

ROBERT NORRIS ADDINGTON

Water Use Patterns and Stomatal Responses to Environment in Longleaf Pine on
Contrasting Sites

(Under the Direction of LISA DONOVAN)

Plants growing in different environments may require variable stomatal behavior to regulate their water loss. This study investigated how variation in water supply at two contrasting sites influenced water use and stomatal responses to environment in mature longleaf pine (*Pinus palustris* Mill.). At low vapor pressure deficits (D), maximum rates of leaf stomatal conductance (g_s), photosynthesis (A_{net}), sap-flux scaled transpiration (E_L), and mean canopy stomatal conductance (G_{Si}) were higher for trees on a sandy (xeric) site relative to trees on a sandy-loam (mesic) site in southwest Georgia, USA. Trees on the xeric site, however, showed a more sensitive stomatal closure response to increasing D, and a greater increase in instantaneous water use efficiency from morning to afternoon relative to mesic site trees. Use of a multiplicative model that incorporated global solar radiation (R_g), D, and leaf water potential (Ψ_L) explained an average 71% of the variation in G_{Si} on the mesic site and 76% on the xeric site, and indicated that soil water limitation played a more important role in regulating G_{Si} on the xeric site. Enhanced stomatal sensitivity to D in xeric site trees is consistent with higher rates of stomatal conductance at low D, and may be necessary in avoiding critically low Ψ_L associated with the soil moisture limitation. Other factors that may contribute to the site-differences in maximum leaf gas exchange include leaf nitrogen and/or tree height.

INDEX WORDS: *Pinus palustris*, stomatal sensitivity, drought, soil texture

WATER USE PATTERNS AND STOMATAL RESPONSES TO ENVIRONMENT IN
LONGLeAF PINE ON CONTRASTING SITES

by

ROBERT NORRIS ADDINGTON

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ROBERT NORRIS ADDINGTON

Approved:

Major Professor: Lisa Donovan

Committee: Robert Mitchell
Timothy Harrington

Electronic Version Approved:

Gordhan L. Patel
Dean of the Graduate School
The University of Georgia
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CHAPTER 1
INTRODUCTION

Many plants are capable of existing across habitats that differ in soil water supply. Longleaf pine (*Pinus palustris* Mill.) is a species native to the Coastal Plain of the southeastern U.S. that occupies a wide ecological gradient (Christensen 1988). Its distribution across gradients is dictated by the frequency of fire, which serves to exclude hardwood competitors (Ware et al. 1993). Where fire is maintained, *P. palustris* persists across a range of site-types, from sandhills characterized by deep, sandy soils, to flatwoods with finer textured soils often underlain by dense clay layers (Myers 1990). Changes in soil texture across these sites influence the supply of soil water and may present trees with very different challenges regarding water acquisition and transport and the maintenance of favorable water status and gas exchange. These challenges are negotiated largely through the action of stomata, which function to regulate plant water loss.

Water movement through the soil-plant-atmosphere continuum occurs along a gradient of declining water potential that originates in the atmosphere. Leaf water potential declines as the water vapor pressure gradient between the sub-stomatal cavity and the air immediately surrounding the leaf increases, creating a water potential gradient from leaf to root to soil that drives the flow of water along the continuum. Stomatal conductance is dependent upon a continuous supply of water to the leaves, and stomatal closure responses are often correlated with decreases in hydraulic conductance along the soil-leaf pathway (Sperry et al. 1993, Andrade et al. 1998, Hubbard et al. 1999, Meinzer et al. 1999). Although the mechanisms through which stomata sense changes in leaf relative water content are not fully understood (Cowan 1995), the role that stomata play in maintaining leaf water potential above a critical threshold has been well demonstrated

(Tyree and Sperry 1988, Sperry et al. 1993, Saliendra et al. 1995). Several studies suggest that stomata function to prevent excessive xylem cavitation and hydraulic failure that occur if leaf water potential becomes too negative (Cochard et al. 1996, Lu et al. 1996, Sperry et al. 1998).

The degree of stomatal sensitivity to environmental factors reflects the plants' efforts to avoid hydraulic failure. Stomatal closure is induced by a number of environmental variables, including high atmospheric vapor pressure deficit (D), low light or solar radiation, and soil moisture deficit (Jarvis 1976, Whitehead et al. 1981, Sandford and Jarvis 1986, Livingston and Black 1987, Aphalo and Jarvis 1991, Bréda et al. 1993, review in Whitehead 1998). Maximum stomatal conductance generally occurs in the morning hours, once leaves are light saturated and when D is low. Reductions in maximum rates from morning to afternoon occur as D increases, with a steeper decline indicating a more sensitive stomatal response (Oren et al. 1999). Imposed on this response is the limitation set by soil water supply. Soils vary in their hydraulic properties as a function of soil texture. Coarser soils provide less resistance to water flow and lose moisture and conductivity at higher water potentials relative to finer textured soils (Buckman and Brady 1969). Plants on coarse soils may therefore exhaust their water supply at higher soil water potentials and may show a more sensitive stomatal response to declining soil water potential relative to plants on finer textured soils, so as to avoid hydraulic failure (Sperry et al. 1998, Hacke et al. 2000).

Plants that exist across moisture gradients have been shown to make adjustments in their architecture to maintain hydraulic compatibility with their soils. Changes in canopy structure and tree height across texture gradients have been reported, with

canopies becoming more open and trees reaching lower maximum height growth as soils become coarser (Aber et al. 1982). A general shift in allocation to below ground structures is often observed as soils become drier (Comeau and Kimmins 1989, Gower et al. 1994, Albaugh et al. 1998), and may serve to maximize water extraction. Increased rooting depth and root to leaf area ratio were observed for *Pinus taeda* on sandy versus loamy soils, and enabled trees on sand to maintain a similar water extraction potential as trees on loam (Hacke et al. 2000). These adjustments also helped to buffer sandy-site trees against soil drought. By having a deeper root system, sandy site trees were able to access more stable water sources deep in the soil profile during drought (Hacke et al. 2000).

The objective of this study was to determine how mature *P. palustris* occupying sites with different soil water holding capacity differed in their water use and status, and in their stomatal responses to environmental factors. A severe growing-season drought allowed for further assessment of the variation in these characters under limiting soil moisture conditions. Leaf water potential and gas exchange were measured throughout a growing season for trees growing on a sandy (xeric) site and a sandy-loam (mesic) site. Water use efficiency, defined as the ratio of photosynthetic carbon gain to transpirational water loss, was inferred from leaf gas exchange data and from leaf carbon isotope ratios. Whole-plant estimates of water use (E) and stomatal conductance (G_s) were scaled from sap-flux data, and relationships between G_s and environmental variables were quantified using a multiplicative approach. Based on previous work for these sites citing soil moisture as the dominant factor controlling productivity (Mitchell et al. 1999), it was hypothesized that mesic site trees would show higher water use per unit leaf area and

higher maximum rates of gas exchange, and have lower water use efficiency relative to xeric site trees. It was also predicted, however, that mesic site trees would experience more water stress during drought due to more limited rooting depth. Other factors including tree height and leaf nitrogen that have been shown to affect plant gas exchange were also evaluated.

CHAPTER 2
MATERIALS AND METHODS

Study sites

The study was conducted at the Joseph W. Jones Ecological Research Center, located on an 11,500 ha preserve known as Ichauway in the Coastal Plain region of southwestern Georgia, USA (31°N, 84°W). The region's climate is described as humid-subtropical with mean daily temperatures ranging from 21-34°C in summer to 5-17°C in winter (Goebel et al. 1997). Precipitation is evenly distributed throughout the year, with an annual mean of 1310 mm.

Pinus palustris is the dominant tree species at Ichauway and can be found across a wide range of site types, from mesic flatwoods characterized by loamy soils, to xeric sandhills with deep, sandy soils (Goebel et al. 1997). Two plots representing the extreme soil moisture conditions on which *P. palustris* occurs at Ichauway were established. These plots were part of an earlier study that evaluated patterns of above-ground productivity (see Mitchell et al. 1999). One plot was located on soils with higher water holding capacity (40 cm water per m soil), classified as Aquic Arenic Kandiudults, and with significant accumulation of clay below 0.5 m soil depth. This plot (hereafter referred to as mesic) contained 121 pine trees over an area of 0.525 ha. The other plot (termed xeric) was located on soils with lower water holding capacity (18 cm water per m soil), classified as Typic Quartzipsamments, and with no significant accumulation of clay within the upper 3 m of soil. This plot was 1.317 ha in area and contained 71 pine trees and 68 oak trees, the majority of which were turkey oak (*Quercus laevis*). *Pinus palustris* stands at both sites are second-growth, uneven-aged stands that regenerated naturally following timber harvests between 1900 and 1920 (Palik and Pederson 1996). Prior to the study, diameter at 1.3 m stem height was measured for every pine tree in each

plot. Total tree height was measured on a sub-sample of approximately 30 trees per plot and a relationship between diameter at 1.3 m and height was developed (Figure B.1). Age was determined for each tree from increment cores taken for the Mitchell et al. (1999) study. Mean age and diameter at 1.3 m were similar for both plots. Soil and stand characteristics are shown in Table A.1. In 1998, scaffolding towers were constructed on each site and allow access to the canopies of 3 trees on the xeric site and 4 on the mesic site.

Leaf area dynamics

Tree leaf area was estimated from branch harvests performed both at the beginning and end of the growing season. Trees representing the full range of sizes in each stand were randomly selected along transects adjacent to each plot. For the pre-season harvest, $n = 17$ on the mesic site and $n = 15$ on the xeric site. For each tree, diameter at 1.3 m, total height, and height and diameter at the base of the crown were measured. Crown length was determined by subtracting the height at the crown base from the total height, and then the crown was divided into thirds. The diameter of every branch in each third was measured by climbing the trees. Two branches from each crown third were randomly selected for harvesting so that $n = 6$ branches per tree. Needles from each of the harvested branches were collected and transported to the laboratory for drying to constant mass. A relationship between projected leaf area (cm^2) and leaf dry weight (g) (i.e. specific leaf area, SLA: $\text{cm}^2 \text{g}^{-1}$) was developed for needle sub-samples collected from each branch. Projected leaf area was measured using a LI-3100 Area Meter (Li-Cor Instruments, Lincoln, NE, USA). Total leaf mass for each branch was corrected for the

weight of the fascicle and was multiplied by the SLA to yield total leaf area. From this, an allometric relationship between branch diameter and leaf area was developed for each crown third on each site and used to estimate the leaf area of the branches not harvested on the trees for which branch diameter had been measured. Because the variation tended to increase with increasing branch diameter, the assumption of constant variance was met by developing relationships for each crown third separately, since most of the large branches were in the lower third. In all cases, log-log transformation was still needed to satisfy the assumption of constant variance. Re-converted values were summed for each tree to get whole tree leaf area, and a relationship between diameter at 1.3 m stem height and total leaf area was developed. This relationship was then applied to every tree in the stand to get total stand leaf area. Leaf area index (LAI, $\text{m}^2 \text{m}^{-2}$) was determined by dividing the total stand leaf area by the ground area.

The pre-season harvest provided leaf area index at the beginning of the growing season, or at time 0, denoted LAI_{t_0} . Seasonal changes in leaf area were determined for another study (S. Jack, D. McConville, M.C. Sheffield unpublished data) by measuring percent needle elongation and senescence in the tower-accessible trees and calculating LAI at any given point during the season (at time x , denoted LAI_{t_x}) as follows:

$$\text{LAI}_{t_x} = \text{LAI}_{t_0} + (\text{LAI}_{t_0}(\text{Net}_x) - \text{LAI}_{t_0}(\text{Nst}_x)) \quad (1)$$

where Net_x is percent needle elongation at time x , and Nst_x is percent needle senescence at time x . Needle elongation was measured every 2 weeks for 27 branches (~110 shoots) on each site and Net_x was calculated as the needle length at t_x divided by the maximum needle length that occurred at the end of the season. Needle senescence was measured by tying individual needles to their corresponding shoots using monofilament line. When

the needle senesced, it remained hanging from the shoot until collected at the same time that needle elongation measurements were made. Approximately 600 needles on each site were tied and N_{st_x} was calculated as the number of needles senesced at t_x relative to the total number of needles tied. Branch harvests were performed again at the end of the growing season on $n = 6$ trees per site to get an end of year estimate of LAI. This, combined with pre-season LAI and measurements of elongation and senescence, was used to develop a model that predicted the daily dynamics of LAI throughout the measurement period for each site.

Environmental measurements

The study period extended from March-October, 2000. Global solar radiation (R_g , $W m^{-2}$) was measured at a weather station located between the sites using a LI-200S pyranometer (Li-Cor Instruments, Lincoln, NE, USA). Daily values represent sums ($MJ m^{-2}$). Air temperature (T_A) and relative humidity (RH) were recorded on each site at two-thirds canopy height using HOBO H8 T_A -RH sensors (HOBO Computer Corp., Bourne, MA, USA). Two-minute T_A and RH values were averaged over a 30-minute interval and used to calculate vapor pressure deficit, D (kPa), based on the following equations adapted from Goff and Gratch (1946):

$$V_S = 0.611 \exp^{(17.27 \cdot T_L)/(T_L + 237)} \quad (2)$$

$$D = (RH/100) \cdot V_S - V_S \quad (3)$$

where T_L is leaf temperature and V_S is saturated water vapor pressure (kPa). In calculating D , T_A was substituted for T_L , assuming close coupling between the canopy and the atmosphere. This assumption is often made for open-canopy coniferous systems

where high atmospheric turbulence maintains leaf temperature close to air temperature (Monteith and Unsworth 1990). To test this assumption for the sites in this study, simultaneous point measurements of T_L and T_A were taken throughout the canopy over a range of T_A 's using thermocouples attached to microprocessor thermometers (Model HH21, OMEGA Engineering, Inc., Stamford, CT, USA). There was no significant difference between T_A and T_L for either site (mesic, $P = 0.904$; xeric, $P = 0.898$). Tests were also performed to determine whether or not there was a vertical gradient in D within the canopy. This was done by simultaneous measurement of T_A and RH in the upper and lower canopy on each site over the course of a few days. No difference in D between upper and lower canopy was found for either site (mesic, $P = 0.870$; xeric, $P = 0.644$). For comparing tree water use patterns to vapor pressure deficit at daily scales, a daytime-averaged vapor pressure deficit (D_D) was calculated as the mean D when $R_g > 5 \text{ W m}^{-2}$ for each day.

Volumetric soil moisture content (θ) at 0-30 cm and 0-90 cm soil depths was measured bi-weekly using time domain reflectometry (TDR) (Topp et al. 1980). During the drought period measurements were made weekly. Pairs of stainless steel rods were inserted vertically in the soil at ten locations within each site and θ was measured using a cable tester (1502B, Tektronix, Beaverton, Oregon, USA).

Leaf water potential and leaf gas exchange

Leaf water potential (Ψ_L) was measured at predawn (0500 h), morning (~1000 h), and midday (~1300 h) for the three tower-accessible trees on each site approximately every 2 weeks throughout the study period using a Scholander-type pressure chamber

(PMS Instruments, Corvallis, OR, USA). Fascicles were collected from the same branches in the upper and lower thirds of the canopy on each measurement date. Because the tower platforms on the mesic site were an average 6.8 m taller than those on the xeric site, all site comparisons of Ψ_L use a height correction factor of 0.01 MPa per m height.

Leaf-level stomatal conductance (g_s), photosynthesis (A_{net}), and intercellular CO_2 concentration (c_i) were measured every 4-5 weeks throughout the study period for the three tower-accessible trees on each site using a LI-6400 portable photosynthesis system equipped with a LI-6400-02B artificial light source (Li-Cor Instruments, Lincoln, NE, USA). Measurement of c_i was used as an indicator of instantaneous water use efficiency (WUE), where a higher c_i represents less conservative water use. The ratio of A_{net} to g_s was also used to indicate instantaneous WUE. All measurements were made at light saturation (photon flux density $> 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) and constant atmospheric CO_2 concentration ($C_A = 350 \mu\text{mol m}^{-2} \text{s}^{-1}$). Needle temperature was kept within 1°C of ambient air temperature and relative humidity inside the chamber was also maintained near ambient. Selected fascicles were taken from sunlit parts of the crown and allowed to equilibrate inside the chamber before beginning measurements. Data was then recorded every 15 s for a 3 min interval using the auto-log feature of the LI-6400. After measurement, needles were stored on ice and transported to the laboratory for determination of leaf area. Needle radius to the nearest 0.01 mm was measured for each needle using digital calipers and was used to calculate all-sided surface area inside the chamber assuming that needles approximate the area of a cylinder (Svenson and Davies 1992).

Measurements of g_S and A_{net} were conducted so that they corresponded with every other measurement of Ψ_L . Diurnal measurements (~0900, 1100, 1300, 1500 h) were made at the same positions in the upper and lower thirds of the canopy on each measurement date on each site, and on different age-classes of needles (current year v. previous year) once new needles reached 50% of total elongation. Equipment limitation precluded simultaneous measurements at both sites, so the following strategy was invoked: xeric site trees were measured at 0900 h, mesic site trees at 1100 h, xeric site trees at 1300 h, and mesic site trees at 1500 h. On the following day the measurement schedule was reversed. The data was then compiled to represent g_S and A_{net} in the morning hours (0900-1100 h) and afternoon (1300-1500 h) separately by averaging the measurements taken for each of these periods over the 2-day measurement interval. Measurements were made on sunny days and weather conditions (i.e. solar radiation and vapor pressure deficit) were always similar over the two days per measurement period (checked using t-tests).

Leaf nitrogen content and carbon isotope ratio

In September 2000, current-year needles from 30 trees on each site were collected for leaf nitrogen (N) and leaf carbon isotope ratio ($\delta^{13}C$) analyses. Leaf $\delta^{13}C$ was used as an indicator of seasonally integrated water use efficiency (WUE), whereby a less negative $\delta^{13}C$ indicates higher WUE (Farquhar et al. 1989). Selected trees represented the range of tree size classes in each stand. On each tree, 4 sunlit branch tips (one from each of the four cardinal directions) were collected from mid to upper-canopy using a shotgun. Needles were pooled by cardinal direction and specific leaf area was measured.

All samples were then oven dried (70°C for 48 h) and ground to pass a 500 μm mesh screen size using a ball mill grinder. Total leaf N was determined on a CHN analyzer (Perkin-Elmer Corp., Norwalk, CT, USA) and leaf $\delta^{13}\text{C}$ was determined by continuous mass flow spectrometry (Dave Harris, University of California Davis Stable Isotope Facility).

Sap flux density measurements

Sap flux density (J_s , $\text{g m}^{-2} \text{s}^{-1}$) was measured in the xylem of seven trees on each site, selected to represent the range of tree size classes present on each site. Three of the selected trees on each site were trees accessible by the scaffold towers (Table A.2). Equipment failure and power limitations (the sites do not have power lines) prevented continuous measurement of all seven trees on each site, so the three tower-accessible trees were measured continuously, and the additional four trees on each site were measured off and on throughout the study period. Dynamax Thermal Dissipation Probes (TDPs, Dynamax, Inc., Houston, TX, USA) were used to measure J_s . Each probe consisted of a heated (constant energy input) and reference (non-heated) needle. Needles were inserted radially into hydroactive xylem, with the heated needle positioned ~ 5 cm above the reference needle. Each needle contained a thermocouple, and the temperature difference (dt) between the thermocouple pair was measured and converted to sap flux according to an empirically derived equation provided in Granier (1987):

$$J_s = 119 \cdot (dt_m/dt - 1)^{1.23} \quad (4)$$

where dt is the temperature difference between the heated and reference needle, and dt_m is the maximum dt , which occurs under conditions of zero flux. All probes were

insulated from solar radiation to prevent thermal gradients. Longitudinal stem temperature gradients were evaluated by comparing the temperature difference of a heated/unheated probe pair to an unheated/unheated probe pair positioned adjacent, similar to that described in Goulden and Field (1994). Sap flux data were recorded by data loggers (CR-10, Campbell Scientific, Inc., Logan, UT, USA) every minute and averaged over a 30 min interval.

Probes were installed in the outer 30 mm of xylem at a stem height of 1.3 m on the north side of all trees. Variation in J_S with azimuth, radial depth, and height on the bole was tested for the three tower trees on each site and applied to all measured trees. For these tests, probes were installed 1) on the south side of the trees to detect variation with azimuth, 2) at 30-60 mm xylem depth to detect radial variation, and 3) at 7 m height on the bole to detect time lags between water uptake and transpiration that may result due to water stored in the stem. Each test was conducted over a period of at least 10 days and was used to weight J_S for the entire measurement period, assuming that the variation in these ratios remains constant throughout the season.

Scaling sap flux to transpiration and stomatal conductance

Measurements of J_S were used to estimate transpiration and stomatal conductance. Transpiration per unit leaf area was calculated both at the individual tree level and the stand level. Individual tree estimates were necessary for the calculation of stomatal conductance as described below, and stand-level estimates were more relevant for making site comparisons in water use patterns. It should be pointed out, however, that

use of the term “stand-level” refers to estimates scaled to every pine tree in each plot and neglects the oak component on the xeric site and the understory on both sites.

At the individual tree level, transpiration per unit leaf area (E_{Li} , $\text{kg m}^{-2} \text{s}^{-1}$) was calculated using weighted J_S and the sapwood to leaf area ratio ($A_S:A_L$; Oren et al. 1998) as follows:

$$E_{Li} = J_S \cdot (A_S:A_L) \quad (5)$$

Sapwood area for each tree was determined from $n = 4$ increment cores per tree.

Sapwood length was determined by visual inspection of the core and converted to area based on the area of a circle, subtracting the area represented by the heartwood and by the bark. The calculation of E_{Li} was weighted for radial variation in J_S by multiplying the flux in each depth interval (0-30, 30-60 mm) by the corresponding sapwood area in each depth interval. In cases where the sapwood depth extended beyond 60 mm, J_S was scaled using the flux measured from 30-60 mm, assuming no radial trend in J_S beyond 60 mm. Probes were never inserted into heartwood. To account for variation with azimuth, J_S was calculated for both the north and south sides of the trees and then averaged.

At the stand-level, transpiration per unit leaf area (E_L , mm d^{-1}) was calculated using J_S as above, the sapwood area to ground area ratio ($A_S:A_G$), and the leaf area index (LAI) as follows:

$$E_L = (J_S \cdot (A_S:A_G))/LAI \quad (6)$$

Because only three of the seven trees on each site were measured continuously, the percent of the stand transpiration represented by these three trees was determined during times when all seven trees were measured and then used to scale data to the stand level during the times that only three trees were measured.

Stomatal conductance for individual trees (G_{Si} , $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) was calculated using E_{Li} and the following equation derived from Whitehead and Jarvis (1981):

$$G_S = (G_v T_a \rho E_{Li}) / D \quad (7)$$

where G_v is the universal gas constant adjusted for water vapour ($0.462 \text{ m}^3 \text{ kPa K}^{-1} \text{ kg}^{-1}$), T_A is the air temperature (in degrees K), ρ is the density of water (998 kg m^{-3}), and D is the vapor pressure deficit (kPa).

Data analyses

Multivariate repeated measures analysis of variance (ANOVA) with between-subject factors (site) was used to test for site differences in environmental variables (D_D and θ) and tree physiological characteristics (Ψ_L , g_S , A_{net} , c_i , E_L). Analysis of D_D used date as the within-subject effect while θ used date and depth. Within-subject factors for Ψ_L , g_S , A_{net} , and c_i included date, time of day, crown position, and needle age class. Comparisons among the means were performed using pre-planned orthogonal contrasts. Site differences in specific leaf area (SLA), leaf nitrogen, and leaf carbon isotope composition were tested using analysis of covariance with site as the main effect (and crown position for SLA analyses), and tree size as the covariate. For tests of azimuth and radial variation in sap flux density (J_S), repeated measures ANOVA was conducted on the daily sums of J_S using probe location as the within-subject effect. Cross correlation analyses between diurnal patterns of J_S measured at 1.3 m stem height and J_S at 7 m stem height was used to determine the time-lag associated with stored water. The J_S at both heights was compared with environmental variables using the same procedure. All of

these analyses were performed using GLM and ARIMA procedures in SAS v. 8.1 (SAS Institute, Cary, NC, USA).

Sap flux scaled stomatal conductance of individual trees (G_{Si}) was evaluated relative to environmental variables using boundary line analyses (Webb 1972, Livingston and Black 1987, Rico et al. 1996, Martin et al. 1997, Schäfer et al. 2000). The procedure followed for this study is described in more detail in Schäfer et al. (2000). Based on other studies, G_{Si} was expected to respond primarily to global solar radiation (R_g) and vapor pressure deficit (D) (Whitehead et al. 1981, Massman and Kaufmann 1991, Köstner et al. 1992, Martin et al. 1997). Water stress due to soil moisture deficit was also expected to play a role in limiting G_{Si} (Bréda et al. 1993). To account for this, predawn leaf water potential (Ψ_L), as an indicator of plant water status, was also incorporated into the analyses. Half-hourly G_{Si} data were partitioned first into nine R_g classes (increments of 100 W m^{-2} from 0 to 900 W m^{-2}). Within each R_g class, G_{Si} data was further partitioned into 0.2 kPa D intervals. Scatter plots of G_{Si} vs. D (w/ D at 0.2 kPa intervals) were created for each R_g class and the upper boundary of G_{Si} was determined by selecting all points falling above 1 standard deviation of the mean for each 0.2 kPa D interval. Selected data for each D interval was then averaged, yielding a maximum mean G_{Si} for each D interval in each R_g class. Mean G_{Si} 's across the D intervals for each R_g class were then related to the natural logarithm of D using the following function modified from Lohammar et al. (1980):

$$G_{Si} = G_{Si\text{ref}} - (m) \cdot \ln D \quad (8)$$

where $G_{Si\text{ref}}$ is a reference G_{Si} because, as a result of the function, it represents G_{Si} at $D = 1 \text{ kPa}$ (Oren et al. 1999). Because the G_{Si} values used to generate this function were

maximum mean G_{Si} taken from the boundary-line analysis, G_{Siref} can be used as a proxy for the maximum G_{Si} that occurred in each R_g class. Furthermore, since G_{Siref} is always the G_{Si} at $D = 1$ kPa, its use facilitates comparison of G_{Si} among different R_g classes. Using this procedure, G_{Siref} was determined for each R_g class. To determine the point at which R_g became limiting to G_{Siref} , G_{Siref} in each R_g class was normalized by the maximum G_{Siref} that occurred under high R_g , yielding a percent reduction in G_{Siref} (denoted % G_{Siref} from maximum) as a function of declining R_g . This procedure was then repeated with predawn Ψ_L , using six Ψ_L classes (increments of 0.1 MPa from -0.40 to -1.0 MPa). For each predawn Ψ_L class, G_{Siref} was determined and a reduction function describing the percent reduction in G_{Siref} with declining predawn Ψ_L was generated as described above. The relationship between G_{Si} and D under non-limiting R_g and predawn Ψ_L was then analyzed following Oren et al. (1999).

After separating the effects of R_g , D , and predawn Ψ_L on G_{Si} as described above, a nonlinear multiple constraint function was used to predict the response of G_{Si} under various combinations of R_g , D , and predawn Ψ_L as proposed by Jarvis (1976):

$$G_{Si} = G_{Siref} \cdot f(R_g) f(D) f(\Psi_L) \quad (9)$$

where $f(R_g)$, $f(D)$, and $f(\Psi_L)$ represent the reduction functions generated from the boundary line analyses. The G_{Si} was determined for any combination of R_g , D , and Ψ_L by first predicting G_{Siref} (proxy for maximum G_{Si}) from R_g , and then reducing G_{Siref} by D and Ψ_L (Jarvis 1976, Livingston and Black 1987, Bréda et al. 1993, Martin et al. 1997). Predicted values of G_{Si} were compared to actual values using simple linear regression and the associated coefficients of variation were taken as the percent variation of G_{Si}

explained. Relationships between G_{Si} and soil moisture contents (θ) at 0-30 cm and 0-90 cm soil depths were also developed and included in the above model (substituted for Ψ_L) to determine how well θ performed relative to predawn Ψ_L in explaining variation in G_{Si} . All curve-fit statistics for these procedures were performed using SigmaPlot v. 5.0 (SPSS Inc., San Rafael, CA, USA).

CHAPTER 3

RESULTS

Leaf area

Pine leaf area index (LAI) was higher on the mesic site relative to the xeric site, reflecting the differences in pine density between the sites (Table A.1). Maximum pine LAI occurred in September for both sites, reaching $1.43 \text{ m}^2 \text{ m}^{-2}$ for the mesic site and $0.52 \text{ m}^2 \text{ m}^{-2}$ for the xeric site. It should be noted that these estimates of LAI only represent the pine component on each site. Oaks co-dominate the xeric site and are not represented, and understory LAI is not represented for either site. Although total pine leaf area was higher on the mesic site, leaf area on an individual tree basis and at a given diameter breast height (DBH) was higher for xeric site trees. Leaf area to sapwood area ratio ($A_L:A_S$) was also higher for xeric site trees. These patterns are depicted in Table A.2.

No significant difference in specific leaf area (SLA, $\text{cm}^2 \text{ g}^{-1}$) between sites was observed ($P = 0.131$; Table A.3). There was a slight decrease in SLA from lower to upper crown on both sites, but differences due to crown position were not significant ($P = 0.173$), and no significant site \times crown position interaction was detected ($P = 0.6145$).

Environmental conditions

Total precipitation over the course of the measurement period was 89% of normal, based on a 42-year mean for this area (Figure B.2a). Precipitation was unevenly distributed over the measurement period, with most (69%) occurring between the months of July and October. Drought persisted prior to July, during which time precipitation was 52% of normal. Seasonal trends were present in both global solar radiation (R_g) and daytime averaged vapor pressure deficit (D_D), with both variables reaching their

maximum in mid-June (Figure B.2b, B.2c). Because R_g was measured in an open area located near the sites, differences in canopy light environment between sites could not be reported. There was no statistically significant difference in D_D between sites ($P = 0.145$), though D_D tended to be slightly higher at the xeric site. Volumetric soil moisture content (θ) was significantly higher for the mesic site relative to the xeric site at both 0-30 cm and 0-90 cm soil depths ($P < 0.0001$ for both depths; Figure B.2d). On the mesic site, θ from 0-90 cm was significantly higher than θ from 0-30 cm ($P = 0.016$), reflecting the accumulation of clay with depth at this site. On the xeric site, however, θ from 0-90 cm was significantly lower than θ from 0-30 cm ($P = 0.006$). It could not be determined whether or not this anomaly reflects the actual conditions at this site or is an artifact of the θ calculations. A sharp decline in θ associated with the drought occurred for both sites. On the mesic site, θ from 0-30 cm was reduced to 35% of its maximum and θ from 0-90 cm reached 52% of max. On the xeric site, θ reached 38% and 34% of max at 0-30 cm and 0-90 cm, respectively.

Leaf water potential and gas exchange

There was no significant effect of crown position (upper crown v. lower crown) on leaf water potential (Ψ_L) for either site (Table A.4). Both date ($P < 0.0001$) and time of day ($P = 0.0012$) were significant factors affecting Ψ_L , however no significant interactions with site were present for either factor (Figure B.3). Differences between sites in Ψ_L (using height-corrected data) were not significant for either predawn ($P = 0.509$), morning ($P = 0.985$), or afternoon ($P = 0.190$).

Crown position had no significant effect on g_S , A_{net} , or c_i (Table A.4). Needle age class (current year v. previous year) was also tested and found to be insignificant. Data were therefore pooled across crown positions and needle age classes and used to compare morning versus afternoon g_S , A_{net} , and c_i for each site. Significant site \times time of day interactions were present for each of the characters due to declines in afternoon rates of g_S and A_{net} and diurnal increases in intrinsic water use efficiency (WUE) that occurred to a greater degree for the xeric site relative to the mesic site (Table A.4). Seasonal patterns of g_S and A_{net} presented in Figures B.4a-d were segregated by morning and afternoon. Morning measurements represent maximum g_S and A_{net} for each site (Figures B.4a, c) and afternoon data are included to illustrate the disproportionate morning to afternoon reduction exhibited by xeric site trees (Figures B.4b, d).

Leaf nitrogen and carbon isotope ratio

Leaf nitrogen (N) content was significantly higher for xeric site trees relative to mesic site trees, both when expressed on a mass ($P < 0.0001$) and an area basis ($P < 0.0001$; Table A.5). Significant differences between sites in leaf carbon isotope ratio ($\delta^{13}C$) were also reported ($P < 0.0001$), with xeric site trees showing a less negative $\delta^{13}C$, reflecting a greater or more conservative seasonally integrated water use efficiency (Table A.5)

Within-tree variation in sap-flux density, J_S

Mean values for J_S on the south sides of trees on the mesic site were 7% higher than that measured on the north sides. On the xeric site, J_S on the south side was 36%

higher than that measured on the north side (Table A.6), even after correcting for longitudinal stem temperature gradients, which were present on the south but not the north sides of trees on the xeric site. The differences recorded across sites may be due to the differences in degree of canopy openness between sites. The test for radial variation showed similar reductions in J_S from outer to inner xylem on both sites and was consistent with reductions found for other pines (Phillips et al. 1996, Ewers and Oren 2000). The ratio of inner xylem J_S to outer xylem J_S was 0.39 for the mesic site and 0.41 for the xeric site (Table A.6). To determine if there was a significant lag between water uptake and transpiration, and therefore a significant effect of stored water, simultaneous measurements of J_S at 1.3 m stem height and at 7 m stem height were compared using cross-correlation analysis (data not shown). No significant lag between the two probe positions was detected (i.e. highest percent correlation occurred at 0 minutes). Probes at both positions, however, lagged environmental variables by 0.5 hour, indicating some effect of stored water. To determine whether or not this would affect analysis of relationships between J_S -scaled stomatal conductance (G_{Si}) and environmental variables, G_{Si} was calculated from J_S at each stem height separately and the percent error between the two calculations determined. This percent error was less than 10% at high D (i.e. $D > 0.6$ kPa; see also Ewers and Oren 2000), indicating that stored water can be considered negligible at high rates of transpiration and stomatal conductance. Therefore in analyzing relationships between sap-flux scaled stomatal conductance and environmental factors, data where $D < 0.6$ kPa was deleted.

Water use patterns

Seasonal patterns of daily transpiration per unit leaf area (E_L) scaled to every *P. palustris* tree on each site were similar to patterns observed for gas exchange at the leaf level (Figure B.5). Early in the season, while daytime averaged vapor pressure deficit (D_D) was still low and before soil moisture was limiting, daily E_L tended to be higher for the xeric site relative to the mesic site. This difference disappeared later in the season so that no significant effect of site was detected in the analysis ($P = 0.319$). However, a significant site \times date interaction was detected ($P < 0.0001$). Under non-limiting soil moisture conditions, E_L increased asymptotically with increasing D_D on both sites (Figure B.6). While these patterns indicate a feedback response of stomata to D_D as E_L increased for both sites, the fact that the xeric site showed higher E_L at lower D_D and lower E_L at higher D_D relative to the mesic site suggests that this response is stronger for trees on the xeric site.

Stomatal response to environment

Relationships between sap flux scaled stomatal conductance (G_{Si}) and global solar radiation (R_g), vapor pressure deficit (D), and predawn leaf water potential (Ψ_L) were described by reduction functions generated from the boundary line analyses. The percent reduction in stomatal conductance at $D = 1$ kPa (G_{Siref}) was used to construct relationships with R_g and Ψ_L . The following function provided a good fit to the relationship between G_{Siref} and R_g on both sites (mesic, $r^2 = 0.96$, $P < 0.0001$; xeric, $r^2 = 0.96$, $P < 0.0001$):

$$\%G_{Siref} = a \cdot (1 - \exp(-b \cdot R_g)) \quad (10)$$

On both sites, G_{Siref} reached 90% of maximum at similar R_g levels (Figure B.7). No significant interaction between R_g level and site was detected ($P = 0.950$), indicating that there was no significant difference in the overall shapes of these curves.

Reductions in G_{Siref} attributed to predawn Ψ_L were described by a negative linear function (Figure B.8). Slopes of this relationship were significantly different ($P = 0.0003$), with G_{Siref} declining more steeply with decreasing predawn Ψ_L in xeric site trees relative to mesic site trees, indicating a higher degree of sensitivity to Ψ_L on the xeric site. During the drought, declines in predawn Ψ_L were associated with decreasing soil moisture content (θ) on both sites (Figure B.9). To determine how well θ performed relative to predawn Ψ_L in describing variation in G_{Si} , relationships between G_{Siref} and soil moisture content (θ) were developed using the following function:

$$\%G_{Siref} = a \cdot (1 - \exp(-b \cdot \theta))^c \quad (11)$$

which provided a good fit to the data on both sites (mesic, $r^2 = 0.97$, $P = 0.028$; xeric, $r^2 = 0.99$, $P = 0.031$ for θ at 0-30 cm soil depth) (Figure B.10). Soil moisture in the 0-90 cm profile fluctuated in similar ways to that at 0-30 cm (Figure B.2d) and provided an equally good fit to the data (mesic, $r^2 = 0.96$, $P = 0.041$; xeric, $r^2 = 0.96$, $P = 0.036$).

Over the same range of D , the reduction in G_{Si} from maximum was greater for xeric site trees, indicating a greater stomatal sensitivity to D for this site (Figure B.11). Slopes of this relationship were significantly different between sites ($P = 0.0041$). To further evaluate stomatal sensitivity to D , the relationship between G_{Si} and D was linearized by natural log transformation of D , and the resulting slope (i.e. $-dG_{Si}/d\ln(D)$) was plotted against the y-intercept, which occurs at $D = 1$ kPa (G_{Siref}) as in Oren et al.

(1999). Slopes above 0.6 indicate greater stomatal sensitivity to D and stricter stomatal regulation of minimum leaf water potential, while slopes < 0.6 indicate lower stomatal sensitivity to D and less strict stomatal regulation of minimum leaf water potential. The slope of this relationship was 0.53 for the mesic site and 0.61 for the xeric site (Figure B.12), indicating again that stomatal sensitivity to D is greater on the xeric site and that xeric site trees more strictly regulate minimum leaf water potential.

Use of the multiplicative model in Equation 9 showed that R_g and D alone described between 59 and 72% (average 65%) of the variation in G_{Si} on the mesic site and between 58 and 80% (average 67%) of the variation in G_{Si} on the xeric site. Inclusion of predawn Ψ_L increased the fit to an average 71% on the mesic site and 77% on the xeric site. Comparison of model fits with and without predawn Ψ_L showed that predawn Ψ_L explained more of the variation in xeric site trees relative to mesic site trees (10% v. 6%), reflecting the greater sensitivity to this variable in xeric site trees. Using soil moisture (at both depths) instead of predawn Ψ_L in the model slightly reduced the fit to an average 70% on the mesic site and 72% on the xeric site. Inclusion of air temperature (T_A) and relative humidity (RH) in the model did not improve the fit for either site, most likely because these variables are already accounted for by the vapor pressure deficit term (D) (Aphalo and Jarvis 1991).

CHAPTER 4
DISCUSSION

In this study, *P. palustris* occupying sites that differed in soil water supply showed different patterns of leaf gas exchange and water use and different degrees of stomatal sensitivity to environmental factors. Seasonal trends in leaf stomatal conductance (g_S), photosynthesis (A_{net}), and transpiration per unit leaf area (E_L) were present on both sites, with maximum values occurring in March and April, before soil moisture became limiting. The hypothesis that maximum rates of g_S , A_{net} , and E_L under non-limiting light and soil moisture conditions would be higher for trees on the mesic site was not supported. At low vapor pressure deficits, high radiation and non-limiting predawn leaf water potential, maximum rates of g_S , A_{net} , and E_L were higher for xeric site trees. In April, g_S and A_{net} were $87.46 \text{ mmol m}^{-2} \text{ s}^{-1}$ and $6.11 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$, respectively, for the mesic site, and $107 \text{ mmol m}^{-2} \text{ s}^{-1}$ and $8.12 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$, respectively, for the xeric site. Maximum rates of E_L (averaged for April) were 0.46 mm d^{-1} for the mesic site and 0.54 mm d^{-1} for the xeric site. Estimates of mean canopy stomatal conductance (G_{S_i}) at a reference vapor pressure deficit (i.e. $G_{S_{\text{iref}}}$ at $D = 1 \text{ kPa}$) were also lower for the mesic site ($55.48 \text{ mmol m}^{-2} \text{ s}^{-1}$) relative to the xeric site ($63.92 \text{ mmol m}^{-2} \text{ s}^{-1}$). Values reported here for leaf g_S and A_{net} are similar to those reported for other pines, particularly mature *P. taeda* (Ellsworth 2000), mature *P. ponderosa* (Hubbard et al. 1999, Kolb and Stone 2000), mature *P. contorta* (Schoettle and Smith 1999), and *P. radiata* and *P. sylvestris* (summarized in Teskey et al. 1994). Ewers et al. (1999) reported rates of E_L for mature *P. taeda* ranging from $0.29 - 0.37 \text{ mm d}^{-1}$ (averaged for August 28 – October 23) that agree well with E_L reported here. Furthermore, estimates of $G_{S_{\text{iref}}}$ in this study are in the same range ($39 - 85 \text{ mmol m}^{-2} \text{ s}^{-1}$) reported by Ewers et al. 2000 for mature *P. taeda*.

Species or individuals that show high stomatal conductance at low vapor pressure deficit (D) also generally show a more sensitive stomatal closure response to increasing D (McNaughton and Jarvis 1991, Yong, Wong and Farquhar 1997, Oren et al. 1999). Results from this study are consistent with this observation. While xeric site trees had higher maximum g_S , A_{net} , and E_L at low D, they were also more sensitive to increasing D. Oren et al. (1999) show both theoretically and empirically that enhanced stomatal sensitivity to D is consistent with the role of stomata in regulating minimum leaf water potential to avoid xylem cavitation and hydraulic failure. The response of G_{Si} to D can be linearized by natural log transformation of D, as in equation (8). Since the stomatal sensitivity to D is defined as the decline in G_{Si} per unit increase in D, the slope of the G_{Si} vs. $\ln D$ relationship (i.e. $-dG_{Si}/d\ln(D)$) represents the stomatal sensitivity to D. Oren et al. (1999) demonstrate that, for several species of plants across numerous habitats, when $-dG_{Si}/d\ln(D)$ is plotted against the $G_{Si,ref}$, the slope of the relationship is 0.6. They used a simple hydraulic model to derive a theoretical slope of this relationship and found it to be consistent with the empirically derived slope. The hydraulic model, modified from Whitehead and Jarvis (1981), assumes perfect regulation of minimum leaf water potential by stomata:

$$G_{Si} = (k/A_L)(1/D)(\Delta\Psi_{S-L}) \quad (12)$$

where k/A_L is the leaf specific hydraulic conductance from soil to leaf and $\Delta\Psi_{S-L}$ is the water potential gradient from soil to leaf. The usefulness of this derivation is that it provides an index of stomatal sensitivity (i.e. slope = 0.6) that equates to a perfect regulatory response of stomata to D. Slopes above 0.6 indicate greater stomatal sensitivity to D and stricter stomatal regulation of minimum leaf water potential, while

slopes < 0.6 indicate lower stomatal sensitivity to D and less strict stomatal regulation of minimum leaf water potential. Slopes < 0.6 are expected for drought tolerant species and have been shown for the desert shrubs *Ephedra nevadensis* and *Larrea tridentate* (D. Pataki unpublished data used by Oren et al. 1999). Use of these dependencies in this study suggests that xeric site trees, with a slope equal to 0.61, more strictly regulate minimum leaf water potential compared to mesic site trees, whose slope was 0.53 (Figure B.12).

In addition to the more sensitive response to D , xeric site trees were more sensitive to declining predawn leaf water potential (Ψ_L) associated with soil drought relative to mesic site trees. Several studies suggest that an increase in the sensitivity to this variable is necessary in avoiding hydraulic failure (Sperry et al. 1998, Hacke et al. 2000). Hacke et al. (2000) showed that *P. taeda* occupying sand approached cavitation inducing transpiration rates (known as E_{crit}) at much higher soil water potential than did mesic site trees. In this study, declines in predawn Ψ_L were associated with declines in soil moisture content during drought. While mesic site trees reached a more negative Ψ_L (-0.93 v. -0.82 MPa), indicative of more water stress, there was no difference in the percent reduction of canopy stomatal conductance between sites at this predawn Ψ_L . On both sites, G_{Si} was reduced to roughly 35% of maximum during the peak of the drought.

Inclusion of global solar radiation (R_g), vapor pressure deficit (D), and predawn leaf water potential (Ψ_L) in the multiplicative model in Equation (9) explained an average 71% of the variation in G_{Si} on the mesic site and 77% on the xeric site. The percent variation in G_{Si} explained in this study is similar to that of other studies. Martin et al. (1997) explained an average 66% of the variability in crown conductance of an *Abies*

amabilis forest and Livingston and Black (1987) explained over 70% in conifer seedlings. Substituting soil moisture terms (θ at 0-30 cm and 0-90 cm soil depth) for predawn leaf water potential decreased the fit of the model only slightly (from 71 to 70% on the mesic site and from 76 to 72% on the xeric), indicating that soil moisture in these upper soil profiles does a reasonable job of describing the response to soil moisture deficit. This would argue that the functional rooting zone across sites is represented reasonably well by the soil depths (0-30 and 0-90 cm) at which soil moisture was measured here. An initial assessment of rooting depth distribution from excavation pits to 2 m soil depth indicated that sites were similar in rooting depth distribution, with over 75% of total root biomass contained in the upper 1 m of soil on both sites (R. Addington, unpublished data). *Pinus palustris* is, however, a species characterized by a deep taproot and may have access to water sources at much deeper soil depths than represented by this study. Additional work that identifies water source utilization will improve our understanding of intraspecific variation in functional rooting depth across sites.

Both Ψ_L and θ explained more of the variation in mean canopy stomatal conductance (G_{Si}) on the xeric site than it did on the mesic site, arguing for a more important role of soil water deficit in limiting G_{Si} in xeric site trees. Soil moisture thresholds were developed for both sites as the moisture content below which G_{Si} fell to less than 90% of maximum. Trees on the xeric site breached their θ threshold earlier into the drought and remained below it for more time relative to trees on the mesic site. Trees on the xeric site were below their θ threshold 21.4% of the measurement period, whereas the mesic site trees spent 14.3% of measurement period below its θ threshold (Table A.7). Data from this study year were consistent with a 5-year θ record showing that the

frequency of drought is greater for xeric site trees, i.e. xeric site trees spend proportionately more time below their θ relative to mesic site trees (Table A.7). These interpretations are consistent with information from the tree-ring literature, which suggests that, while mesic groups may be more affected by severe drought because of limited rooting depth, xeric groups are more affected over the long-term, most likely because they experience drought more frequently (Tardif and Bergeron 1997, Abrams et al. 1998).

Leaf nitrogen content was significantly higher for xeric site trees, both when expressed on a mass and an area basis, and may contribute to the higher maximum rates of A_{net} at low D (Table A.5). Patterns of leaf nitrogen were consistent with soil nitrogen mineralization patterns reported for these sites by Wilson et al. (1999). Water and nitrogen availability are inversely correlated on these study sites, such that soil nitrogen mineralization is higher on the xeric site than on the mesic site (Wilson et al. 1999). Hardwood species that exist on the xeric site but that are not present on the mesic site return a higher quality litter to the litter pool, and may contribute to the higher nitrogen availability on the xeric site (Jacqmain et al. 1999). Furthermore, higher soil temperatures on the xeric site may accelerate N mineralization on this site (Wilson et al. 1999). Increases in leaf N are correlated with increases in photosynthetic capacity because nearly all of the biochemical processes involved in photosynthesis require nitrogenous compounds (Field and Mooney 1986, Evans 1989). Furthermore, increases in leaf nitrogen have been shown to increase plant water use efficiency (WUE), i.e. the ratio of carbon assimilated to water lost (Green and Mitchell 1992). By concentrating N in foliage, xeric site trees may achieve higher photosynthetic return per unit water lost

relative to mesic site trees. Information from leaf carbon isotope ratio ($\delta^{13}\text{C}$) suggests that xeric site trees are more WUE (Table A.5), however, gas exchange measurements failed to show a significant difference between sites in instantaneous water use efficiency (c_i or the ratio of A_{net}/g_s). Whether or not site-differences in leaf $\delta^{13}\text{C}$ are attributable to soil water supply, and not other environmental factors (i.e. irradiance) (Walcroft et al. 1997), could not be determined. However, since sites were similar in precipitation, air temperature, and vapor pressure deficit, and because effort was made to sample sunlit foliage, results suggest that differences in integrated WUE are related to differences in soil water supply. Measurements of instantaneous WUE showed interactions with time of day, suggesting that WUE increased diurnally to a greater extent in xeric site trees (Table A.4). Higher (less negative) $\delta^{13}\text{C}$ may therefore reflect greater midday diffusional limitations to CO_2 on the xeric site (Farquhar et al. 1989). The increased sensitivity of stomata to D for this site is consistent with this interpretation.

Differences in tree height between sites may also be related to the patterns of leaf gas exchange observed in this study. Mesic site trees were an average 6 m taller than trees on the xeric site (Figure B.1). Several studies in the recent literature have shown declines in transpiration, stomatal conductance, and photosynthesis with increasing tree height (Yoder et al. 1994, Hubbard et al. 1999, Kolb and Stone 2000, Schäfer et al. 2000). To predict the theoretical decline in canopy stomatal conductance (G_{Siref} at $D = 1$ kPa) related solely to the path length increase with tree height, this study used the hydraulic model of in Schäfer et al. (2000):

$$G_{\text{Siref}} \propto E_L = (1/h_M)(A_S:A_L)(\Delta\Psi_{S-L} - 0.01h_M) \quad (13)$$

where stomatal conductance at $D = 1$ kPa (G_{Siref}) is proportional to transpiration per unit leaf area (E_L), h_M is mid-canopy height, $A_S:A_L$ is sapwood to leaf area ratio, and $\Delta\Psi_{S-L} - 0.01h_M$ is the soil to leaf water potential gradient including the effect of height. The water potential gradient, using predawn leaf water potential to represent Ψ_S , was constant between sites. Modeled values were entirely within the 95% confidence interval of a least square fit to the actual data (Figure B.13), which suggests that increased path length associated with increasing tree height plays some role in limiting maximum stomatal conductance and photosynthesis on the mesic site. An increase in sapwood to leaf area ratio with increasing height was observed, but did not completely compensate for the increase in path length, similar to the findings of Schäfer et al. (2000).

Other factors that may affect tree hydraulic conductance, stomatal conductance, and photosynthesis on these sites but which were not evaluated include differences in tissue permeability related to sapwood anatomical characteristics. Tracheid lumen diameter and length have both been shown to vary with site-quality, with shorter and narrower tracheids being characteristic of resource-poor sites, and associated with greater resistance to water flow (Pothier et al. 1989b). This would argue that trees on resource-limited sites have lower specific hydraulic conductivity and therefore lower rates of gas exchange. Because of the inverse correlation between water and nutrients on the sites in this study, it may be difficult to determine which is the more resource-limited site. However, future measurements of tracheid anatomy and sapwood specific hydraulic conductivity should be done for these sites to determine the degree of variation that occurs and its influence on tree water relations.

Xeric site trees maintained higher rates of water use and gas exchange under non-limiting environmental conditions, but were more sensitive to increasing vapor pressure deficit and decreasing predawn leaf water potential. These patterns led to relatively similar water use and gas exchange over the course of the season between the sites. When averaged over the entire season, there were no differences in water use, stomatal conductance, or photosynthesis between sites, suggesting that these processes were conserved across the sites in this study. Variation in stomatal behavior is one mechanism that may help conserve these processes. Other adjustments, such as shifts in root to leaf area ratio and maximum rooting depth, have been shown to conserve these processes in other systems (Hacke et al. 2000) and likely operate in a similar fashion on the sites in this study. Limits to maximum tree height may also be a means to this end.

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APPENDIX A

TABLES

Table A.1. Soil and stand characteristics for the mesic and xeric sites. Soil texture fractions (percent sand, silt, clay) represent averages for the upper 1 m soil. Water holding capacity is abbreviated WHC and expressed as cm water per m soil. Stand characteristics are for *Pinus palustris* only on each site (oaks codominate xeric site). Values for above-ground net primary productivity (ANPP) are from Mitchell et al. (1999). Values in parentheses for the soil characteristics are ± 1 SE. Values in parentheses for the stand characteristics are ranges.

	Mesic	Xeric
Soil		
Sand fraction (%)	63.4 (1.5)	89.3 (0.8)
Silt fraction (%)	24.3 (3.1)	7.1 (1.1)
Clay fraction(%)	12.4 (4.6)	3.7 (0.3)
WHC (cm m ⁻¹)	40.0	18.0
Stand (characteristics for pine)		
Density (trees ha ⁻¹)	230	54
Basal area (m ² ha ⁻¹)	10.7	2.7
ANPP (Mg ha ⁻¹ yr ⁻¹)	5.0	1.5
Mean diameter at 1.3 m (cm)	21.8 (7.5-52.9)	24.7 (8.6-49.1)
Mean age (years)	44 (19-166)	57 (7-198)
LAI (min-max)	0.8-1.4	0.3-0.5

Table A.2. Characteristics of trees selected for measurement of sap flux density.

Projected leaf area is abbreviated A_L , and A_S is sapwood area calculated from $n = 4$ increment cores per tree.

Site	DBH (cm)	Height (m)	Age (yrs)	Crown length (m)	Crown width (m)	A_L (m²)	A_S (cm²)
Mesic	17.5	17.6	46	8.34	2.79	23.7	211.1
	22.3	18.5	37	10.16	4.55	34.4	343.7
	26.9	21.0	52	10.38	4.64	45.1	488.2
	29.4	18.1	57	7.66	5.10	52.7	542.9
	37.2*	25.7	73	14.56	5.20	75.1	790.8
	39.6*	26.6	70	13.99	5.15	81.2	908.9
	39.8*	24.1	69	11.43	5.28	82.1	948.4
Xeric	16.0	11.1	52	6.29	4.03	24.7	112.8
	20.3	13.6	53	8.23	4.59	36.9	263.5
	22.3	14.9	55	8.22	4.43	45.2	295.8
	27.3*	17.0	47	11.57	5.74	63.3	426.1
	30.0*	17.9	44	12.21	6.88	74.6	522.1
	32.6*	20.1	34	14.34	5.72	86.2	633.7
	36.2	17.7	63	12.01	6.90	104.2	771.3

* designates trees accessible by scaffold towers

Table A.3. Specific leaf area (SLA, $\text{cm}^2 \text{g}^{-1}$) with crown position (lower, middle, upper crown) for mesic and xeric sites. Values represent means from branch harvests (mesic, $n = 46$; xeric, $n = 39$). Standard errors (± 1 SE) are included in parentheses. Different letter designations across sites and crown positions indicate significant differences at $P < 0.05$.

	Mesic	Xeric
Specific Leaf Area (g m^{-2})		
<i>Crown position</i>		
Upper	31.44 (0.99) ^a	33.58 (0.72) ^a
Middle	33.68 (1.67) ^a	33.87 (0.71) ^a
Lower	33.81 (1.25) ^a	34.67 (0.72) ^a

Table A.4. Within-site variation in leaf water potential (Ψ_L , height corrected), stomatal conductance (g_s), photosynthesis (A_{net}), intercellular CO_2 concentration (c_i), and instantaneous water use efficiency (WUE, A_{net}/g_s) averaged for the entire measurement period (excluding drought period). Measurements were conducted during morning (0900-1100 h) and afternoon (1300-1500 h) and at two crown positions (lower and upper) for $n = 3$ trees per site. Numbers in parentheses are ± 1 SE. Letter designations show where significant differences were detected within each site for each character. Means followed by a different letter designation are significantly different at $P < 0.05$.

Mesic	Crown Position		Time of Day	
	<i>Lower</i>	<i>Upper</i>	<i>Morning</i>	<i>Afternoon</i>
Ψ_L (MPa)	-1.11(0.39) ^a	-1.30(0.23) ^a	-1.08(0.01) ^a	-1.60(0.07) ^b
g_s (mmol m ⁻² s ⁻¹)	50.43(2.81) ^a	55.64(2.8) ^a	55.22(2.74) ^a	50.27(7.31) ^a
A_{net} (μ mol m ⁻² s ⁻¹)	4.12(0.16) ^a	4.68(0.15) ^a	4.78(0.26) ^a	4.75(0.39) ^a
c_i (ppm)	190.6(4.6) ^a	187.8(6.0) ^a	191.0(6.3)	187.2(6.4)
WUE (μ mol mmol ⁻¹)	0.092(0.004) ^a	0.093(0.004) ^a	0.092(0.004) ^a	0.092(0.004) ^a
Xeric	Crown Position		Time of Day	
	<i>Lower</i>	<i>Upper</i>	<i>Morning</i>	<i>Afternoon</i>
Ψ_L (MPa)	-1.17(0.39) ^a	-1.37(0.21) ^a	-1.19(0.03) ^a	-1.64(0.04) ^b
g_s (mmol m ⁻² s ⁻¹)	59.96(3.26) ^a	56.12(2.86) ^a	73.39(6.01) ^a	54.98(5.30) ^b
A_{net} (μ mol m ⁻² s ⁻¹)	4.65(0.17) ^a	4.56(0.16) ^a	5.59(0.39) ^a	3.86(0.31) ^b
c_i (ppm)	195.82(4.6) ^a	188.94(4.62) ^a	200.29(4.17) ^a	181.44(4.99) ^b
WUE (μ mol mmol ⁻¹)	0.087(0.003) ^a	0.092(0.004) ^a	0.085(0.003) ^a	0.095(0.003) ^b

Table A.5. Leaf nitrogen content (top panel) and seasonally integrated water use efficiency, $\delta^{13}\text{C}$ (bottom panel), for $n = 30$ trees per site. Values for leaf N are expressed both on a mass basis (%) and an area basis (g m^{-2}). Values in parenthesis are ± 1 SE of the mean. Means for each character followed different letter designations indicate significant differences at $P < 0.05$.

	Mesic	Xeric
Leaf Nitrogen Content		
Mass based (%)	0.787 (0.014) ^a	0.857 (0.014) ^b
Area based (g m^{-2})	2.60 (0.049) ^a	2.91 (0.043) ^b
Leaf $\delta^{13}\text{C}$	-28.29(.19) ^a	-26.72(.16) ^b

Table A.6. Ensemble means generated for tests of within-tree variation in sap flux density (J_S , $\text{g cm}^{-2} \text{d}^{-1}$) measured at 1.3 m stem height. Each value represents mean of 3 trees per site averaged over the test period, which extended from August 29 – October 19, 2000. Values in parentheses are ± 1 SE. Means followed by the same letter both within and across columns are not significantly different at $P > 0.05$.

	Mesic	Xeric
Probe location (xylem depth)		
J_S north (0-30mm)	37.37 (± 7.5) ^a	47.03 (± 4.3) ^a
J_S north (30-60mm)	14.57 (± 2.61) ^b	19.28 (± 6.32) ^b
J_S south (0-30mm)	39.98 (± 12.89) ^a	64.04 (± 6.74) ^c

Table A.7. Percent of time mesic and xeric site trees spent above and below their soil moisture (θ) thresholds (mesic θ threshold = $0.087 \text{ m}^3 \text{ m}^{-3}$; xeric = $0.056 \text{ m}^3 \text{ m}^{-3}$) during the study year (year 2000) and for the 5 years previous (1995-1999).

Site	Year 2000 (%Time)		1995-1999 Mean (%Time)	
	Above	Below	Above	Below
Mesic	85.7	14.3	87.9	12.1
Xeric	78.6	21.4	76.6	23.4

APPENDIX B

FIGURES

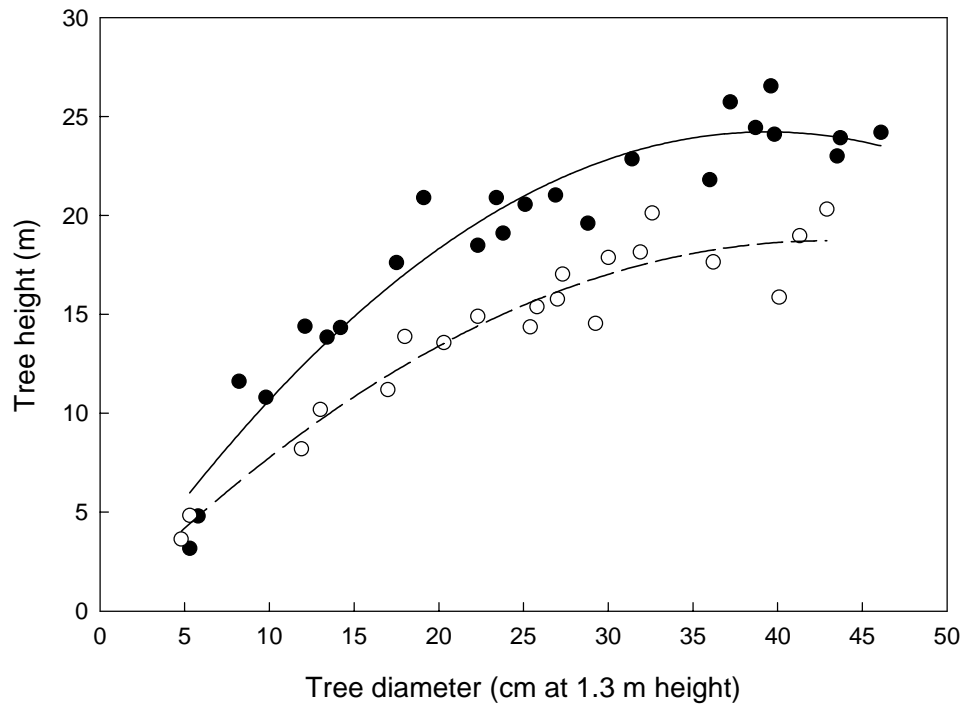


Figure B.1. Tree height versus diameter at 1.3 m stem height for mesic (closed circles) and xeric (open circles) sites.

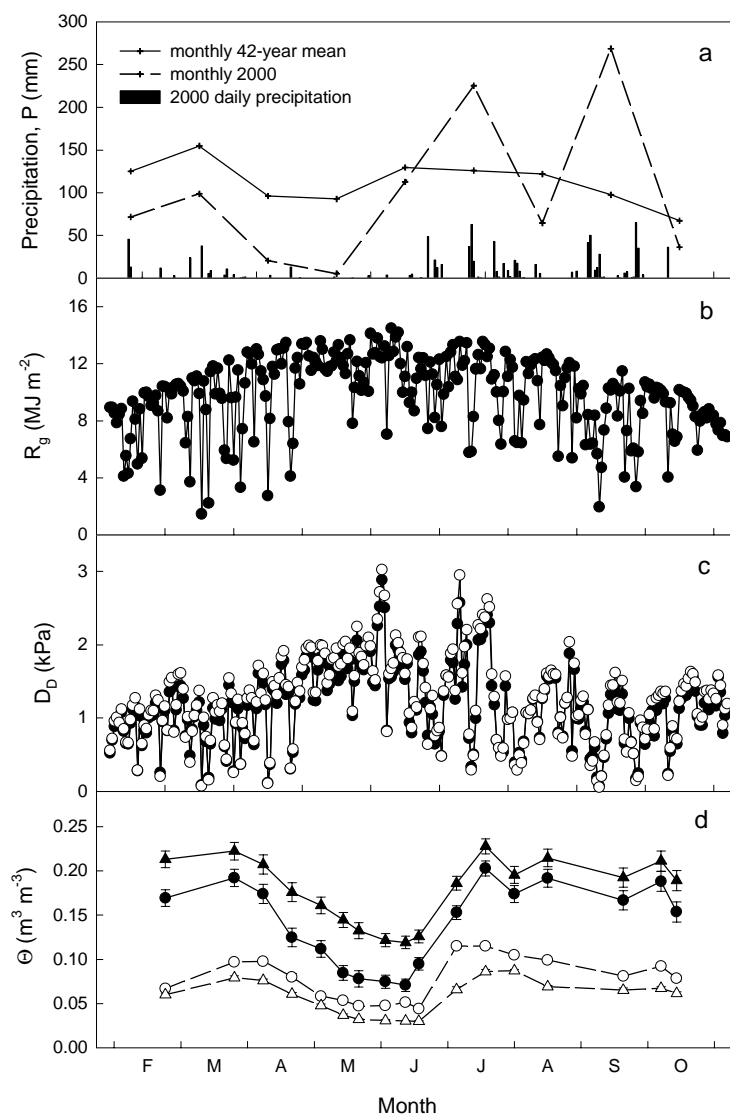


Figure B.2. (a) Daily precipitation (P), (b) daily average global radiation (R_g), (c) daytime averaged atmospheric vapor pressure deficit (D_D) for mesic (closed circle) and xeric (open circle) site, and (d) soil volumetric water content (θ) at to 30 cm (circles) and 90 cm (triangles) soil depth on mesic (closed symbols) and xeric (open symbols) sites. Error bars are ± 1 SE.

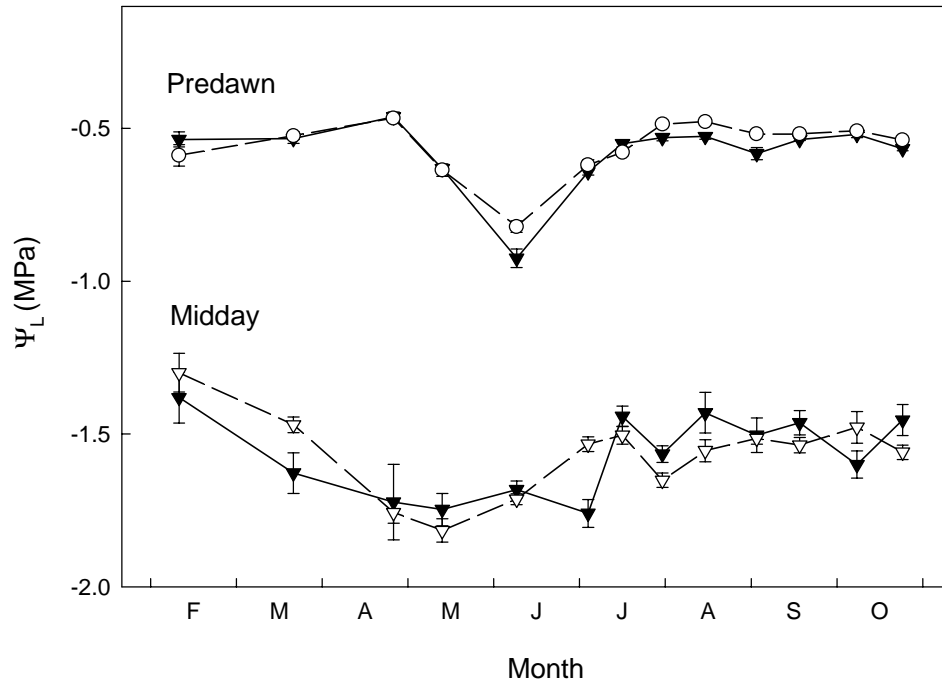


Figure B.3. Seasonal course of predawn (circles) and midday (triangles) leaf water potential (Ψ_L) for mesic (closed symbols) and xeric (open symbols) sites. All data are corrected for site-differences in tree height using 0.01 MPa per m height. Values represent means of $n = 3$ trees per site. Error bars are ± 1 SE.

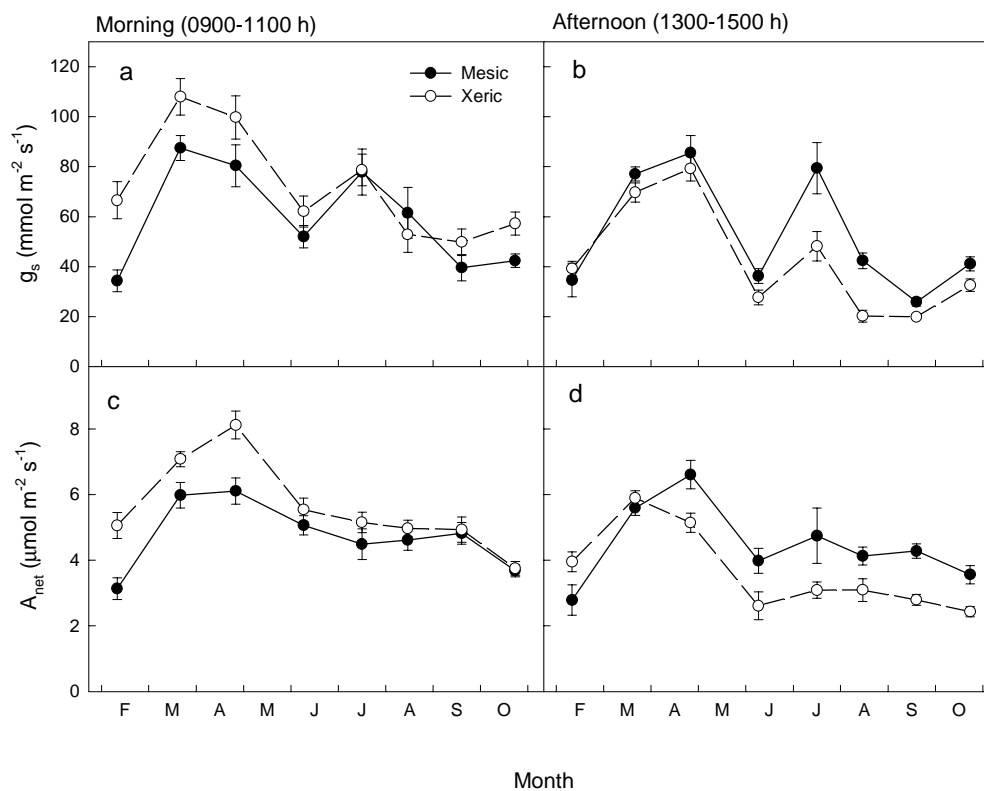


Figure B.4. Seasonal course of leaf gas exchange for morning (0900-1100 hrs) and afternoon (1300-1500 hrs) for $n = 3$ trees per site on mesic (closed circles) and xeric (open circles) site. (a) Morning stomatal conductance, g_s , (b) afternoon g_s , (c) morning photosynthesis, A_{net} , and (d) afternoon A_{net} . Error bars are ± 1 SE.

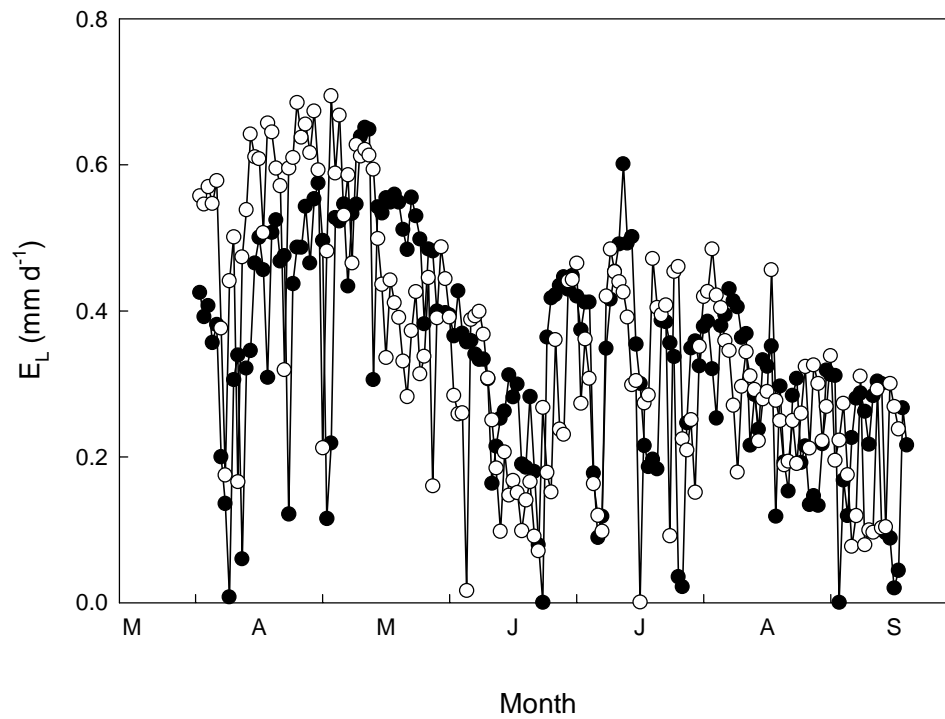


Figure B.5. Seasonal course of daily transpiration per unit leaf area (E_L) for mesic (closed circle) and xeric (open circle) sites scaled to every *Pinus palustris* in each stand.

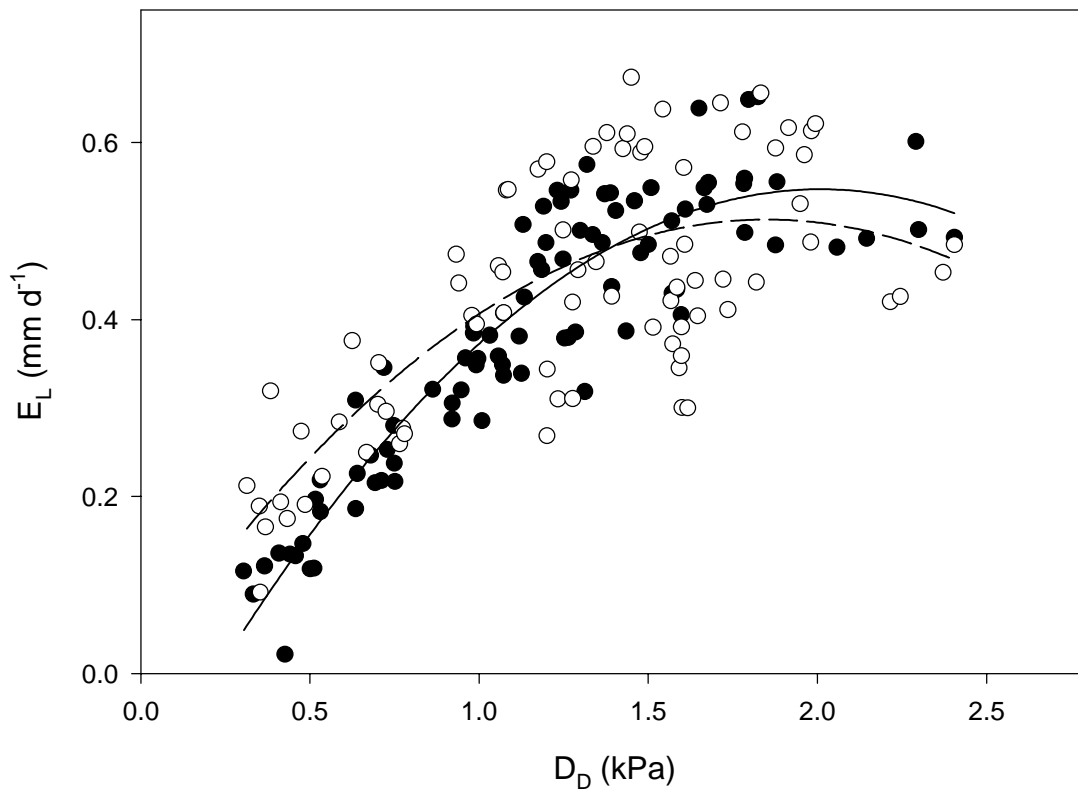


Figure B.6. Daily transpiration per unit leaf area (E_L) versus daytime-averaged vapor pressure deficit (D_D) under non-limiting soil moisture conditions for mesic (closed circle, solid line) and xeric (open circle, dashed line) sites.

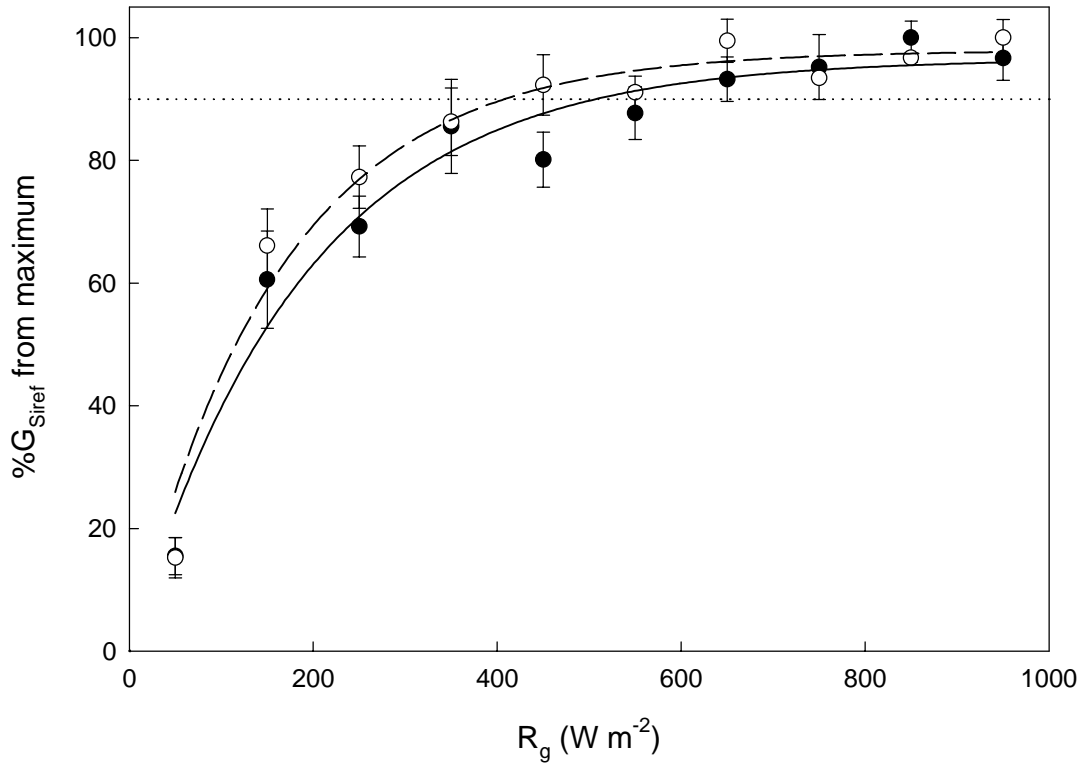


Figure B.7. Percent response of mean stomatal conductance (G_{Siref}) at a reference vapor pressure deficit ($D = 1$ kPa) to global solar radiation (R_g) for mesic (closed symbol, solid line) and xeric sites (open symbol, dashed line). Values represent means of $n = 3$ trees per site, with error bars representing ± 1 SE of mean. Dotted line represents 90% of maximum G_{Siref} .

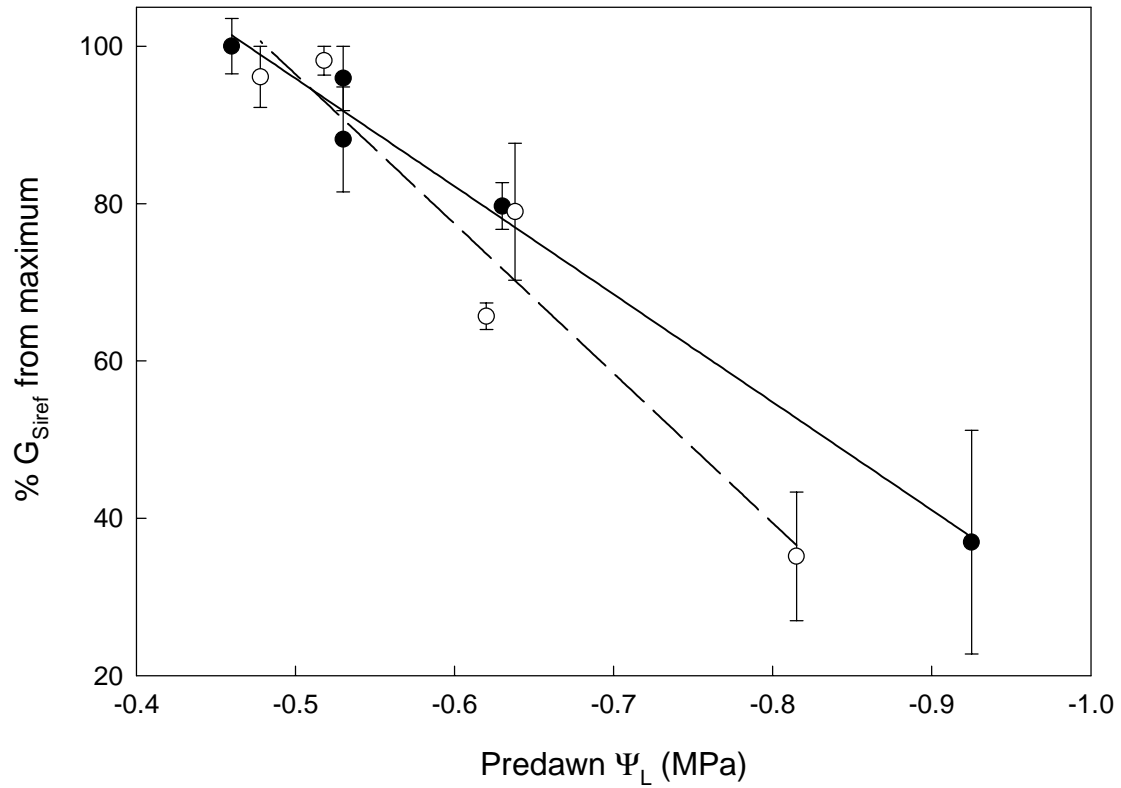


Figure B.8. Percent decline in mean stomatal conductance (G_{Siref} , at $D = 1$ kPa) with decreasing predawn leaf water potential (Ψ_L) for mesic (closed symbol, solid line) and xeric (open symbol, dashed line) sites. Values represent means of $n = 3$ trees per site, with error bars representing ± 1 SE of mean.

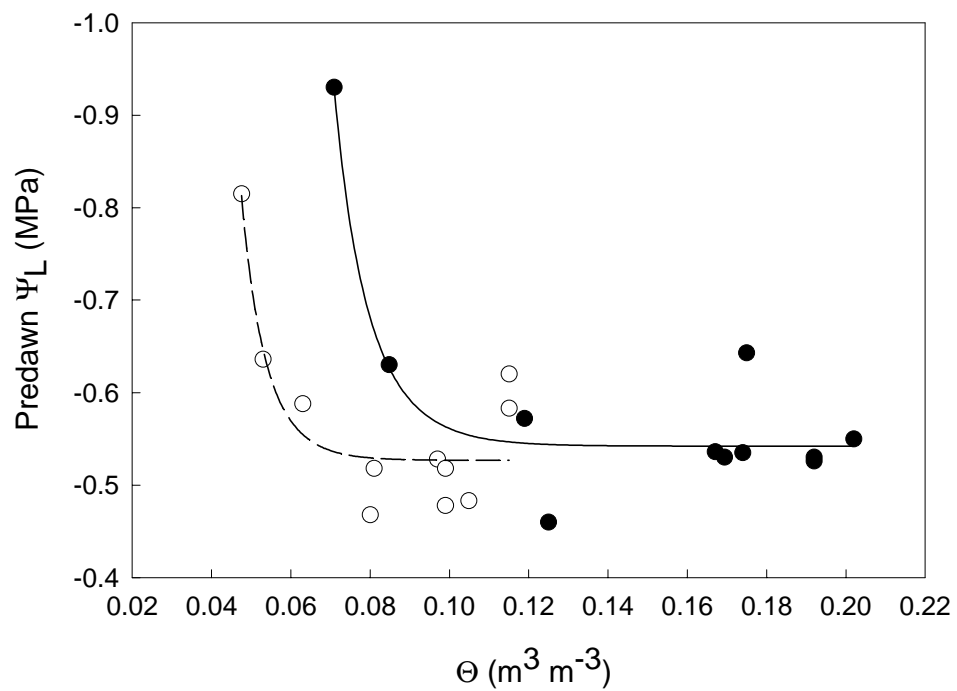


Figure B.9. Predawn leaf water potential (Ψ_L) versus soil moisture content (Θ) at 0-30 cm soil depth for mesic (closed symbols) and xeric (open symbols) sites.

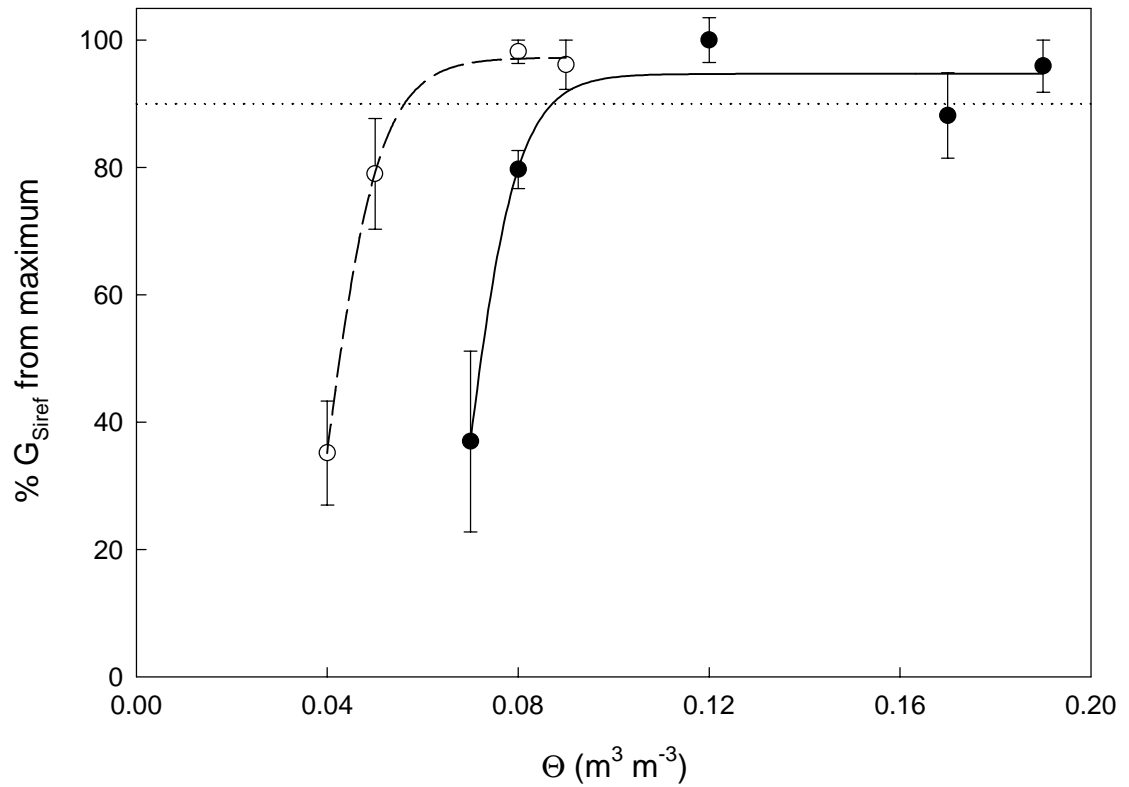


Figure B.10. Percent reduction in mean stomatal conductance (G_{Siref} , at $D = 1$ kPa) with declining soil moisture content (θ) at 0-30 cm soil depth for mesic (closed symbol, solid line) and xeric (open symbol, dashed line) sites. Values represent means of $n = 3$ trees per site, with error bars representing ± 1 SE of mean. Dotted line represents 90% of maximum G_{Siref} .

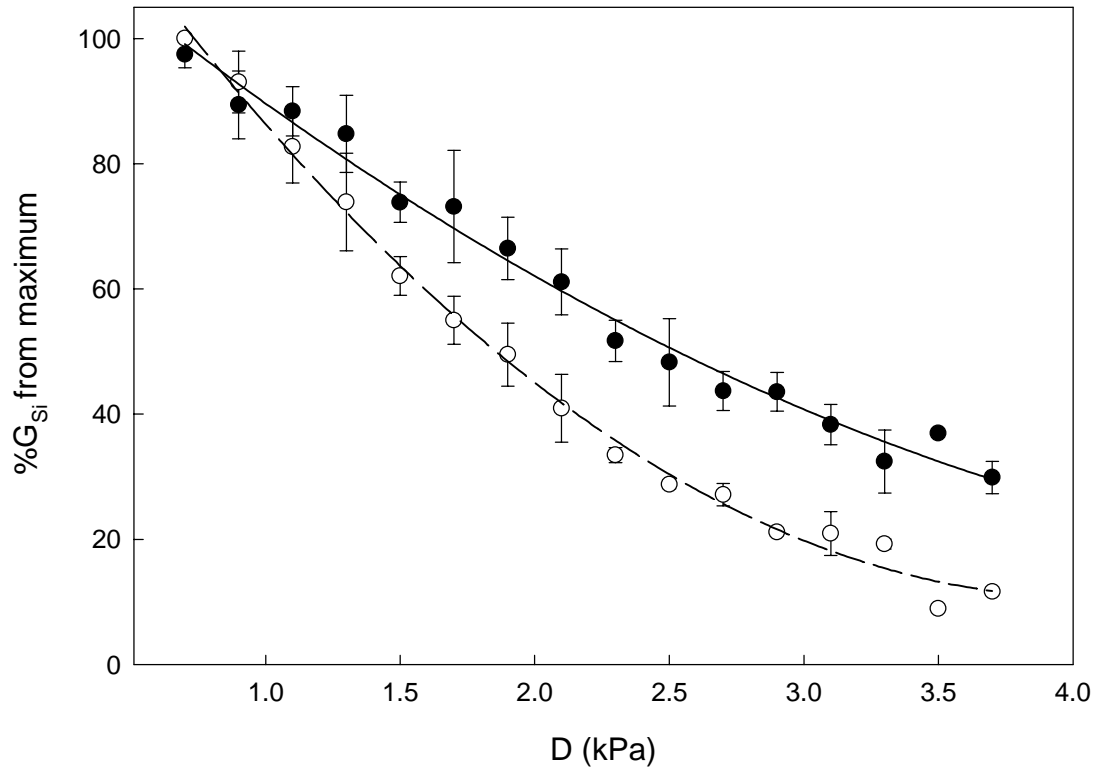


Figure B.11. Percent response of mean stomatal conductance (G_{Si}) to increasing vapor pressure deficit (D) for mesic (closed symbol, solid line) and xeric (open symbol, dashed line) sites. Values represent means of $n = 3$ trees per site, with error bars representing ± 1 SE of mean.

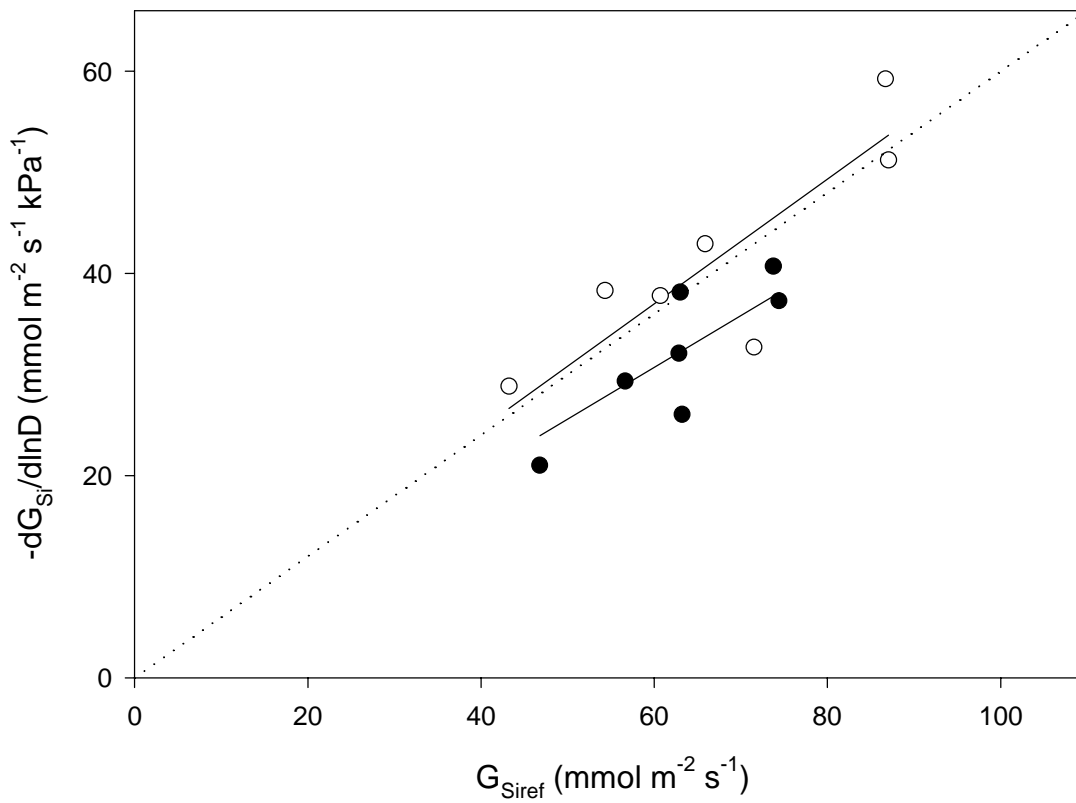


Figure B.12. Stomatal sensitivity ($-dG_{Si}/d\ln D$) as a function of mean stomatal conductance at reference vapore pressure deficit ($G_{Si,ref}$, $D = 1$ kPa) for mesic (closed symbol) and xeric (open symbol) sites.

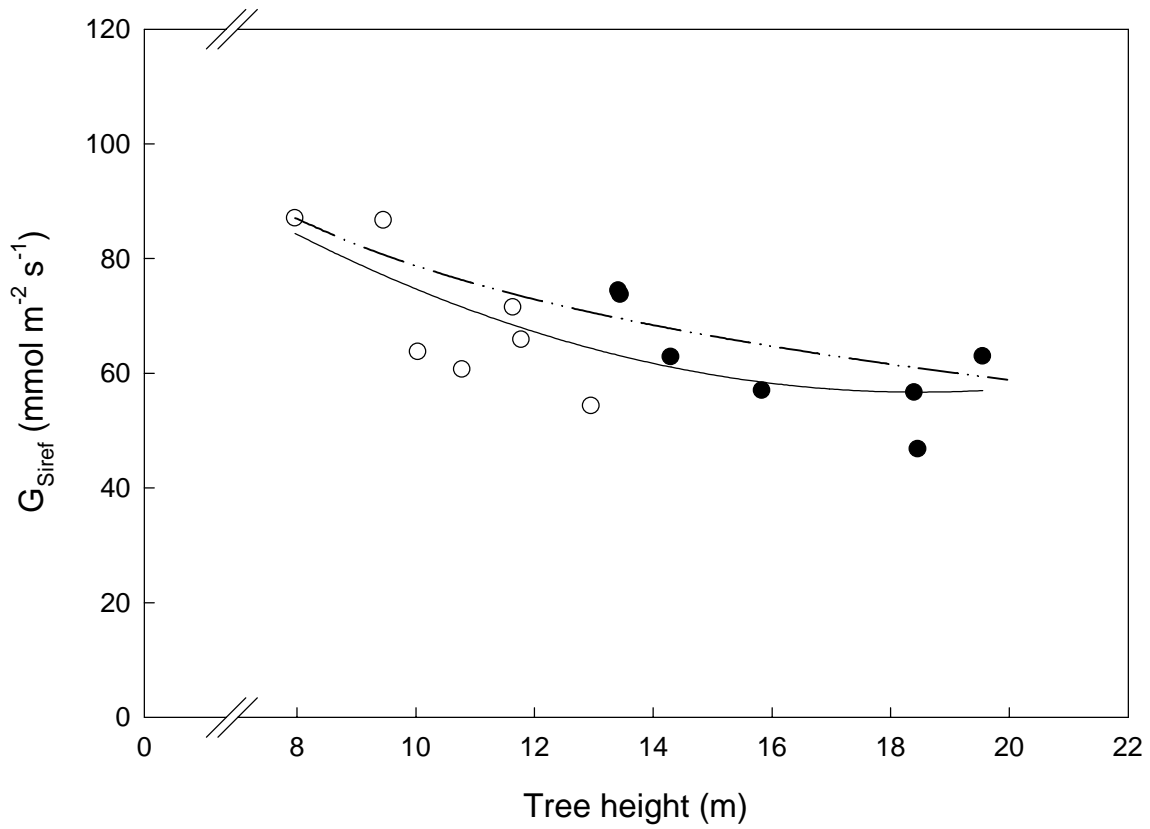


Figure B.13. Decline in mean stomatal conductance at reference vapor pressure deficit (G_{Siref} , $D = 1$ kPa) with increasing tree height across both mesic (solid circles) and xeric (open circles) sites. Solid line shows least square fit to the data, while dash-dotted line shows expected decline with tree height based on the hydraulic model in Equation 13.