte Experimental Range typically receives the majority of moisture between September and June (most of it in the form of snow), with little precipitation received in July and August. The study site is an *Artemisia tridentata* ssp. *vaseyana*/*Festuca idahoensis* habitat type (Winward 1970) at 1360 m elevation. The soil is a Typic Haploxeroll, with textures ranging from loam near the soil surface to gravelly loam at the lower depths (Swanson 1982). Soils are underlain by columnar basalt bedrock at approximately 112 cm.

CLIMATOLOGICAL AND SOIL PARAMETERS

Climatic measurements included precipitation, air and soil temperatures, relative humidity, vapor pressure deficit (VPD), and photosynthetic active radiation (PAR). Daily precipitation and air temperature were measured throughout the year with standard weather bureau equipment 1.6 km from the study site. Air temperature and relative humidity were measured on site with a Psyron battery-powered psychrometer concurrent with plant-water measurements.¹ Vapor pressure deficit was calculated from air temperature and relative humidity recorded with a steady state porometer (Li-1600, LiCor, Inc., Lincoln, NB) during plant-water measurements. Soil temperatures were measured with a soil thermometer at 15 and 45 cm in April, May, and July in 1983, and on each date plant measurements were recorded in 1984. During winter months, soil temperatures were recorded once at 15 and 45 cm in January of 1983 and 1984 when temperature of the upper soil layer was below 0°C. In 1983, soil water content was measured gravimetrically approximately monthly from March to October at 15 cm and in March, July, August, and November at 100 cm. In 1984, soil moisture content was mea-

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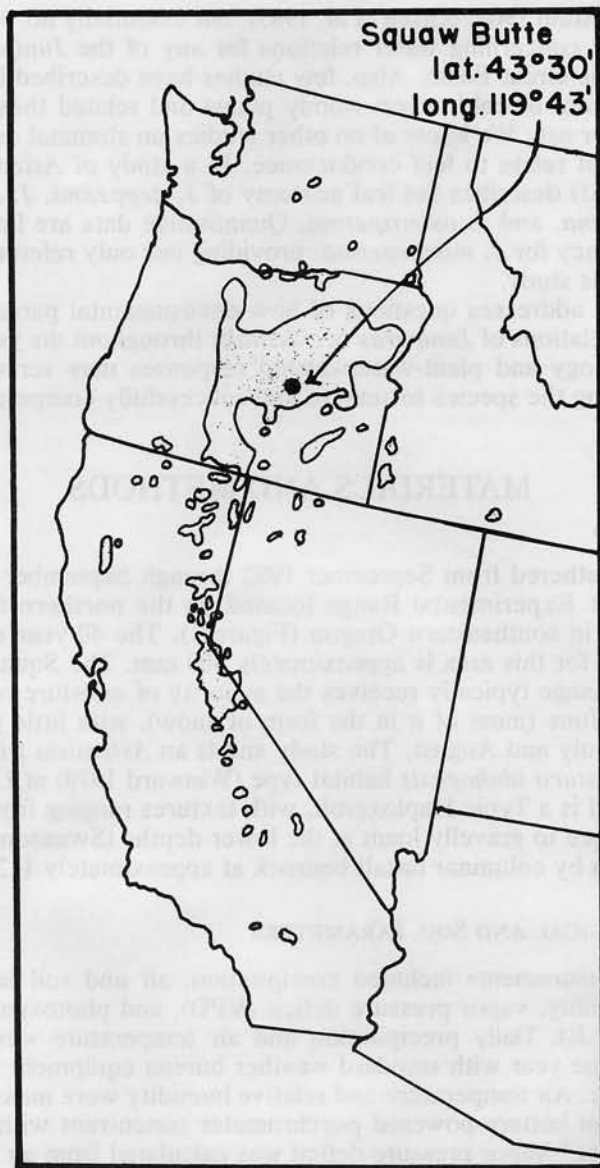


FIGURE 1. Distribution of *Juniperus occidentalis* (from USDA For. Serv. 1965 and Shultz field records) and location of the Squaw Butte Experimental Range.

sured gravimetrically approximately monthly from March through September at 15, 30, 60, and 100 cm. Soil moisture release curves for each horizon in the profile were developed to convert percent soil water to soil water potential (ψ_s). Photosynthetic active radiation was measured by holding a quantum sensor (LI-190S, LiCor, Inc., Lincoln, NB) parallel with the leaf surface during plant water measurements.

PLANT MATERIALS

Six trees within the stand were chosen for study. Ages estimated from core samples ranged from 82 to 123 years old. Tree sizes ranged from 4 to 6 m in

height and 25 to 45 cm in basal diameter at the litter surface. All trees looked healthy, showing no signs of decadence. Trees were located within 80 m of each other. All samples were collected in the lower 2 m of crown. *Juniperus occidentalis* root distribution in the woodland was visually observed in five soil pits excavated to bedrock in the tree interspaces.

LEAF MORPHOLOGY

Leaf samples, for morphological study, were collected in 1984 from branchlets on the north and south sides of the six trees. Samples were sealed in airtight plastic bags, shipped to Utah State University, and maintained at 5°C prior to evaluation. Epidermal and stomatal patterns were examined on individual scale-leaves and on entire branchlets. In order to preserve cuticles and epidermal patterns, entire branchlets and individual leaves were prepared for scanning electron microscopy as fresh specimens and coated with gold-palladium by a low-temperature sputter coat (Polaron E-500 Sputter Coater, Polaron Ins. Inc. Doylestown, PA). An AMR-1000 scanning electron microscope was used for photomicrography. Photographic angles and magnification were replicated for different samples in order to facilitate comparison of stomatal distribution and guard cell size. Area of the leaf surface, number of stomata, and pore size were calculated from the photographs with a sample from each of five branchlets.

PLANT-WATER RELATIONS

Xylem sap potential (ψ_1) was measured on one branchlet for each of the six trees with a pressure chamber (Scholander et al. 1965). Samples were collected on the south side of the tree, sealed in a ziploc bag, placed on ice, and read within five minutes of collection. Leaf conductance (g_1) was measured with a steady state porometer (LiCor, Li-1600) fitted with a cylindrical chamber (LiCor Li-1600-02A). Two branchlets were sampled on the north and south aspects of each tree. At the end of each sampling period, leaf samples on which g_1 was measured were collected and sealed in ziploc plastic bags to determine exposed leaf area with a leaf area meter (LiCor, LI-3100). No correction for overlapping leaf scales were made. Readings from the leaf area meter were multiplied by π to estimate exposed total leaf surface area (the shape of the branchlets were assumed to be cylindrical). Leaf area measurements were then used to correct g_1 data recorded in the field. Transpiration was calculated from simultaneous measurements of g_1 and VPD using the equation $J = (g_1)(VPD)$. Relationships between plant-water parameters, and plant-water parameters with environmental parameters were evaluated using regression analysis. Differences in g_1 between the two tree aspects were evaluated with a paired Student's t-test.

Xylem sap potential and g_1 were measured diurnally in 1984 over a two-day period in May, June, July, and August. Xylem sap potential measurements were recorded at approximately three-hour intervals from predawn to approximately 2100 h. Predawn ψ_1 was measured a half hour before sunrise. Leaf conductance was measured directly following ψ_1 readings excluding the predawn measurement.

Predawn and midday ψ_1 , and midday g_1 , were also recorded, throughout the study, at monthly intervals from March through October with biweekly measurements recorded during the active growth period of May through July. Several measurements were also recorded during winter, when daytime temperatures rose above zero.

Osmotic potential at full and zero turgor were measured by collecting a twig sample from each of the six trees in the morning, once in January, April, June, July, September, and October, 1984. Samples were placed in water and refrigerated for 24 hours, recut under water (Yoder 1984), and a water release curve developed (Richardson and McKell 1980).

RESULTS

CLIMATIC CONDITIONS

Seasonal climatic conditions at the Squaw Butte Experimental Range during 1982–1984 were characteristic of those found in the Great Basin. Monthly mean air temperatures ranged from -13.5°C to 30°C (Figure 2). During December, January, and February, daily maximum temperatures often remained below freezing. Nighttime temperatures frequently dropped below 0°C as late as May. Daytime temperatures in the summer months frequently ranged from 25°C to 35°C , with nighttime temperatures ranging from 5°C to 13°C . Freezing nighttime temperatures begin occurring in September and October. Soil temperatures followed a seasonal pattern similar to air temperatures. In both years soil temperature in the upper 15 cm dropped below 0°C during winter months. At 30 and 45 cm soil depths, winter temperatures ranged between 1°C and 4°C . Diurnal change in soil temperature decreased with depth.

Precipitation during the study averaged 115% and 150% of normal in 1983 and 1984, respectively. Soil water in the upper 15 cm remained near -0.03 MPa through mid-May and then rapidly decreased to or below -1.5 MPa (Figure 2). Soil moisture at 60 and 100 cm, however, remained above -0.2 and -0.03 MPa, respectively, throughout the study. In years with less precipitation, ψ_s throughout the soil profile dropped below -1.5 MPa by late summer (Miller et al. 1986).

LEAF MORPHOLOGY

Mature leaves of *Juniperus occidentalis* are reduced to small scales, which range from 0.9 mm to 1.2 mm in length. The juniper leaf scale, as seen in transection, forms an oblique triangle. In outline, the leaf is triangular with minutely serrate margins (Figure 3). Leaf margins are slightly recurved, creating a slight "cupping," which seals one leaf against the other. Leaves closely overlap on the branches, forming a chain-line cylinder of scales. The adaxial surfaces are not exposed to sunlight or air movement and abaxial surfaces are only partially exposed. The leaf epidermis is heavily cuticularized to the extent that cell lumina are nearly obliterated. Epidermal walls are straight. Leaves are reduced to scales with a low surface-to-volume ratio.

Stomates on mature leaves of *Juniperus occidentalis* are distributed on both adaxial and abaxial surfaces. The distribution is unequal, however, in that none occur on exposed abaxial surfaces. Here, stomates are restricted to the base of the leaf, near the margins, and in the region entirely covered by the adjacent subtending scale leaf (Figures 3a–3b). Stomates are absent on the abaxial side from the lowermost leaves on the branch where leaf bases are exposed. The majority of stomates are located on the adaxial surface (Figure 3c). Here they are evenly distributed near the leaf margins from the base to the apex and are equally dispersed on either side of the midrib. Stomates do not occur adjacent to the point of leaf attachment or immediately adjacent to the midrib. Guard cells are raised above the level of adja-

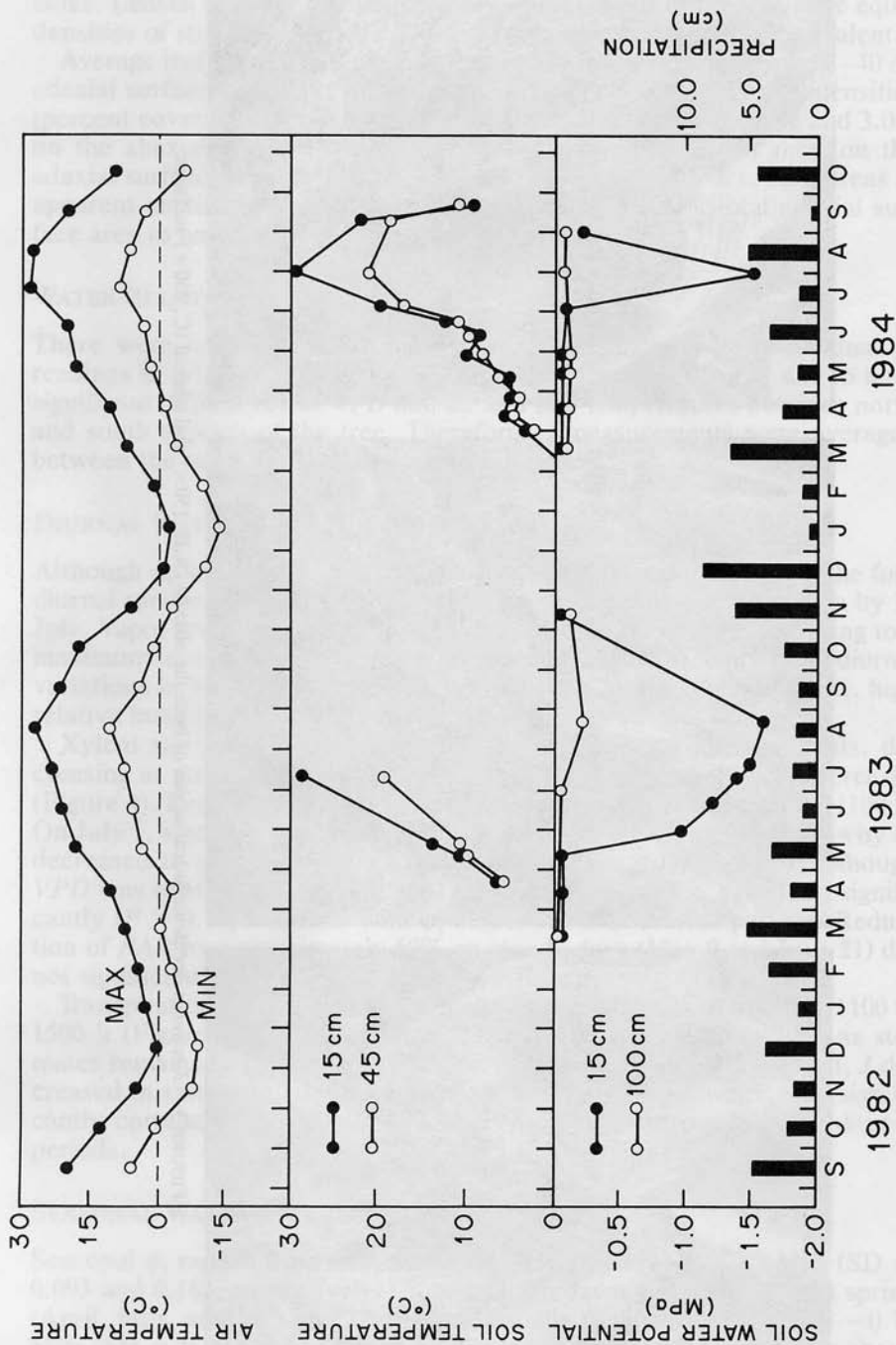


FIGURE 2. Seasonal climatic conditions on the Squaw Butte Experimental Range and soil water and temperature on the study site.

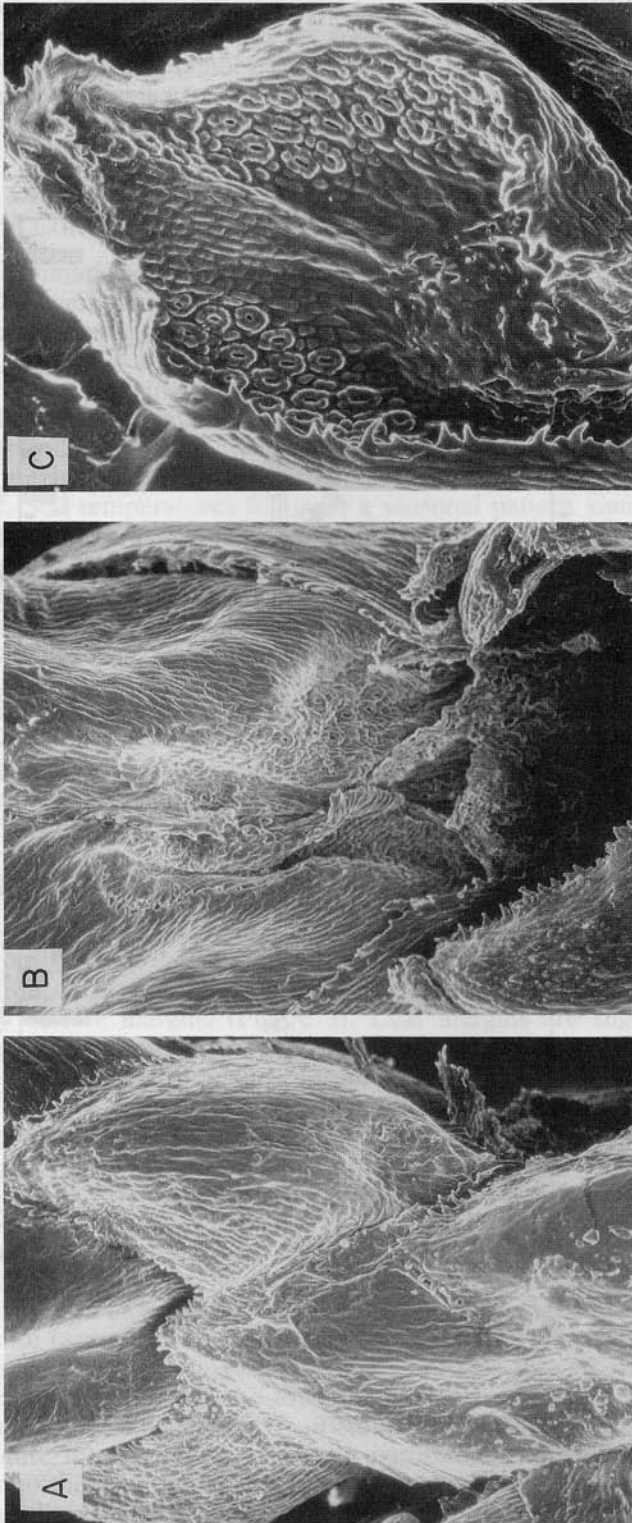


FIGURE 3. *Juniperus occidentalis* leaf scales of both the abaxial (A,B; 150 \times) and adaxial (C; 250 \times) surfaces.

cent epidermal cells while stomatal pores are slightly depressed below the plane of subsidiary cell walls.

Leaf position apparently does not affect stomatal size or stomatal densities. Leaves sampled from north and south portions of the tree have equal densities of stomates. Guard cell length and pore size are also equivalent.

Average leaf area is 1.78 mm² and stomatal numbers range from 36–40 on adaxial surfaces and 8–10 stomates on abaxial surfaces. Stomatal densities (percent coverage per mm²) average 12.3% on the adaxial surface and 3.0% on the abaxial surface. Stomatal frequencies are 21–22 per mm² on the adaxial surface, and 4.5–5.7 per mm² on the abaxial surfaces. Pore areas at apparent maximal stomatal openings range from 1.0% of total adaxial surface area to only 0.25% of the total abaxial surface area.

WATER RELATIONS

There were no significant differences ($P > 0.10$) between individual g_1 readings in relation to location on the tree. This was probably due to non-significant differences in VPD and air and leaf temperatures between north and south aspects of the tree. Therefore g_1 measurements were averaged between the north and south side of each tree.

DIURNAL WATER CYCLES

Although ψ_s was not limiting in the lower soil depths during any of the four diurnal runs in 1984, ψ_s in the upper 30 cm dropped below -1.5 MPa by 31 July. Vapor pressure deficits ranged from 2.16 to 27.5 g m⁻³ increasing to a maximum level by 1400 h for each diurnal run (Figure 4). Only small diurnal variations in VPD occurred on May 9 and June 21 due to cloud cover, high relative humidity, and cool air temperatures.

Xylem sap potentials were highest during predawn measurements, decreasing as atmospheric stress, VPD, PAR, and air temperatures increased (Figure 4). Leaf conductance was usually highest between 0800 and 1100 h. On July 1, stomates did not appear to fully open, which may explain why ψ_1 decreased to only -1.5 MPa (standard deviation (SD) = 0.101) although VPD was relatively high (27.5 g m⁻³). Diurnal changes in g_1 did not significantly ($P > 0.10$) correlate with ψ_1 across the four diurnal periods. Reduction of PAR by approximately 50% on cloudy days (May 9 and June 21) did not significantly ($P > 0.10$) influence daytime g_1 .

Transpiration, a product of VPD and g_1 , generally peaked between 1100 to 1500 h (Figure 4). During daylight, J increased with VPD as long as stomates remained at least partially open. However, as stomates closed, J decreased in spite of a continued increase in VPD. Transpiration was significantly correlated with ψ_1 ($P < 0.05$, $r = -0.83$) across the four diurnal periods.

SEASONAL WATER CYCLES

Seasonal ψ_1 ranged from a high of -0.5 MPa to a low of -2.7 MPa (SD = 0.093 and 0.163, respectively) (Figure 5). Predawn ψ_1 was highest in spring (April, May, and June) for both years, usually ranging from -0.5 to -0.75 MPa (SD = 0.093 and 0.095, respectively). At this time ψ_s was at or above field capacity throughout the soil profile, and VPD was generally below 15 g m⁻³. The only exception was May 23, 1983, when predawn ψ_1 dropped to -1.2 MPa (SD = 0.129). During the previous six days, maximum VPD

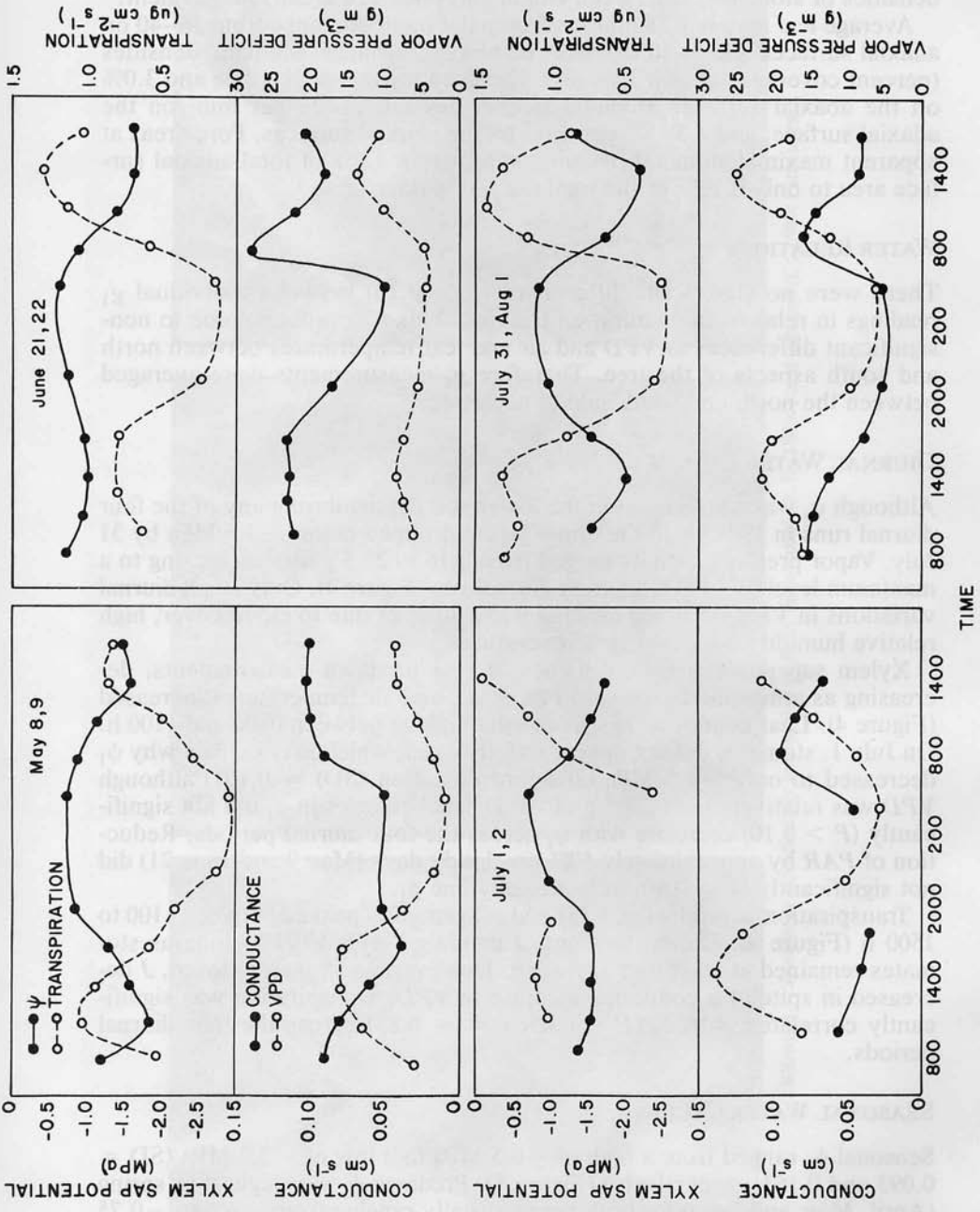


FIGURE 4. *Juniperus occidentalis* diurnal xylem sap potential (ψ_1), transpiration, leaf conductance, and vapor pressure deficit (VPD) in 1984. Data missing on July 1, 2 due to rain.

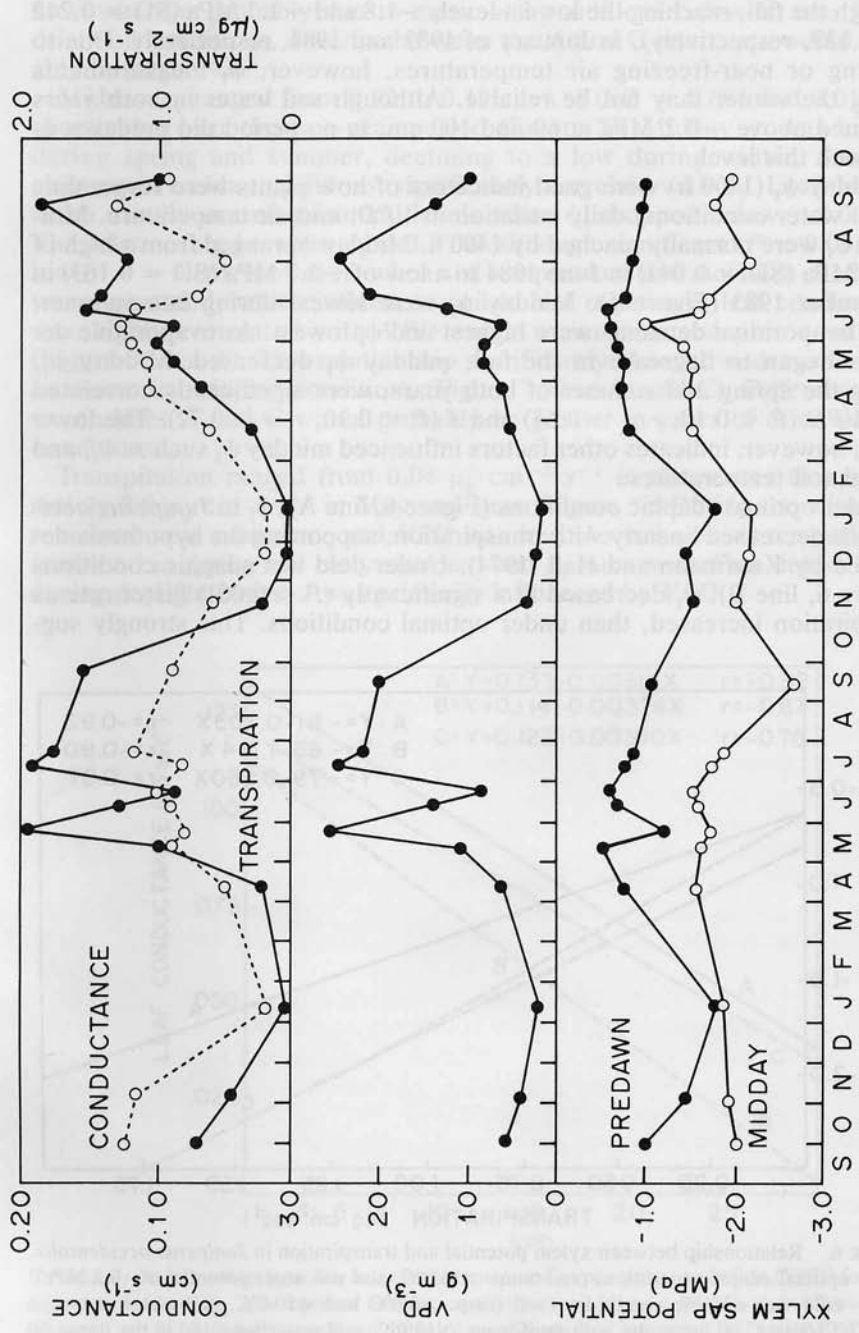


FIGURE 5. Seasonal plant water parameters and vapor pressure deficit (VPD) for *Juniperus occidentalis*.

levels averaged 25.6 g m^{-3} , well above the mean for this time of year. As daylength, daily VPD , and temperatures increased during the summers of 1983 and 1984, predawn ψ_1 decreased even though soil water at the lower depths remained near field capacity. Predawn ψ_1 continued to decline through the fall, reaching the lowest level, -1.8 and -1.7 MPa (SD = 0.242 and 0.137, respectively), in January of 1983 and 1984, respectively. Due to freezing or near-freezing air temperatures, however, ψ_1 measurements during the winter may not be reliable. Although soil water in both years remained above -0.2 MPa at 60 and 100 cm, in no period did predawn ψ_1 approach this level.

Midday ψ_1 (1400 h) were good indicators of how plants were responding to soil water conditions, daily variation in VPD , and air temperature. Minimum ψ_1 were normally reached by 1400 h. Midday ψ_1 ranged from a high of -1.0 MPa (SD = 0.041) in June 1984 to a low of -2.7 MPa (SD = 0.163) in September 1983 (Figure 5). Midday ψ_1 were lowest during late summer, when evaporative demands were highest and ψ_s lowest. As evaporative demands began to decrease in the fall, midday ψ_1 decreased. Midday ψ_1 , during the spring and summer of both years, were significantly correlated with VPD ($P < 0.10$, $r = -0.63$) and J ($P < 0.10$, $r = -0.72$). The low r value, however, indicates other factors influenced midday ψ_1 such as ψ_s , and air and soil temperatures.

Under optimal edaphic conditions (Figure 6, line A), ψ_1 in *Juniperus occidentalis* decreased linearly with transpiration, supporting the hypothesis developed by Kaufmann and Hall (1974). Under cold wet edaphic conditions (Figure 6, line B), ψ_1 decreased at a significantly ($P < 0.001$) faster rate as transpiration increased, than under optimal conditions. This strongly sug-

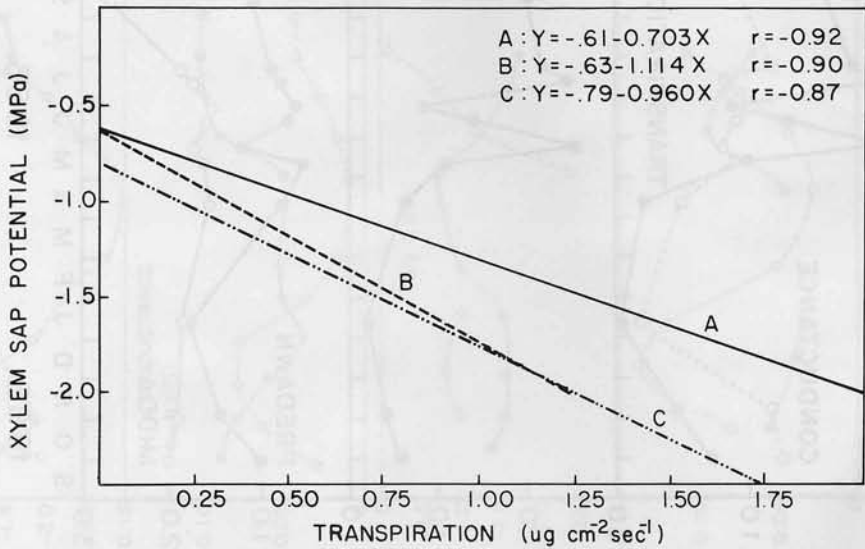


FIGURE 6. Relationship between xylem potential and transpiration in *Juniperus occidentalis*. A = optimal edaphic conditions (soil temp. $>10.0^\circ\text{C}$, and soil water potential ≥ -0.2 MPa); B = cold wet edaphic conditions (soil temp. $>0.0^\circ\text{C}$ and $\leq 10.0^\circ\text{C}$, soil water potential ≥ -0.2 MPa); C = warm dry soils (soil temp. $>10.0^\circ\text{C}$, soil water potential in the upper 60 cm ≤ -0.2 MPa). Slopes B and C are significantly different than A ($P \leq 0.001$); intercept C is significantly different than intercept A ($P \leq 0.001$), A and B intercepts are not significantly ($P \geq 0.10$) different (Neter and Wasserman 1974). A, $n = 33$, SD = 0.175; B, $n = 14$, SD = 0.184; C, $n = 10$, SD = 0.295; each n value is a mean of six measurements.

gests cold soil temperatures increase the soil-to-leaf resistance. Soil-to-leaf resistance also significantly increases ($P < 0.001$) as the upper 60 cm of the soil profile dries (Figure 6, line C). The decrease in predawn ψ_1 of only 0.18 MPa from line A to line C (intercept on the Y axis), during late summer, however, was probably due to mesic soil conditions below 60 cm. Under drier soil conditions, distance between the A and C intercepts would probably be larger.

Midday g_1 ranged from 0.02 to 0.13 cm s^{-1} (SD = 0.004 and 0.016, respectively) over the two-year period (Figure 5). Midday g_1 was highest during spring and summer, declining to a low during winter. Seasonal changes in midday g_1 did not significantly correlate with ψ_1 . Leaf conductance usually neared minimum levels when ψ_1 dropped below -2.0 MPa. The relationship between g_1 and VPD although significant ($P < 0.05$), was low ($r = -0.66$). However, when soil temperature and moisture conditions were separated, which influences soil-to-leaf resistance, leaf conductance was highly correlated with VPD under warm moist edaphic conditions (Figure 7, line A). This relationship significantly changed under cold moist or warm dry edaphic conditions (Figure 7, lines B and C). Differences between lines A and C would probably be greater in years of drier edaphic conditions.

Transpiration ranged from 0.04 $\mu_g \text{ cm}^{-2} \text{ s}^{-1}$ in the winter to approximately 2.0 $\mu_g \text{ cm}^{-2} \text{ s}^{-1}$ in May and June (Figure 5). During the winter, g_1 remained near minimum, and VPD was low. As soil and air temperatures increased in spring and early summer, and g_1 rates neared maximum levels during daylight hours, J was primarily influenced by VPD.

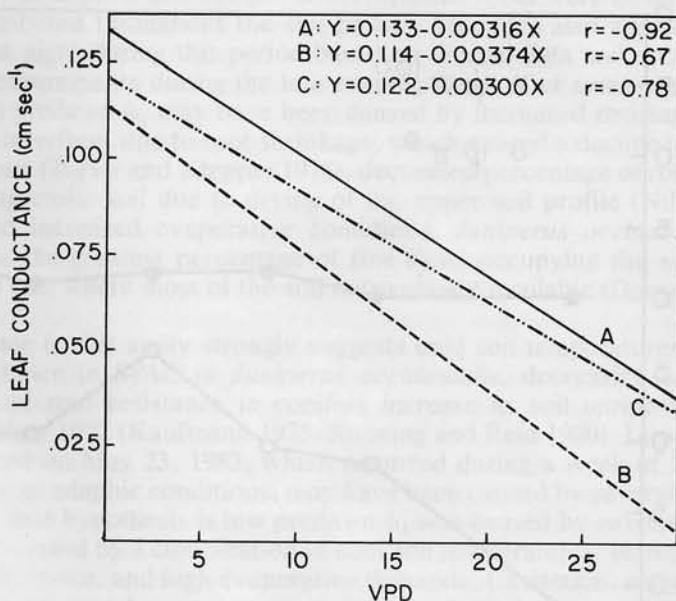


FIGURE 7. Relationship between leaf conductance and vapor pressure deficit (VPD) for *Juniperus occidentalis*. A = optimal edaphic conditions (soil temp. $>10.0^{\circ}\text{C}$, and soil water potential ≥ -0.2 MPa); B = cold wet edaphic conditions (soil temp. $>0.0^{\circ}\text{C}$ and $\leq 10.0^{\circ}\text{C}$, soil water potential ≥ -0.2 MPa); C = warm dry soils (soil temp. $>10.0^{\circ}\text{C}$, soil water potential in the upper 60 cm ≤ -0.2 MPa). Lines B and C are significantly ($P \leq 0.001$) different from A (Neter and Wasserman 1974). A, $n = 14$, SD = 1.108; B, $n = 10$, SD = 1.937; C, $n = 5$, SD = 1.145; each n value is a mean of six measurements.

Osmotic potential at full turgor ranged from -1.8 to -2.0 MPa (SD = 0.166 and 0.163 , respectively), and osmotic potential at zero turgor -2.4 to -4.2 MPa (SD = 0.131 and 0.306 , respectively) (Figure 8). Osmotic potential at full turgor varied little throughout the year while osmotic potential at zero turgor changed 1.8 MPa. In general, seasonal change in osmotic potential at zero turgor reflected a pattern similar to predawn ψ_1 , although osmotic potential at zero turgor reached a maximum later in the summer.

DISCUSSION

Juniperus leaves fit within a classic xeromorphic pattern (Oppenheimer 1970) in many aspects. Structural adaptations in leaf morphology of *Juniperus occidentalis* allow for maximum drought avoidance through low leaf area, low surface-to-volume ratios, thick cuticle layers, and protected stomates. The scale-like leaves of *Juniperus* are significantly more reduced in surface area than the majority of conifers that have elongated needle-like leaves (*Abies*, *Picea*, *Pinus*, *Taxus*, etc.). Stomates on both abaxial and adaxial surfaces are protected from light and freely moving air. Desiccation by wind, sunlight, and VPD may thus be reduced. In comparison, stomates in mesomorphic *Chamaecyparis* species are more or less equally distributed between leaf surfaces and are considerably more abundant (Zobel et al. 1978). Stomatal frequency in this species ranged from 51 – 69 per mm^2 , 3 and 12 times higher than the abaxial and adaxial sides, respectively, in *Juniperus occidentalis*. The reduced number of stomates in *Juniperus occidentalis* provides an additional measure of drought avoidance. Stomatal frequency

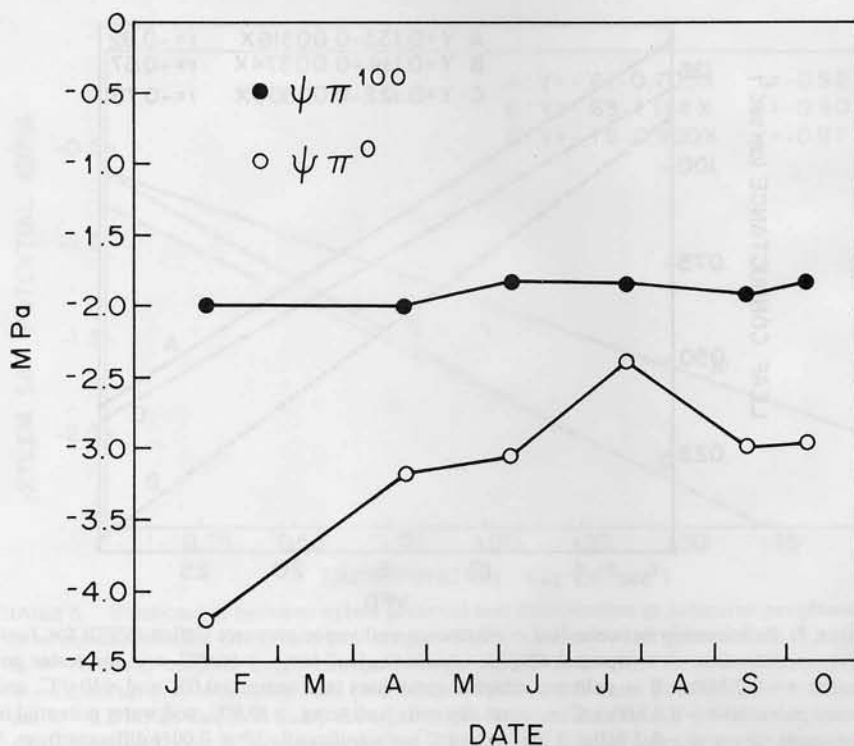


FIGURE 8. Osmotic potentials at full turgor ($\psi_{\pi 100}$) and zero turgor ($\psi_{\pi 0}$) in *Juniperus occidentalis*, 1984.

has been shown to have a high correlation with drought resistance in *Pinus taeda* (Knauf and Bilan 1974) as well as in *P. strobus* and *P. resinosa* (Davies et al. 1974). High boundary layer resistance around the stomates and reduced stomata numbers are probably primary factors causing relatively low levels of g_1 in *Juniperus occidentalis* as compared to other conifers. Although caution should be used in comparing g_1 values reported in the literature (Hinckley et al. 1978), mean maximum g_1 values for *Juniperus occidentalis* are lower (0.08 to 0.13 cm s^{-1}) than values reported for other coniferous species (0.12 to 0.40 cm s^{-1}) (Dysktra 1974, Fetcher 1976, Running 1976, 1980, Jarvis 1980, Murphy and Ferrell 1982, Yoder 1984). Differences in maximum g_1 values between *Juniperus occidentalis* and other conifers may be greater than these estimates because our data are based on only the exposed surface area of the leaf.

Although *Juniperus occidentalis* grows in a drier environment than many other conifers, diurnal and seasonal ψ_1 and g_1 respond similarly to environmental factors. Water status of this plant is influenced by water availability, atmospheric demand, and resistances that occur in the soil-plant-atmosphere continuum (SPAC).

Under optimum environmental conditions in the spring, ψ_1 in *Juniperus occidentalis* declined during the day as stomates opened and evaporative demands increased. Diurnal fluctuations in ψ_1 , occurring in plants grown under ideal conditions, can be explained by physical limitations of water movement through the plant (Kramer 1937, Klepper 1968, Kaufmann and Hall 1974). Seasonal differences between ψ_s and predawn ψ_1 also reflect resistances in water flux from soil to leaves. Predawn ψ_1 declined with the progression of summer drought, even though soil water remained available in the lower depths, and *Juniperus occidentalis* roots were observed to be well distributed throughout the soil profile. Stomates also appeared to be closing at night during this period based on diurnal data and spot conductance measurements during the late evening hours after sundown. The decrease in predawn ψ_1 may have been caused by increased resistance at the soil root interface, due to root shrinkage, which caused a decline in the root soil contact (Taylor and Klepper 1978), decreased percentage of root surface contacting moist soil due to drying of the upper soil profile (Nilsen et al. 1983) and increased evaporative conditions. *Juniperus occidentalis* may also have the greatest percentage of fine roots occupying the soil profile above 60 cm, where most of the soil nutrients are available (Doescher et al. 1986).

Evidence in this study strongly suggests cold soil temperatures increase the resistance in SPAC in *Juniperus occidentalis*, decreasing ψ_1 . Others have found root resistance in conifers increase as soil temperatures decrease below 10°C (Kaufmann 1975, Running and Reid 1980). Low predawn ψ_1 reported on May 23, 1983, which occurred during a week of high VPD and cool wet edaphic conditions, may have been caused by several possibilities. The first hypothesis is low predawn ψ_1 was caused by cavitation in the sapwood caused by a combination of cool soil temperatures, increasing soil-to-leaf resistance, and high evaporative demands. Cavitation, caused by the decline in sapwood water content, decreased predawn ψ_1 of Scots pine (*Pinus sylvestris*) under well-watered, high evaporative conditions (Waring et al. 1979). The second hypothesis is low predawn ψ_1 was caused by stomates remaining open at night during late spring. Although we have no data to support or disclaim this hypothesis, stomates were observed to remain

open during one set of porometer readings in the spring of 1982 at 2300 and 2400 h. This phenomenon has also been observed in Douglas-fir (*Pseudotsuga menziesii*) during bud break (Waring 1987, personal communication). In winter, if ψ_1 are reasonable estimates of water status, low predawn ψ_1 and midday g_1 are probably caused by restricted water flow, due to freezing soil temperatures, frozen stem water, and low air temperatures. Hickley et al. (1978) reported that continued water loss in winter months by forest trees, at minimum rates, eventually promoted low ψ_1 . Others have also reported that low predawn ψ_1 during the winter was a response to frozen soils and the inability of plants to recharge transpired water (Solo 1974, Lassoie and Dougherty 1976, Lassoie et al. 1983).

Stomates closed, with one exception (September 14, 1983), when ψ_1 dropped below -2.0 MPa. Similar results have been found in other conifers where stomates closed between -1.8 and -2.0 MPa (Hinckley et al. 1978), and -1.4 and -2.5 MPa (Lopushinsky 1969, Jarvis 1980). The poor correlation between g_1 and ψ_1 ($r = 0.12$) and the occurrence of closed stomates at $\psi_1 > -2.0$ MPa partially supports the threshold theory for *Juniperus occidentalis*. Under this theory stomates are normally unresponsive to ψ_1 until reaching some critical ψ_1 , which causes closure (Hsiao and Acevedo 1974, Jarvis 1980). Hinckley et al. (1983) concluded that stomatal closure occurred near the turgor loss point. Although stomates closed at ψ_1 near -2.0 MPa in *Juniperus occidentalis*, adjustment of g_1 did occur at $\psi_1 < -2.0$ MPa. Leaf conductance decreased with increasing VPD at a faster rate under conditions of cold soil temperatures or dry soils than under optimal edaphic conditions. Kaufmann (1982) concluded differences in absolute humidity between leaf and air to be a primary stomatal control factor.

Osmotic adjustment may be a primary mechanism by which *Juniperus occidentalis* adapts to drought conditions in late summer and winter. Reduction of osmotic potential at zero turgor during the summer would aid in turgor pressure maintenance as water content in the plant decreases (Turner and Jones 1980). Maintenance of turgor potential is essential for plant growth, continued root exploration and CO_2 fixation (Hsiao 1973).

CONCLUSIONS

Juniperus occidentalis is well adapted to growing under the semiarid conditions of the Great Basin. The absence of stomates on exposed leaf surfaces, thick cuticles, and reduced stomata density appear to be important mechanisms in reducing water loss through transpiration under high evaporative conditions. This may increase the competitive advantage of this plant by allowing it to display larger total leaf area for increased carbon fixation. The evergreen character of this species also allows it to display maximum leaf surface area during favorable growing conditions early in the spring.

It is clear no single factor influences g_1 . Leaf conductance was affected by soil temperature, soil moisture, and evaporative demands. Soil temperatures below 10°C appeared to limit water movement into and through the plant reducing ψ_1 and g_1 . Leaf conductance did not correlate with ψ_1 ; however, stomates usually closed when ψ_1 dropped below -2.0 MPa. *Juniperus occidentalis* has been thought to utilize soil water during the winter since it displays green leaves throughout the year. Water use during the winter, however, was minimal due to cold soil and air temperatures, low VPD, and minimum g_1 .

LITERATURE CITED

- ADAMS, M. S., and B. R. STRAIN. 1968. Photosynthesis in stems and leaves of *Cercidium floridum*: spring and summer diurnal field response and relation to temperature. *Oecol. Plant.* 3:285-295.
- BUCKHOUSE, J. C., and J. L. MATTISON. 1980. Potential soil erosion of selected habitat types in the high desert region of central Oregon. *J. Range Manage.* 33:282-285.
- BURKHARDT, J. W., and E. W. TISDALE. 1976. Causes of juniper invasion in southwestern Idaho. *Ecology* 57:472-484.
- CARAHER, D. L. 1978. The spread of western juniper in central Oregon. P. 3-7 in *Proc. western juniper ecology and management workshop*, R. E. Martinn et al. (eds.). USDA For. Serv. Gen. Tech. Rep. PNW-74.
- DAVIES, W. J., T. T. KOZLOWSKI, and K. J. LEE. 1974. Stomatal characteristics of *Pinus resinosa* and *Pinus strobus* in relation to transpiration and antitransparent efficiency. *Can. J. For. Res.* 4:571-574.
- DOESCHER, P. S., R. F. MILLER, and A. H. WINWARD. 1984. Soil chemical patterns under plant communities dominated by big sagebrush (*Artemisia tridentata*) in eastern Oregon. *J. Soil. Sci.* 48:659-663.
- DYSKTRA, G. F. 1974. Photosynthesis and carbon dioxide transfer resistance of lodgepole pine seedlings in relation to irradiance, temperature, and water potential. *Can. J. For. Res.* 4:201-206.
- EDDLEMAN, L. 1983. Some ecological attributes of western juniper. P. 32-34 in *Research in rangeland management*. Agric. Exp. Stan. Oregon State Univ., Corvallis Spec. Rep. 682.
- FETCHER, N. 1976. Patterns of leaf resistance to lodgepole pine transpiration in Wyoming. *Ecology* 57:339-345.
- HINCKLEY, T. M., J. P. LASOIE, and S. W. RUNNING. 1978. Temporal and spatial variations in the water status of forest trees. *For. Sci. Monogr.* 20. P. 72.
- HINCKLEY, T. M., ET AL. 1983. Drought relations of shrub species: Assessment of the mechanisms of drought resistance. *Oecology* 59:344-350.
- HSIAO, T. C. 1973. Plant responses to water stress. *Ann. Rev. Plant Physiol.* 24:519-70.
- HSIAO, T. C., and E. ACEVEDO. 1974. Plant responses to water deficits, water-use efficiency and drought resistance. *Agric. Meteorol.* 14:59-84.
- JARVIS, P. G. 1980. Stomatal response to water stress in conifers. P. 105-122 in *Adaptation of plants to water and high temperature stress*, N. C. Turner and P. J. Kramer (eds.). Wiley, New York.
- JOHNSON, T. N., JR. 1963. Anatomy of scalelike leaves of Arizona junipers. *Bot. Gaz.* 124:220-224.
- KAUFMANN, M. R. 1975. Leaf water stress in Engelmann spruce. *Plant Physiol.* 56:841-844.
- KAUFMANN, M. R. 1982. Leaf conductance as a function of photosynthetic photon flux density and absolute humidity differences from leaf to air. *Plant Physiol.* 69:1018-1022.
- KAUFMANN, M. R., and A. E. HALL. 1974. Plant water balance—its relationship to atmospheric and edaphic conditions. *Agric. Meteorol.* 14:85-98.
- KLEPPER, B. 1968. Diurnal patterns of water potential in woody plants. *Plant Physiol.* 43:1931-1934.
- KNAUF, T. A., and M. V. BILAN. 1974. Needle variation in loblolly pine from mesic and xeric seed sources. *For. Sci.* 20:88-90.
- KRAMER, P. J. 1937. The relation between rate of transpiration and rate of absorption of water in plants. *Am. J. Bot.* 24:10-15.
- LASSOIE, J. P., and P. M. DOUGHERTY. 1976. Fall and winter gas exchange rates in eastern red cedar. *Plant Physiol. Suppl.* 57:45.
- LASSOIE, J. P., ET AL. 1983. Ecophysiological investigations of understory eastern red cedar in central Missouri. *Ecol.* 64:1355-1366.
- LOPUSHINSKY, W. 1969. Stomatal closure in conifer seedlings in response to leaf moisture stress. *Bot. Gaz.* 130:258-263.
- MILLER, R. F., ET AL. 1986. Growth and internal water status of three subspecies of *Artemisia*

- tridentata*. P. 347–352 in *Biology of Artemisia and Chrysothamnus*, E. D. McArthur and B. Welch (eds.). USDA Interm For and Range Exp Sta Gen Tech Rep INT-200.
- MURPHY, E. M., and W. K. FERRELL. 1982. Diurnal and seasonal changes in leaf conductance, xylem water potential, and abscisic acid of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] France) in five habitat types. *For. Sci.* 28:627–638.
- NILSEN, E. T., ET AL. 1983. Diurnal and seasonal water relations of the desert phreatophyte *Prosopis glandulosa* (honey mesquite) in the Sonoran Desert of California. *Oecology* 64:1381–1393.
- OPPENHEIMER, H. R. 1970. Drought resistance of cypress and thuja branchlets. *Israel J. Bot.* 19:418–425.
- RICHARDSON, S. G., and C. M. MCKELL. 1980. Water relations of *Atriplex canescens* as affected by the salinity and moisture percentage of processed oil shale. *Agron. J.* 72:946–950.
- RUNNING, S. W. 1976. Environmental control of leaf water conductance in conifers. *Can. J. For. Res.* 6:104–112.
- RUNNING, S. W. 1980. Environmental and physiological control of water flux through *Pinus contorta*. *Can. J. For. Res.* 10:82–91.
- RUNNING, S. W., C. P. Reid. 1980. Soil temperature influences on root resistance of *Pinus contorta* seedlings. *Plant Physiol.* 65:635–640.
- SALO, D. J. 1974. Factors affecting photosynthesis in Douglas-fir. Ph.D. Diss., Univ. of Wash., Seattle. 150 p. Diss. Abstr. 35/08:3765-D.
- SCHOLANDER, P. F., ET AL. 1965. Sap pressure in vascular plants. *Science* 148:339–346.
- SLAYTER, R. O. 1961. Internal water balance of *Acacia aneura* F. Muell. P. 137–146 in *Relation to Environmental Conditions*. Madrid Symp. Plant-water relationships in arid and semiarid conditions. Proc. UNESCO, 1959.
- SWANSON, S. R. 1982. Infiltration, soil erosion, nitrogen loss and soil profile characteristics of Oregon lands occupied by three subspecies of *Artemisia tridentata*. Ph.D. Diss., Oregon State Univ., Corvallis. 140 p.
- TAYLOR, H. M., and KLEPPER, B. 1978. The role of rooting characteristics in the supply of water to plants. *Adv. Agron.* 30:99–128.
- TURNER, N. C., and M. M. JONES. 1980. Turgor maintenance by osmotic adjustment: A review and evaluation. P. 87–103 in *Adaptation of plants to water and high temperature stress*, N. C. Turner and P. J. Kramer (eds.). Wiley, New York.
- WARING, R. H., D. WHITEHEAD, and P. G. JARVIS. 1979. The contribution to stored water to transpiration in Scots pine. *Plant Cell Environ.* 2:309–319.
- WINWARD, A. H. 1970. Taxonomic and ecologic relationships of the big sagebrush complex in Utah. Ph.D. Diss., Univ. of Idaho, Moscow. 80 p.
- YODER, B. J. 1984. Comparative water relations of *Abies grandis*, *Abies concolor* and their hybrids. MS Thesis, Oregon State Univ., Corvallis. 110 p.
- ZOBEL, D. B., T. P. LIN, and V. T. LIU. 1978. Stomatal distribution on leaves of three species of chamaecyparis. *Taiwania* 23:1–6.