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Influence of Vapor Pressure Deficit and Soil Moisture on Gas Exchange of *Juniperus occidentalis*

Abstract

An unusual combination of meteorological events allowed comparison of gas exchange for juvenile and adult *Juniperus occidentalis* under contrasting conditions of soil moisture and vapor pressure during August 1987 and August 1988. Responses of carbon dioxide assimilation, leaf conductance, transpiration, and intercellular carbon dioxide concentrations to changes in photosynthetic photon flux density, leaf temperature, and xylem water potential were measured for juvenile and adult trees. Carbon dioxide assimilation was significantly higher for juveniles with high soil water. Adult assimilation and conductance for both juveniles and adults were not significantly different in 1987 and 1988. Similar diurnal curves of leaf conductance in 1987 and 1988 were associated with different amounts of transpiration because of high vapor pressure deficits in 1987 and low soil water in 1988. Although stomata of juvenile *J. occidentalis* were more responsive than adult stomata, juveniles did not restrict transpiration when vapor pressure deficits were high; adults had higher water-use efficiencies. With vapor pressure deficits > 3.5 kPa, fluctuations in leaf conductance of juvenile *J. occidentalis* indicated stomatal closure and reopening in ~ 20 minute cycles from 1000 to 1630 hr. Increases in air temperatures and vapor pressure deficits can be expected to have less effects on physiological processes of *J. occidentalis* than would variations in available soil moisture.

Introduction

Scenarios of future climatic change predict increasing air temperatures with concomitant increases in water vapor pressure deficits experienced by plants; patterns of precipitation and soil moisture are also predicted to change (Schlesinger and Mitchell 1987, Hansen *et al.* 1988, Manabe and Wetherald 1987). In a localized region, increased air temperatures may or may not be accompanied by decreased precipitation and soil moisture (Manabe and Wetherald 1987, Running and Nemani 1989). Information on the response of naturally established trees to unusual, but natural, combinations of soil moisture and vapor pressure deficits can provide insight as to which environmental factors are most limiting and how native species may respond to predicted alterations of climatic regimes.

An unusual precipitation event ($P < 0.001$) during July, 1987, produced 95 mm of precipitation at Redmond, OR, compared to the average July precipitation of 7.4 mm (NOAA 1982). During August 1987, a period of high air temperatures and high water vapor pressure deficits occurred while soil water content was higher ($P < 0.10$) than was soil water content during August, 1988, a summer with precipitation similar to the long term average at Redmond (NOAA 1982). Soil moisture was unusually high for almost a month prior to the

August 1987 measurements and was low for the month prior to the August 1988 measurements. This month long period of preconditioning allowed the trees used in this research to equilibrate with soil moisture conditions.

Mean maximum and mean minimum air temperatures were similar for the month preceding the measurements in 1987 and 1988 (Miller *et al.* 1992). However, the extreme maximum air temperature of 42.5 °C on 10 Aug 87 was considerably above the highest August mean maximum air temperature of 30 ± 3.6 °C measured at Redmond, OR, from 1951 to 1980 (NOAA 1982). This combination of unusual precipitation and extreme air temperature produced experimental conditions that allowed comparison among *Juniperus occidentalis*, which were in a similar phenological stage at the same field site, under contrasting environmental regimes of high soil moisture and high vapor pressure deficits in August, 1987, versus low soil moisture and relatively low vapor pressure deficits in August, 1988.

Data for the two August periods, which focused on small trees with juvenile foliage and large trees with adult foliage, were part of a larger 15 month study on the seasonal course of physiological processes for *J. occidentalis* (Miller *et al.* 1992). Analysis of the two August data sets indicated contrasting patterns of physiological responses that provided the opportunity to explore the plasticity

of naturally established trees by focusing on a detailed analysis and comparison of diurnal responses of juvenile and adult trees. Presentation of this type of detailed analysis was not possible for the total 15 month data set. The two August periods were chosen because they contained interesting contrasts in plant responses to differing environmental conditions.

Juniperus occidentalis Hook. subsp. *occidentalis* is a native North American conifer that has spread and increased in density in eastern Oregon during the last 100 years (Dealy *et al.* 1978). Under the present climatic regime, *J. occidentalis* currently occupies 1,145,000 ha in central Oregon (Dealy *et al.* 1978); it has successfully invaded non-degraded communities and communities degraded by grazing animals and by fire suppression (Young and Evans 1981). The tolerance of *J. occidentalis* to low soil moisture and high vapor pressure deficits may determine its ability to withstand increases in air temperatures and decreases in precipitation predicted with increased levels of greenhouse gasses and may effect its ability to continue to spread and increase in density in eastern Oregon.

Objectives of this research were to measure the response of carbon dioxide assimilation, leaf conductance, and intercellular carbon dioxide concentrations to changes in photosynthetic photon flux density, leaf temperature, and xylem water potential as the result of contrasting combinations of soil moisture and ambient vapor pressure deficits.

Methods

The research site, located 12.8 km west of Redmond, Oregon (44° 16' N, 121° 20' W), is a gentle, west-facing slope at 1050 m elevation. The soil is a well drained loamy-skeletal, Aridic Haploxeroll derived from Mazama volcanic ash over tuff, with a uniform silty loam texture down to a hard pan at about 70 cm. Annual precipitation at Redmond averages 217 mm, 89% of which occurs from October to June (NOAA 1982). The plant community at the research site was similar to the *Juniperus/Artemisia/Agropyron-Chaenactis* association described by Driscoll (1964).

Juniperus occidentalis has needle-like juvenile leaves which are replaced by scale-like adult leaves as the plant matures (de Laubenfels 1953). Trees with only juvenile foliage may be up to 26 yrs old and over 1 m tall (Miller *et al.* 1990). Two juveniles

and 2 adults were measured in 1987 and 4 juveniles and 4 adults in 1988. Juveniles had 100% juvenile foliage and were 30 to 60 cm tall; the estimated height of adults was 4 to 4.5 m. Juveniles large enough to support diurnal sampling were located first and adults growing near-by were selected, based on proximity and the requirement that the south side of the tree be in full sun through the day. Branchlets used for physiological measurements were on the south side of the tree, 10 cm to 1.5 m above the ground surface.

Diurnal measurements of physiological processes were made on 8 and 10 August 1987 and on 2 and 3 August 1988. This paper will focus on 10 August 1987 when each tree was measured 36 times during the day with conditions of high soil moisture and high vapor pressure deficits (H) and on 2 August 1988 when each tree was measured 15 times with conditions of low soil moisture and low vapor pressure deficits (L).

Carbon dioxide assimilation and relative humidity were measured using an Analytical Development Corporation I.CA-2 portable infrared gas analyzer system and a PLC(C) Parkinson leaf chamber with a volume of 137 cm³. Leaf conductance, transpiration, intercellular carbon dioxide concentrations, and water vapor pressure deficits inside the cuvette were calculated. Photon flux density (400-700 nm) was measured with a LiCor 190 SB quantum sensor; leaf and air temperatures were measured with fine gauge copper/constantan thermocouples and a Campbell Scientific CR 10 data logger. Vapor pressure deficits in the cuvette were calculated using leaf temperatures measured in the cuvette. Xylem water potentials were measured with a PMS Instruments pressure chamber. Data were reduced using a BASIC program (Miller 1990) based on equations from Wexler (1976, 1977), Nobel (1983), Campbell (1986), and Ball (1987). Soil moisture was measured gravimetrically during each measurement period (Hillcl 1971).

Similar amounts of foliage tissue were used for gas exchange measurements in both years; dry mass of juvenile foliage was 0.3458 g in 1987 and 0.3326 g in 1988; dry mass of adult foliage was 0.5115 g in 1987 and 0.5052 g in 1988. The tissue was produced during the period of rapid branchlet elongation from May through early August (Miller *et al.* 1992). The same tissue was measured repeatedly throughout the day. Carbon dioxide assimilation, leaf conductance, and transpiration data were presented on a dry mass basis

because measurements of dry mass were considered more accurate than leaf area measurements (Miller *et al.* In prep). Daily totals of carbon dioxide assimilation per gram of foliage were calculated by integrating under measured diurnal curves.

Significance of differences between a single observation and a sample mean was determined using a special case of the Student's *t*-test (Sokal and Rohlf 1981). Diurnal response curves of physiological processes between years were compared using two-tailed Mann-Whitney tests (Zar 1984, Potvin *et al.* 1990). For each Mann-Whitney test, the data on one process, i.e., carbon dioxide assimilation for juvenile *J. occidentalis* in 1987 and in 1988, were ranked; a separate test was used to compare the same process for large-adults in 1987 and in 1988. Statistical significance levels were set at $P < 0.05$, but probabilities levels greater than 0.05 are reported because biological significance and statistical significance are not always synonymous.

Results

During the four month period prior to the August measurements, precipitation at Redmond, OR, was 146 mm in 1987 and 63 mm in 1988; the average precipitation for April through July is 63 mm at Redmond (NOAA 1982). Gravimetric soil water content was higher on 10 Aug 87 than 2 Aug 88 ($P < 0.10$). Water contents at 0-5, 10-15, 25-30, and 45-50 cm depths were 1.53, 9.2, 11.1, and 7.5% on 10 Aug 87 and 0.8, 4.2, 5.4, and 6.1% on 2 Aug 88.

Diurnal curves of photosynthetic photon flux density ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$, *PFD*) on 10 Aug 87 and 2 Aug 88 were similar, but daytime air temperatures and water vapor pressure deficits were significantly higher during the 10 Aug 87 measurement period ($P < 0.003$ and 0.05 , respectively) (Fig. 1A). Leaf temperatures for juvenile and adult *J. occidentalis* in the cuvette were also significantly higher on 10 Aug 87 than 2 Aug 88 ($P < 0.03$, and < 0.05 , respectively). During the 10 Aug 87 measurements, maximum leaf temperatures were > 35 °C and water vapor pressure deficits in the cuvette were > 4 kPa from 1130 to 1600 hr.; while on 2 Aug 88 maximum leaf temperatures were < 33 °C, through the day and water vapor pressure deficits in the cuvette were > 4 kPa only from 1430 to 1530 hr (data not shown). The letters H and L will be used to remind the

reader that soil moisture and vapor pressure deficits were high on 10 Aug 87 and low on 2 Aug 88.

The highest rates of carbon dioxide assimilation, $17.2 \text{ nmol g}^{-1} \text{ s}^{-1}$, were measured for juvenile *J. occidentalis* on 10 Aug 87 (H). Diurnal curves of assimilation for juveniles was significantly higher on 10 Aug 87 (H) than 2 Aug 88 (L) ($P < 0.02$) (Fig. 1B), and daily total carbon dioxide assimilation was 71% higher on 10 Aug 87 (H) than on 2 Aug 88 (L), $425 \mu\text{mol g}^{-1} \text{ d}^{-1}$ versus $248 \mu\text{mol g}^{-1} \text{ d}^{-1}$.

The highest carbon dioxide assimilation for adults, $10.5 \text{ nmol g}^{-1} \text{ s}^{-1}$ was also measured on 10 Aug 87 (H), but the highest rate for 2 Aug 88 (L) was only slightly lower, $10.1 \text{ nmol g}^{-1} \text{ s}^{-1}$. Statistical tests did not indicate a significant difference in diurnal curves of assimilation in adults on 10 Aug 87 (H) and 2 Aug 88 (L) because rates during the morning were similar (Fig. 1B). However, during the afternoon of 10 Aug 87 (H) carbon dioxide assimilation remained at levels similar to those measured during the morning; on 2 Aug 88 (L) assimilation declined steadily after 1200 h. Therefore, total daily carbon dioxide assimilation for adults was 25% greater on 10 Aug 87 (H) than on 2 Aug 88 (L), $356 \mu\text{mol g}^{-1} \text{ d}^{-1}$ versus $284 \mu\text{mol g}^{-1} \text{ d}^{-1}$.

Diurnal curves of intercellular carbon dioxide concentrations (c_i) for juvenile and adult *J. occidentalis* were significantly lower on 10 Aug 87 (H) than 2 Aug 88 (L) ($P < 0.002$ and 0.001 , respectively). In both years, the lowest c_i were measured for adults, $282 \mu\text{mol}$ on 10 Aug 87 (H) and $308 \mu\text{mol}$ on 2 Aug 88 (L) (Fig. 1c).

Patterns of the response of carbon dioxide assimilation to the diurnal course of photosynthetic photon flux density, 400-700 nm (*PFD*) for juvenile *J. occidentalis* (Fig. 2A) were more dissimilar on 10 Aug 87 (H) and 2 Aug 88 (L) than were the patterns for adults during the two measurement periods (Fig. 2B). The high juvenile assimilation rates measured on 10 Aug 87 (H) were not present with similar levels of *PFD* on 2 Aug 88 (L). Adult carbon dioxide assimilation was similar in the morning in both years, but no afternoon hysteresis occurred on 10 Aug 87 (H); therefore, the response of assimilation to *PFD* for adult *J. occidentalis* was similar in the morning and afternoon during 10 Aug 87 (H).

Carbon dioxide assimilation for juvenile *J. occidentalis* was 80% of maximum with leaf

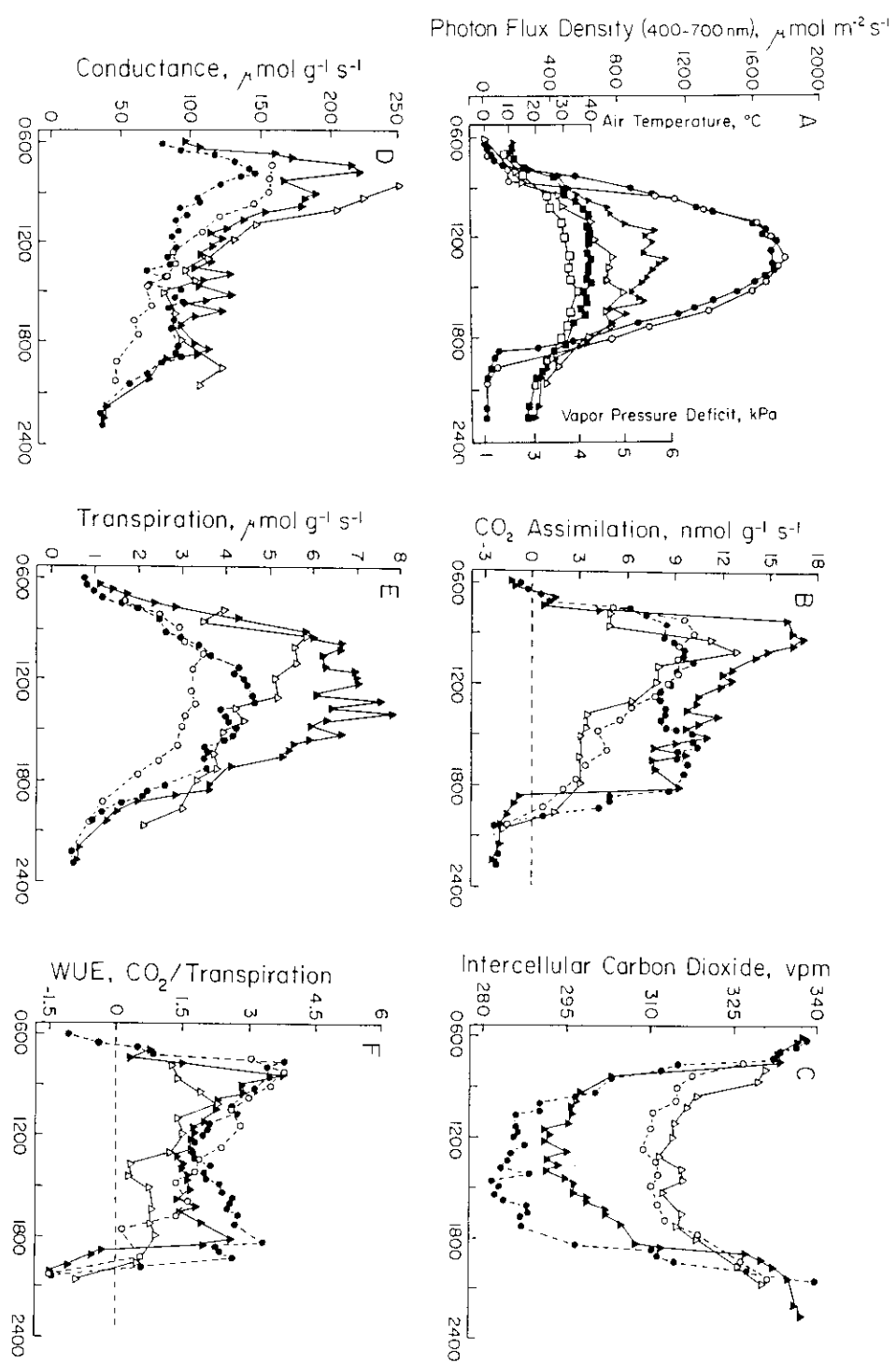


Figure 1. The diurnal course of (A) photosynthetic photon flux density (400-700 nm) ($\mu\text{mol m}^{-2} \text{s}^{-1}$) on August 10, 1987 (●) and August 2, 1988 (○), of air temperature ($^{\circ}\text{C}$) Aug 10-87 (■) and Aug 2-88 (□), and of vapor pressure deficit (kPa) Aug 10-87 (▲) and Aug 2-88 (△). The diurnal course of (B) carbon dioxide assimilation, (C) intercellular carbon dioxide, (D) leaf conductance, (E) transpiration, and (F) water use efficiency (WUE) of juvenile *J. occidentalis* on Aug 10-87 (▲) and Aug 2-88 (△) and of adults on Aug 10-87 (●) and Aug 2-88 (○).

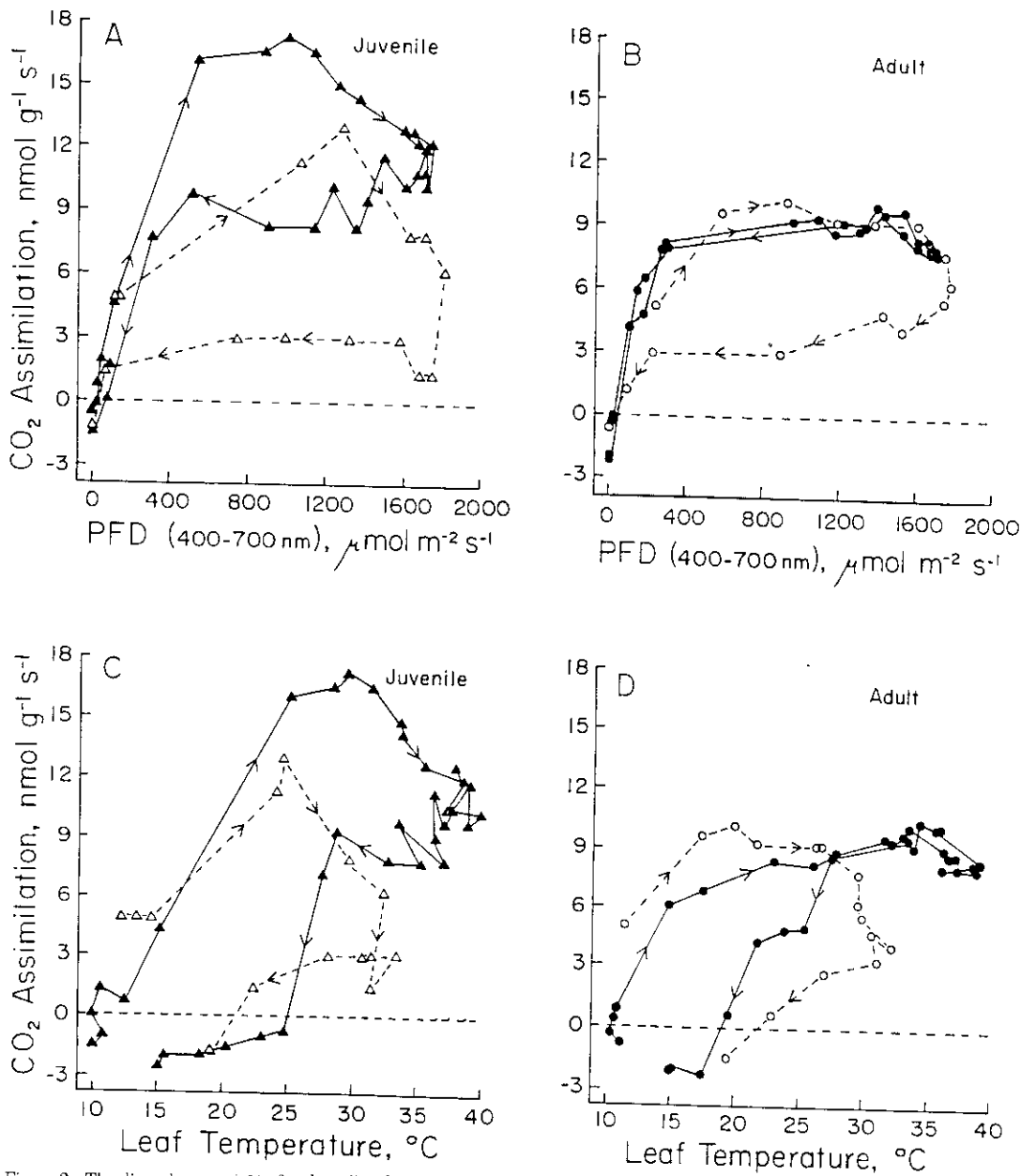


Figure 2. The diurnal course (→) of carbon dioxide assimilation ($\text{nmol g}^{-1} \text{s}^{-1}$) as a function of (A and B) photon flux density (400-700 nm PFD, $\mu\text{mol m}^{-2} \text{s}^{-1}$) and (C and D) leaf temperature ($^{\circ}\text{C}$) of juvenile *J. occidentalis* on Aug 10-87 (\triangle) and Aug 2-88 (\blacktriangle) and of adults on Aug 10-87 (\circ) and Aug 2-88 (\bullet).

temperatures of 23-34.5 $^{\circ}\text{C}$ on 10 Aug 87 (H) (Fig. 2C) and with temperatures of 23-27 $^{\circ}\text{C}$ on 2 Aug 88 (L) (Fig. 2D). For adults, assimilation was 80% of maximum over a broader range of leaf temperatures, 22-39 $^{\circ}\text{C}$ on 10 Aug 87 (H) and 15-29 $^{\circ}\text{C}$ on 2 Aug 88 (L).

Maximum leaf conductances (stomatal plus cuticle and boundary layer) for juveniles were 222 and 253 $\mu\text{mol g}^{-1} \text{s}^{-1}$ on 10 Aug 10 (H) and 2 Aug 88 (I), respectively; maximum conductances for adults were 145 and 157 $\mu\text{mol g}^{-1} \text{s}^{-1}$ for the two August measurements (Fig. 1D). Diurnal leaf

conductance curves for juvenile and for adult *J. occidentalis* were similar during the two years; however, juvenile diurnal transpiration was significantly higher on 10 Aug 87 (H) than on 2 Aug 88 (L) ($P < 0.02$) (Fig. 1E) as the result of differences in vapor pressure deficit (Fig. 1A). Transpiration for adults was also higher on 10 Aug 87 (H) than 2 Aug 88 (L) ($P < 0.16$) (Fig. 1E). Total daily transpiration was 35% higher for juvenile *J. occidentalis* on 10 Aug 87 (H) than 2 Aug 88 (L), 252 $\text{mmol g}^{-1} \text{d}^{-1}$ versus 187 $\text{mmol g}^{-1} \text{d}^{-1}$, and 32% higher for adults, 162 $\text{mmol g}^{-1} \text{d}^{-1}$ versus 122 $\text{mmol g}^{-1} \text{d}^{-1}$.

The diurnal pattern of leaf conductance plotted against water vapor pressure deficits for juvenile and adult *J. occidentalis* on 10 Aug 87 (H) indicated a pattern of stomatal closure and reopening during approximately 20 minute cycles from 1100 to 1630 hr (Fig. 3A and 3B), when water vapor pressure deficits were > 3.5 kPa. On 2 Aug 88 (L), leaf conductance declined more rapidly over a narrower range of water vapor pressure deficits and the pattern of cyclical stomatal closure was less pronounced than on 10 Aug 87 (H) (Fig. 3A and 3B).

Xylem water potentials for juvenile and adult *J. occidentalis* were significantly less negative throughout the day on 10 Aug 87 (H) than 2 Aug 88 (L) ($P < 0.001$ and 0.003, respectively). Pre-dawn and mid-day xylem water potentials were -0.5 and -2.2 MPa and -0.4 and -1.95 MPa, respectively, for juvenile and adult *J. occidentalis* on 10 Aug 87 (H). On 2 Aug 88 (L) pre-dawn and mid-day potentials were -2.4 and -4.1 MPa for juvenile and -2.0 and -3.3 for adult trees.

On 10 Aug 87 (H), the diurnal response of leaf conductance to whole plant water status, as measured by xylem water potentials, indicated repeated stomatal closure and reopening within a narrow range of xylem water potentials, -1.6 to -2.2 MPa for juvenile (Fig. 3C) and -1.1 to -1.95 MPa for adult *J. occidentalis* (Fig. 3D). The range of conductance values on 2 Aug 88 (L) was similar to the range measured on 10 Aug 88 (H) for both juvenile and adult *J. occidentalis*, but oscillations were not observed on 2 Aug 88 (L).

Juvenile water-use efficiency (carbon dioxide assimilation/transpiration, *WUE*) was significantly higher on 10 Aug 87 (H) than on 2 Aug 88 (L) ($P < 0.001$) (Fig. 1F). On 10 Aug 87 (H) adult *WUE* had a bimodal pattern with peaks in the

morning and afternoon; on 2 Aug 88 (L) adult *WUE* declined steadily throughout the day (Fig. 1F), but the diurnal curves were not significantly different ($P < 0.24$).

Discussion

Physiological processes for juvenile *J. occidentalis* in eastern Oregon were more responsive to environmental conditions than were similar processes for adult trees. Carbon dioxide assimilation for juveniles varied 71% more with the measured range of *PDF* and 74% more with the measured range of leaf temperatures than did assimilation for adults. Leaf conductance for juveniles was 39% and 26% more variable with the measured range of vapor pressure deficits and xylem pressure potentials than was conductance for adults.

The lack of hysteresis in the response of adult *J. occidentalis* assimilation to *PDF* on 10 Aug 87 (H) indicated that, with adequate soil moisture, high rates of adult carbon dioxide assimilation were maintained throughout the day, declining only when light levels were below $300 \mu\text{mol m}^{-2} \text{s}^{-1}$.

The similarity of diurnal curves of conductance on 10 Aug 87 (H) and 2 Aug 88 (L) in both juvenile and adult *J. occidentalis* indicated a similar degree of stomatal opening on both days despite differences in soil water and vapor pressure deficits during the two August periods. Daily transpirational loss of water appeared to be controlled more by environmental conditions of soil moisture availability and vapor pressure deficit than by the physiological mechanism of stomatal opening and closing.

The cyclical response of juvenile *J. occidentalis* conductance on 10 Aug 87 (H) when *VPD* was > 4 kPa may indicate a feed forward response of stomata (Cowan 1977, Farquhar 1978) to high vapor pressure deficits or may be caused by an overshoot in leaf water content or by CO_2 feedback loops controlling stomatal aperture (Weyers and Meidner 1990). However, cycles of stomatal closure on 10 Aug 87 (H) were not sufficient to reduce carbon dioxide assimilation or transpiration of juvenile *J. occidentalis*. Integrating under the 10 Aug 87 (H) diurnal curves with and without the reductions resulting from stomatal closure indicated only a 5% reduction in daily assimilation and a 3% reduction in transpiration due to stomatal closure. The cycle pattern of juvenile stomatal closure was not evident on 2 Aug 88 (L) even though

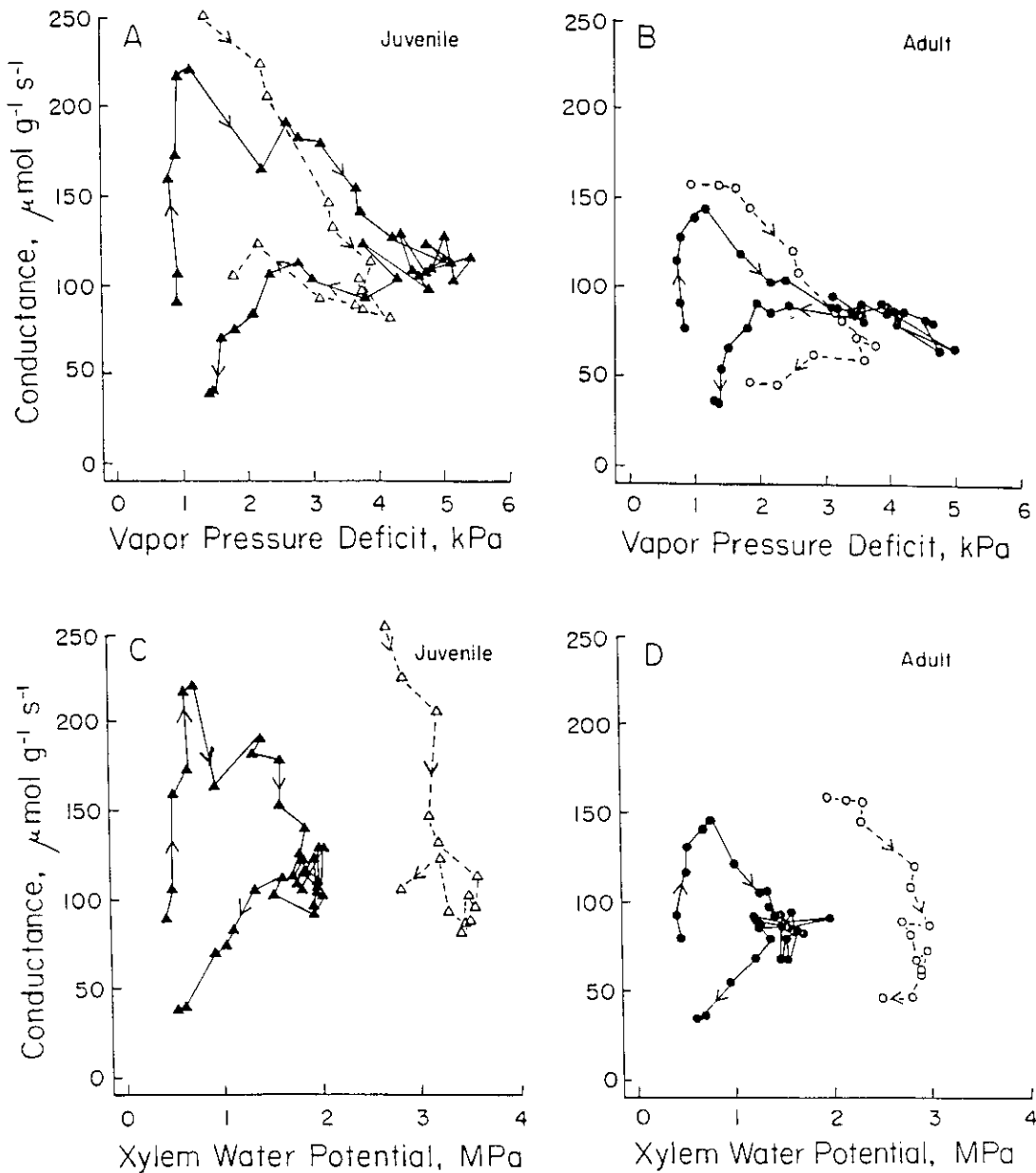


Figure 3. The diurnal course (\rightarrow) of leaf conductance ($\mu\text{mol g}^{-1} \text{s}^{-1}$) with (A and B) vapor pressure deficit (kPa) and (C and D) xylem water potential (MPa) of juveniles *J. occidentalis* on Aug 10-87 (\blacktriangle) and Aug 2-88 (\triangle) and of adults on Aug 10-87 (\bullet) and Aug 2-88 (\circ).

the average soil moisture at 0-50 cm depth was 44% lower and pre-dawn xylem pressure potentials were almost 5x more negative than on 10 Aug 87 (H).

Stomata of adult *J. occidentalis* did not appear to have the same feed forward response to vapor

pressure deficits as was measured in juveniles. Location of adult leaf stomata on the adaxial surface, not exposed to air movement, and on the abaxial surface, covered by the adjacent scale leaf (Miller and Shultz 1987), may reduce the sensitivity of the response of adult leaf conductance to high vapor pressure deficits.

An additional trigger for stomatal closure may be generated by a regulatory coupling of the rate of foliar water loss with the moisture environment of roots (Bates and Hall 1981, Gollan *et al.* 1985). Differences in the response of leaf conductance to high vapor pressure deficits in juvenile and adult *J. occidentalis* on 10 Aug 87 (H) may be related to the larger volume of soil available for water extraction by the extensive root system of adult *J. occidentalis*. Water supply from adult roots may have kept up with evaporative demand on 10 Aug 87 (H), while signals from the smaller juvenile root system triggered cyclical stomatal closure to more closely balance supply and demand. Therefore, the cyclical patterns of stomatal closure and resulting fluctuations in carbon dioxide assimilation and conductance were less pronounced in adults than juveniles on 10 Aug 87 (H). Reich and Hinckley (1989) concluded that leaf conductance of *Quercus marilandica* and *Quercus rubra* was controlled by root or soil water potential and speculated that differences in their fine roots systems or cavitation affected plant hydraulic conductance when soils were dry.

Although stomata of juvenile *J. occidentalis* were more responsive than adult stomata to vapor pressure deficits and xylem water potentials, juveniles did not restrict transpiration when vapor pressure deficits were high. Assimilation rates of juveniles were not high enough to compensate for their high transpiration; adult *J. occidentalis* with less responsive stomata and lower rates of assimilation had higher *WUE* on 10 Aug 87 (H) than did juveniles.

It has been suggested that carbon dioxide assimilation and leaf conductance do not respond in parallel to temperature (Morison 1987). In *Agropyron desertorum*, conductance did not change greatly with leaf temperature, so changes in assimilation rates were attributed to direct effects of temperature (Nowak *et al.* 1988). On 10 Aug 87 (H), the correlation between assimilation and leaf temperature was stronger for juvenile and adult *J. occidentalis* ($r^2 = 0.58$ and 0.71 , respectively) than was the correlation between leaf conductance and leaf temperature ($r^2 = 0.02$ and 0.005 , respectively). However on 2 Aug 88 (L), the pattern was reversed; the correlation between carbon dioxide assimilation and leaf temperature for juvenile and

adults was low ($r^2 = 0.0005$ and 0.004 , respectively), and the correlation between leaf conductance and leaf temperature was higher ($r^2 = 0.66$ and 0.36 , respectively). For *J. occidentalis* the effects of temperature on assimilation and leaf conductance appears to be influenced by soil moisture availability, but high leaf temperatures of up to 39°C did not appear to have a direct effect on assimilation.

Processes of carbon dioxide assimilation and leaf conductance do not appear to be strongly coupled in juvenile and adult *J. occidentalis* at the research site in eastern Oregon; they responded independently to variations in air temperature, vapor pressure deficits, and soil moisture. The positive effect of high soil water in August was a more important factor influencing carbon dioxide assimilation in *J. occidentalis* than were the negative effects of vapor pressure deficits > 4 kPa on stomatal closure and leaf conductance.

Conclusions

Juvenile and adult *J. occidentalis* in eastern Oregon are able to tolerate a wide range of leaf temperatures and vapor pressure deficits. Periods of above average temperatures and vapor pressure deficits, if associated with adequate soil moisture, should not adversely affect their physiological processes. Established adult trees are more buffered against variations of soil moisture than are juveniles. The responsiveness of juvenile *J. occidentalis* to soil moisture is advantageous under favorable conditions. However, the depression of juvenile assimilation and the relative inability of their stomata to restrict water loss when soil water resources are limited may reduce their establishment, competitive ability, and the spread of *J. occidentalis* in eastern Oregon during periods of reduced precipitation.

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