Comparative Plant Water Relations and Soil Water Depletion Patterns of Three Seral Shrub Species on Forest Sites in Southwestern Oregon

Susan G. Conard, Steven R. Sparks, and Jon C. Regelbrugge

ABSTRACT. We compared stomatal conductance, transpiration, plant water potential, and soil moisture depletion patterns for three shrub species common on early seral forest sites in southwestern Oregon following logging or fire. Our goal was to determine which of these species were more likely to be the strongest competitors with regenerating conifers. The three species, *Arctostaphylos patula* Greene, *Ceanothus sanguineus* Pursh., and *Holodiscus discolor* (Pursh.) Maxim., were selected to represent a range in leaf morphology and expected water use patterns. Diurnal patterns of leaf conductance, plant water potential, and environmental parameters were measured throughout the growing season, along with seasonal patterns in soil moisture. As with any data obtained under ambient field conditions, environmental parameters and exact timing of measurements varied among shrubs. To better evaluate the response of individual species to common environmental parameters, we constructed models of leaf conductance based on field data and used these models to estimate responses of conductance and transpiration to averaged environmental conditions. This allowed us to better compare species responses to seasonal and diurnal trends in environmental variables. C. *sanguineus typically* had the highest transpiration rates per unit leaf area, and *H. discolor* the lowest; however, due to much higher leaf area indices of *H.* discolor, the two species depleted soil moisture at about the same rate. C. *sanguineus and A. patula* both had high predawn water potentials throughout the season, even when soil water potential at 1 m depth was less than -1.2 Mpa, suggesting that these species, but not *H.* discolor, had roots in deeper soil layers. We predict that the two deciduous species, *C. sanguineus* and *H. discolor*, will be stronger competitors for soil moisture than *A. patula,* at least in the top meter of soil. In contrast, *A. patula* and C. *sanguineus* are capable of depleting moisture from deeper in the soil and may therefore strongly compete even with deep-rooted conifers late in the season. Our use of empirical models allowed us to compare species responses to common environmental conditions, which facilitated ecological interpretation of species differences in water use patterns. By early August, soil water potentials under all species were low enough to significantly inhibit conifer transpiration, photosynthesis, and growth. For. Sci. 43(3):336-347.

Additional Key Words: Stomatal conductance, transpiration, water use, soil moisture.

IN MANY FORESTS OF THE PACIFIC NORTHWEST and California, seasonal water deficits limit establishment and growth of conifers following logging (Walstad et al. 1987, Tappeiner et al. 1992). Neighboring broadleaf shrubs and trees, many of which sprout or establish seedlings very quickly after fire or logging, can reduce the amount of soil moisture available for the regenerating conifers (Carter et al. 1984, Lanini and Radosevich 1986, Shainsky and Radosevich 1986, Petersen et al. 1988, White and Newton 1989, Pabst et al. 1990, Wang et al.1995), thereby impeding conifer seed-

---

Susan G. Conard and Jon C. Regelbrugge, Pacific Southwest Research Station, USDA Forest Service, 4955 Canyon Crest Dr., Riverside, CA, 92507 (909-680-1542; FAX 909-680-1501; E-mail: /s j.regelbrugge/out=s27105a@mhs-fswa.attmail.com); Steven Sparks, Division of Math and Science, Arizona Western College, P.O. Box 929, Yuma, AZ 85366-0929 (520-344-7719; FAX 520-344-7730; E-mail: ssparks@awc.cc.az.us). Susan Conard's current address is Vegetation Management and Protection Research, USDA Forest Service, P.O. Box 96090, Washington, DC 20090-6090 (202205-1561; Fax: 202-205-2497; E-mail: sgconard@aol.com).

Acknowledgments: The research reported here was supported by cooperative agreement with the Pacific Northwest Research Station, USDA Forest Service, PNW-82-328, and was started while the senior author was Postdoctoral Research Associate at Oregon State University. Many thanks are due Lynn Evans and Carol Whittaker for their able assistance in the field, and David Randall for statistical and analytical advice.

Manuscript received April 28, 1995. Accepted April 1, 1996.

ling establishment and growth. Conifer sapling growth may be suppressed for many decades by competing shrubs (Skau et al. 1970, Gratkowski et al. 1973, Bolsinger 1980, Conard and Radosevich 1982, Walstad et al. 1987, Conard and Sparks 1993), until shrubs are eventually shaded out by conifer canopy closure.

Plant species differ in their transpiration rates, patterns of root distribution, and responses to water stress. These different patterns of water use likely result from differences among species in morphological and physiological characteristics that affect the rate of soil moisture depletion and the distribution of water removal at different soil depths. Natural communities of the Pacific Northwest contain seral shrub species of markedly different growth forms and leaf characteristics, ranging from thin-leaved deciduous species to evergreen sclerophylls. We might expect these morphological, and associated physiological, differences to be associated with substantially different responses to environmental conditions and stress. The relative timing, spatial distribution, and maximum potential water removal by co-occurring plants, when coupled with the abilities of those plants to tolerate water deficits, should largely determine the strength of the competitive interactions in a water-limited system. That such differences cause some shrub species to be more vigorous competitors for soil water than others is conventional wisdom. Demonstrations of this idea in wildland systems are lacking, however.

Predicting or quantifying plant water use is difficult because leaf conductance and transpiration are affected by several interdependent factors that tend to vary together under ambient conditions. Stomatal conductance depends on light, vapor pressure deficit from leaf to air, leaf temperature, leaf water potential, soil water potential, and ambient C02 concentrations (Hinckley et al. 1975, Raschke 1975, Burrows and Milthorpe 1976, Jarvis 1976, Reed et al. 1976, Pallardy and Kozlowski 1979, Gollan et al. 1985, Reich and Hinckley 1989, Turner 1991). Recent evidence indicates that seasonal soil drying can increase levels of abscisic acid in the xylem sap, which in turn decreases maximum daily stomatal conductance (Zhang et al. 1987, Wartinger et al. 1990, Turner 1991). However, this relationship may not hold later in the season, when abscisic acid levels may decrease as soil drying continues (Wartinger et al.1990). Relationships between soil water potential, or predawn plant water potential, and diurnal conductance patterns are less clear (e.g., Reich and Hinckley 1989). In the laboratory, each of these influencing factors (driving variables) can be varied singly while the others are held constant. However, in the field these driving variables often vary simultaneously (e.g., Hinckley et al. 1975, Jarvis 1976, Reed et al. 1976, Pallardy and Kozlowski 1979). For example, leaf temperature may affect vapor pressure deficit, and air temperature typically varies diurnally with light. Not only may leaf water potential influence stomatal conductance, and hence transpiration, but the amount of water lostby transpiration will influence leaf water potential, blurring the distinction between response and driving variables. Furthermore, the effects of the driving variables on stomatal conductance are best represented as multiplicative, rather than additive, because if any one of the driving variables occurs in a range that causes stomatal closure, the resulting stomatal conductance will be zero regardless of the values of the other driving variables. The interdependent nature of the driving variables often obscures the simple relationships between leaf conductance and any one of the driving variables when they are derived from field data (Jarvis 1976). Finally, the simple relationships between stomatal conductance and at least two of the driving variables (temperature and light) are nonlinear, and at least one of those relationships, that with light, is likely best represented by a function that is nonlinear in the parameters (Burrows and Milthorpe 1976, Jarvis 1976, Warrit et al. 1980). Because of the complex relationships between stomatal conductance and the environmental driving variables, and because of the spatial and temporal variability in driving variables for field data, we felt that comparisons of patterns of water use among the species would be facilitated by the use of empirical models developed with nonlinear regression techniques, thus allowing us to simulate species' responses to a uniform set of environmental driving variables (Jarvis 1976, Reed et al. 1976, Schulze et al. 1976).

Our objectives were: (1) to estimate and contrast patterns of water use of three shrub species believed to be major competitors with conifers for water using models of leaf conductance developed from field data, and (2) to discuss possible implications of these patterns for relative impacts of these three shrub species on soil moisture and, by implication, conifer performance. The shrub species selected for this study were *Arctostaphylos patula* Greene (Ericaceae), *Ceanothus sanguineus* Pursh. (Rhamnaceae), and *Holodiscus discolor* (Pursh.) Maxim. (Rosaceae) (species nomenclature follows Hitchcock and Cronquist 1973). These species were selected because they span a wide range in leaf morphology from evergreen sclerophyll *(A. patula),* to deciduous semisclerophyll (C. *sanguineus),* to thin-leaved deciduous *(H. discolor)* species.

Materials and Methods

Study Sites

The study sites were in the Siskiyou Mountains of southwestern Oregon approximately 57 km southwest of Medford, in T40S, R2W, Section 30. Soils in the 77 ha clearcut unit were moderately deep sandy loams derived from highly weathered granite parent material. Except for a weak ochric surface horizon, there was little or no profile development. Site elevation was 1460 m, and slopes averaged 15-20°. *Ceanothus sanguineus* (redstem ceanothus), *Arctostaphylos patula* (greenleaf manzanita), and *Holodiscus discolor* (oceanspray) dominated the site. Common associates included *Rubus parviflorus* Nutt. (thimbleberry), *Ribes* spp. (gooseberry), *Berberis spp.* (Oregon grape), and *Arbutus menziesii* Pursh. (Pacific madrone). Conifer species on the site included *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir), *Abies concolor* (Gord & G1end.) Lindl. (white fir), and *Pinus ponderosa* Dougl. ex. Laws. (ponderosa pine). The shrubs ranged from about 1.5 m to 2.5 m tall at the time of the study. Two study areas were established in spring 1983 on opposite aspects within the clearcut unit, at azimuths of 65° (eastfacing slope) and 265° (west-facing slope).

Species Selection

Our study species were selected because we expected their water use patterns to be markedly different. Because there are few species on which comparative data are available, the degree of sclerophylly and evergreenness were used as indicators of expected differences in water use patterns. The selected species span the range, from a thin-leaved deciduous species (H. *discolor*), to a semisclerophyllous deciduous species (C. *sanguineus)* and a sclerophyllous evergreen species (A. *patula).* Three typical individuals of each species were selected within each of the two study blocks. All vegetation was cleared by hand from a 2 m radius around each shrub in spring 1983 to isolate effects of individual shrubs on soil moisture and minimize competitive interactions. Clearing was repeated as needed.

Soil Moisture and Temperature Measurements

Cylindrical gypsum soil moisture blocks (Delmhorst, Inc.) were buried at three depths (25, 50, 100 cm) on the N, S, E, and W sides of each shrub at 1 m from the shrub center. Calibrated copper-constantan thermocouples were buried with the blocks on all 4 sides at 25 cm, on N and S sides at 50 cm, and on the W side at the 100 cm depth. A subsample of 25 blocks was calibrated to -1.5 MPa on a pressure plate in the laboratory using soil from the study site. Regression equations relating soil water potential to resistance were developed from pressure plate calibrations. Soil moisture and temperature were measured with an ohmmeter (Soiltest, Model MC300B) and a microvolt meter (Keithley Instruments, Model 155) with an internal reference junction. Soil moisture readings were corrected for temperature using the calibrations developed by Aitchison et al. (1951). Field measurements took place at 2 wk intervals throughout the summer of 1983 and 4 times during the summer of 1984. We report only data from 1984, as 1983 data indicated some initial adverse effects of disturbance from clearing on stomatal conductance and growth in some of the sample shrubs.

Leaf Area and Shrub Size Measurements

Total leaf area for each shrub was determined by estimating the number of leaves and the average area of a single leaf. On each shrub leaves were counted for 10% of the shrub volume using a triangular frame we devised to enclose 5% of the shrub's volume in a vertical 18° sector radiating from the shrub center. Two radially opposite sectors were sampled. The number of leaves within both 3 dimensional sectors was counted and multiplied by 10 to estimate the number of leaves per shrub.

At least 100 leaves were collected from each shrub to determine the average area of a single leaf. Leaves were collected from the same two volumes sampled for leaf counts. Average leaf area was determined by measuring the total leaf area of the sample with a leaf area meter (LiCor, Model LI 3000), and dividing the total area by the number of leaves in the sample. Total shrub leaf area was then estimated by multiplying the total number of leaves by the average leaf area.

Projected ground area for each shrub was determined by measuring the width of each shrub in two perpendicular directions at the shrub's greatest width. Total leaf surface area was divided by the projected shrub ground area to calculate Leaf Area Index (LAI).

Plant Water Status Measurements

Leaf conductance to water vapor, and leaf and air temperatures were measured on individual leaves with a null-balance porometer (Lambda Instruments, LI-1600). Leaves of A. *patula* are amphistomatous, so two measurements were made on each leaf, one on each side, and the leaf conductance values were added together. Only the adaxial side of the hypostomatous leaves of C. *sanguineus* and H. *discolor* was measured.

Xylem pressure potential of stems, used to estimate leaf water potential, was measured with a pressure chamber (PMS Instruments). Three replicate measurements were made of each variable on each shrub in a block during a 11.5 hr sampling period. These measurements were regarded as subsamples and combined into single summary observations. This procedure was repeated at least 4 (usually 5) times throughout the day. The initial xylem pressure potential measurement for each day was predawn. Porometer measurements were begun as soon as dew had evaporated from the foliage. Predawn water potentials and the first porometer measurement of the day were paired for modeling purposes, on the assumption that water potential did not change between the time of sampling and the time of the initial conductance measurement. Each of the two blocks was sampled on a separate day within a 3 day period. Measurements of soil moisture and temperature were taken during the same sampling periods. Each block was sampled four times during the growing season.

Environmental Measurements

Air temperature and relative humidity were recorded on each block with a 30 day clock drive hygrothermograph (Weathermeasure, Model H311) in a standard ventilated instrument shelter. Photosynthetic photon flux density was measured with a Li-Cor quantum sensor.

Analyses

Modeling Approach

Directly comparing measured leaf conductance and transpiration among species growing under field conditions is difficult. Leaf conductance is influenced by several interdependent driving variables. Because these factors vary spatially and temporally, perceived differences in leaf conductance and transpiration may be confounded by short-term or local differences in environmental driving variables. To ensure that we were observing true differences in responses among species, we developed nonlinear regression models of leaf conductance as a function of environmental and plant variables and used these models to estimate and compare water use among the three species. This allowed us to make comparisons among species without confounding from environmental variation.

The general approach to developing leaf conductance models and using these models to compare water use patterns among species consisted of several steps. The model form was derived analytically from expected relationships of driving variables and leaf conductance, and then nonlinear least squares regression was used to estimate model coefficients for each species separately. Model fit was evaluated using various diagnostic measures. Leaf conductance in relation to environmental driving variables was compared among species by using the model to estimate conductance for each species under common environmental conditions. Instantaneous transpiration rate at several times over the course of a day was calculated using these model-estimated conductances and the leaf-to-air water vapor concentration gradient, and total daily transpiration was estimated by approximating the integral of the diurnal course of instantaneous transpiration. Finally, transpiration per unit leaf area was scaled up to a whole plant basis by multiplying by estimated shrub leaf area, and total mass of water transpired over the season was estimated by approximating the integral of the seasonal course of daily transpiration. This modeling approach is discussed in more detail below.

Model Specification

Models of leaf conductance as a function of vapor pressure deficit (VPD), plant water potential (..$_p$), leaf temperature (LFT), and photosynthetic photon flux density (PPFD) were constructed to estimate and compare water use of the three shrub species. Initial exploratory analysis showed no significant relationships between soil water potential or predawn plant water potential and leaf conductance. Leaf conductance was assumed to be inversely linear with respect to VPD (Jarvis 1976, Kaufmann and Levy 1976, Schulze et al. 1976, Thorpe et al. 1980, Schulze and Hall 1982) and ..$_p$ (Jarvis 1976, Jones and Rawson 1979, Schulze and Hall 1982), a concave quadratic function of LFT (Takakura et al. 1975, Burrows and Milthorpe 1976, Jarvis 1976, Schulze et al. 1976), and a decaying exponential with respect to PPF (Burrows and Milthorpe 1976, Jarvis 1976, Schulze et al. 1976, Warrit et al. 1980, Schulze and Hall 1982). The terms were specified to be multiplicative. The final form of the model is:

$$g=\eta_0(1+\eta_1X_1)(1+\eta_2X_2)(1+\eta_3X_3+\eta_4X_3^{\,2})(1-e^{(-\eta_5x_4)}) \qquad (1)$$

where g= estimated conductance (cm s_{-1} *); $\eta\iota$ = model parameters*; X_1 = VPD (kPa) - 2; X_2 = ..$_p$(-MPa) -10; X_3 = LFT (°C) - 10; X_4 = PPFD (σmole m_{-2} s_{-1}). Constants were subtracted from X_1, X_2, and X_3 to facilitate model convergence. Absolute values of ..$_p$ were used for model fitting (i.e., -..$_p$). We assumed that ambient levels of CO_2 remained constant (e.g., Schulze et al. 1976, Hinckley et al. 1975, Pallardy and Kozlowski 1979).

The model was fitted to the data for each species separately using the SAS NLIN procedure and the Marquardt estimation algorithm (SAS Institute, 1988). Residual plots of the initial model fits indicated that the estimated conductances were locally biased and heteroscedastic. Model parameters were then re-estimated using iterative reweighting.Weights were inversely proportional to the squares of the estimated conductances under the assumption of constant coefficient of variation. This procedure considerably reduced local model bias, although there was still some tendency to underestimate the highest values of leaf conductance for all three species models. The re-estimated models were homoscedastic, and the weighted residuals were approximately normally distributed, except for the C. *sanguineus* model, where the residuals did not appear to be seriously nonnormal (Kolmogorov D statistic, $P < 0.024$). Although residuals were often fairly large (± -25% of the estimated leaf conductance values), the model fits seemed satisfactory, given the complexity of the four-predictor nonlinear model and given the study objectives of comparing the response of leaf conductance (and consequently, transpiration) to the environmental driving variables among the three species.

Inspection of diurnal plots of environmental variables and plant water status indicated that shrub water relations were very similar on the two aspects. We therefore combined the data from the two blocks for model estimation. Analysis of residuals from the conductance models showed no evidence of differences among blocks in conductance response to driving variables (t-test; $P > 0.05$), supporting the combining of blocks.

Reduced models were also estimated by dropping one term at a time from the full model and using the same weights as the full model (the final weights generated by the iteratively reweighted procedure). The mean square errors from the full and reduced models were used to calculate asymptotic F-statistics evaluating the contribution of each of the terms to the model sum of squares.

Species Comparisons

The four-predictor nature of these nonlinear models of leaf conductance made graphical and analytical comparisons of model predictions among the three species difficult. Furthermore, values of independent variables obtained in the field differed within and among species even within a sampling period. To compare expected species responses under identical environmental conditions, we calculated model conductance estimates for each of the three species based on the same (or analogous) input values for the driving variables. To obtain input values, we created an evaluation data set by averaging VPD, LFT, and PPFD across species, for each of the five daily sampling times on each of the four sampling dates (the two sampling dates, one per block, were combined for each of the four seasonal rounds of sampling). By also averaging the time of measurement for each of the five daily sampling rounds, we constructed an average diurnal course for the measured environmental variables (for the purpose of this comparison, we considered LFT to be an environmental variable).

Because ..$_p$ is a biological variable, rather than an environmental variable, it was averaged within species for each time of day on a particular sampling date. Thus, model input values for the species comparisons used average diurnal courses of VPD, LFT, and PPFD that were common to all three species, but used average diurnal courses of ..$_p$ that were appropriate for, and unique to, each species.

These evaluation data were appended to the data used for fitting in the NLIN procedure. Evaluation data were given zero weight, and so did not influence model fitting; their inclusion in the fitting procedure allowed NLIN to calculate estimated conductances for the evaluation data, and their associated error estimates.

Estimated mean leaf conductances were compared between species at each day-time combination of the calculated average diurnal courses of model driving variables by pairwise asymptotic t-tests, using a modified Bonferroni adjustment (Hochberg 1988) to assure that ζ < 0.05 for all comparisons. The error estimates on the model estimated conductances required by these comparisons were those calculated by the NLIN procedure.

Estimated Daily Transpiration

Estimated values of transpiration per unit leaf area (g H_2O cm cm^{-2}s^{-1}) were calculated for each day-time combination of the average diurnal courses of driving variables by multiplying estimated conductances for each time of day by the water vapor concentration gradient (æC_w), which was in turn calculated from average humidity and temperature values. These æC_w values were assumed to be identical among the three species. Error estimates were also scaled by æC_w.

Initial and final measurements of leaf conductance in the field were made at different times of day for the different sampling dates, so the average initial and final values of the environmental driving variables in the evaluation data set (as well as the estimated values of conductance and transpiration) were also at different times on different sampling dates. Furthermore, complete diurnal measurements (from sunrise to sunset) were not available for any of the sampling dates. So, in order to standardize calculated estimators of mean total daily transpiration, we integrated under the diurnal transpiration curves between 0900 hr and 1500 hr using a trapezoidal approximation. The integral of each daily transpiration curve was represented as a function of the regression parameters, whose covariances had been estimated during the fitting of the model. Standard errors of these estimators of mean daily transpiration were then estimated by Taylor series approximation (Mood et al. 1974).

Leaf Area and Shrub Size

Species comparisons of total shrub leaf area, projected shrub area, and leaf area index (LAI; leaf area/shrub area) were carried out by one-way analysis of variance followed by a least significant difference test using ζ = 0.05 (SAS Institute 1988). Shrubs from the two blocks were pooled for each species in these analyses of variance (N= 18).

Estimated Seasonal Transpiration per Shrub

We estimated cumulative transpiration per shrub over the growing season by multiplying estimated transpiration per unit leaf area per day (0900 hr to 1500 hr) by the average shrub leaf area for each species, and then using trapezoidal approximation to integrate under the resulting curve of estimated daily transpiration per shrub. Cumulative transpiration per shrub was estimated for that portion of the growing season between our first and last sampling dates, June 12 and August 23.

Results and Discussion

Diurnal patterns of VPD, LFT, and PPFD (averaged across all shrubs and both sampling days for each of the four seasonal sampling periods) were similar for the four sampling dates (Figure 1), although maximum VPD and LFT increased progressively between June 12 and August 7. The final sampling date, August 21, was somewhat cooler and cloudy, with environmental parameters similar to those earlier in the season. Diurna of ..p varied substantially among the four averaged sampling dates and among the three species (Figure 2). The lowest daily minimum values of ..p occurred on the August sampling dates. Minimum ..p for *H. discolor* on these dates (~ -2.5 --3.0 MPa), was substantially lower than for the other two species (~ -2.0 MPa) (Figure 2). *A. patula* and C. *sanguineus* attained fairly high (> -0.7 MPa) predawn ..p

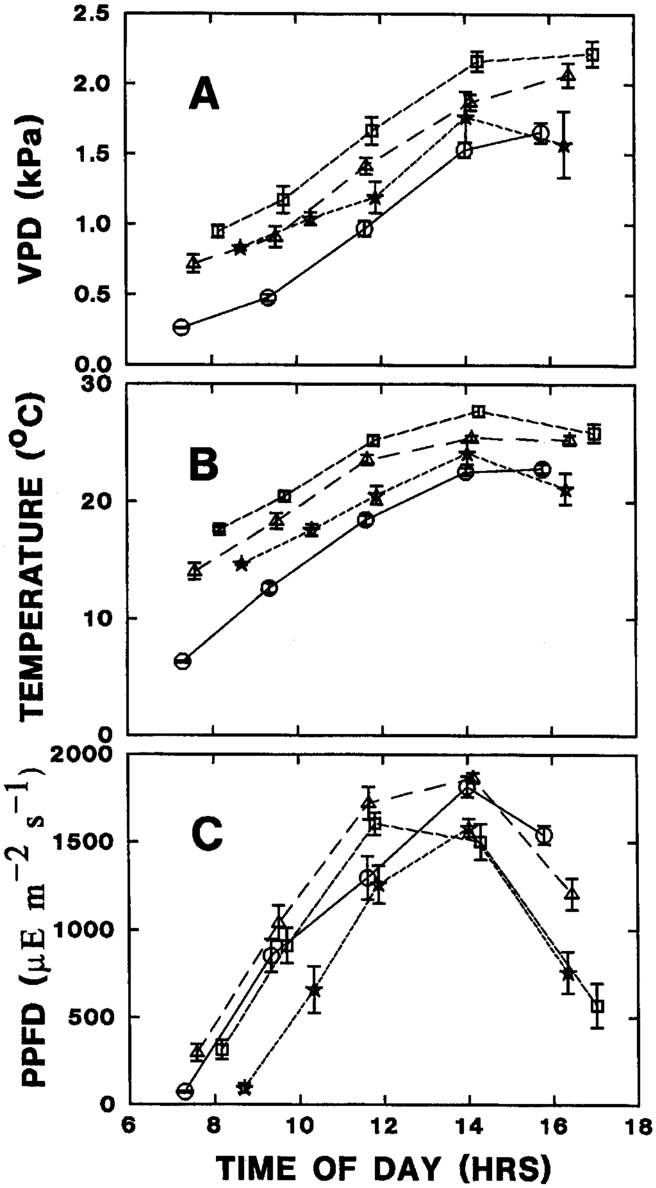

Figure 1. Average diurnal courses of vapor pressure deficit (VPD, kPa; A), leaf temperature (°C; B), and photosynthetic photon flux density (PPFD, σEinsteins m^{-2} s^{-1}; C) for four sampling cycles. Values are means (± one SE) of 18 shrubs (6 shrubs for each of 3 species for a particular sampling cycle of 2 days (June 12 and 13(O), July 10 and 12 (æ), August 7 and 9 ( ), and August 21 and 23 (*)). These average values were input into the models estimating leaf conductance for each species to facilitate species comparisons.

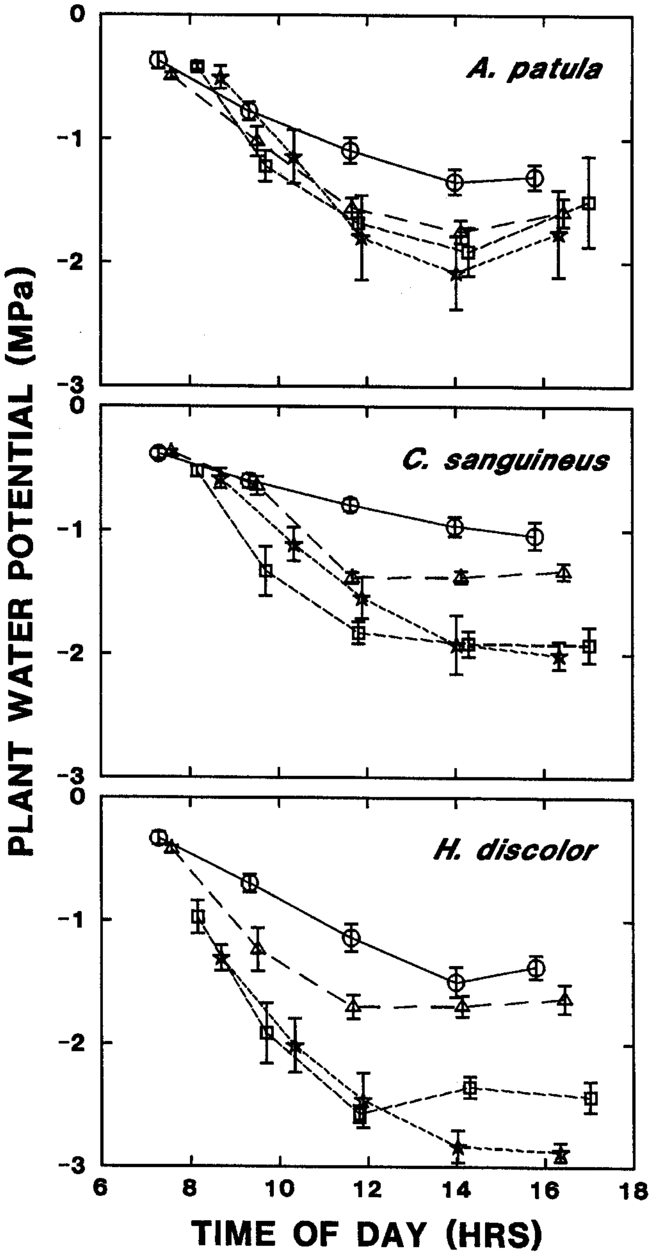

Figure 2. Average diurnal courses of plant water potential (MPa, as estimated by xylem pressure potential) for A. patula, C. sanguineus, and H. discolorfor four sampling cycles. Values are means (± one SE) of six shrubs for each species for a particular sampling cycle of 2 days [June 12 and 13 (O), July 10 and 12 (æ), August 7 and 9 ( ), and 21 and 23 August (*). Although the first measurements of the day were made predawn, they are shown here at the times of measurement of the conductance and environmental values they were paired with for modeling purposes (see Methods). These average values were input into the models predicting leaf conductance for each species to facilitate species comparisons.

throughout the season; *H. discolor* predawn ..p decreased to -1.0 to -1.3 MPa in August. High daily predawn ..p for *A. patula* and C. *sanguineus* shrubs indicate that throughout the season these shrubs had access to fairly wet soils, although perhaps at some depth.

Model Estimation

Parameter estimates for models estimating leaf conductance (g) as a function of VPD, ..p , LFT, and PPFD for each species are shown in Table 1. The signs of the estimated parameters were, for the most part, consistent with hypothesized relationships between leaf conductance and each driving variable: a negative linear relationship between g and VPD, a concave quadratic relationship between g and LFT, and a decaying exponential relationship between g and PPFD (Table 1). Asymptotic F-statistics calculated by comparing the full and reduced models indicated that the terms for each of these variables (VPD, LFT, and PPFD) contributed significantly to the models for all 3 species (Table 2).

Parameter estimates for the relationship between g and ..p were more problematic. The hypothesized relationship between g and ..p would suggest a negative sign for η_2, which is the outcome observed for *H. discolor* (Table 1). The positive estimate for η_2 in the *A. patula* model is of low magnitude and is not significantly different from 0 (Table 2); in fact, the ..p term in the *A. patula* model is the only term which does not contribute significantly to the model sum of squares for any of the three leaf conductance models (Table 2). The significant positive sign for η_2 in the C. sanguineus model (Tables 1, 2) suggests that, over the domain of the driving variables, the marginal relationship between *g* and ..p for that species is a positive one. Possibly the range in the values of ..p for C. *sanguineus* and *A. patula* is too small for this value to influence the stomatal conductance. The relationship for C. *sanguineus* may well be spurious, especially given the multiplicative and interdependent nature of the driving variables; i.e., the apparent relationship could be the result of the influence of one or more of the other driving variables. A similar, counterintuitive relationship between ..p and *g* derived from nonlinear models has been reported elsewhere (Pallardy and Kozlowski 1979), and underscores the need for caution in interpreting parameter estimates involving interdependent predictors (e.g., Hall 1982).

Species Comparisons

Observed leaf conductances for each of the four sampling periods indicate similar diurnal patterns for the three species on the June and July sampling dates, but with greater differences among the species on the August sampling dates (Figure 3). Observed leaf conductances were, particularly for August, highest for C. *sanguineus* and lowest for *H. discolor*, with intermediate values observed for A. *patula.* The relatively thin, mesophytic leaves of *H. discolor* make it more prone to wilt and close stomata in response to water stress than the other two species. The high conductances of C. *sanguineus* relative to A. *patuia* are similar to patterns observed by Conard and Radosevich (1981) for C. *velutinus* and *A. patula.* How this is related to leaf morphology is not clear; however, *Ceanothus* species in general seem to maintain high conductance under apparently adverse environmental conditions.

Seasonal patterns of leaf conductance also differed among the species. For all species, leaf conductances increased between June and July, perhaps reflecting the influence of soil warming on soil water availability, or changes in environmental driving variables such as increased LFT and PPFD. For C. *sanguineus,* leaf conductance remained high through July and August. Conductance in *A. patula* was maximum in July, but dropped slightly in

Table 1. Parameter estimates for nonlinear regression models of leaf conductance as a function of vapor pressure deficit, plant water potential,[a] leaf temperature, and photosynthetic photon flux density, for each of three shrub species. The model form used in the regression is shown below.

$$g=\eta_0(1+\eta_1 X_1)(1+\eta_2 X_2)(1+\eta_3 X_3+\eta_4 X_3^2)(1-e^{(-\eta_5 X_4)})$$

where:

g = estimated conductance (cm sec^{-1})

ηi = model parameters

X_1 = vapor pressure deficit (kPa) - 2

X_2 = plant water potential (-MPa) - 10

X_3 = leaf temperature (°C) - 10

X_4 = photosynthetic photon flux density (σEinsteins $m^{-2}s^{-1}$)

	η_0	η_1	η_2	η_3	η_4	η_5
A. patula	0.1856	-0.6115	0.015	0.1767	-0.0008	0.0143
C. sanguineus	0.3972	-0.5288	0.0374	0.0844	-0.0025	0.0139
H. discolor	0.2129	-0.5080	-0.268	0.1604	-0.0025	0.0102

[a] Absolute values were input into the model for plant water potential.

NOTE: Constants were subtracted from X_1, X_2, and X_3 to facilitate model convergence.

August. *H. discolor* conductance peaked in July, followed by a sharp drop on both August sampling dates.

Estimated diurnal courses of leaf conductance from the three species' models are shown in Figure 4. These values were generated by the models using the mean diurnal courses of driving variables shown in Figures 1 and 2. Estimated diurnal courses of leaf conductance for each of the four sampling periods shown in Figure 4 are similar to the observed diurnal courses of leaf conductance in Figure 3. As with the observed leaf conductances, the models generally predict the highest values of leaf conductance for C. *sanguineus,* the lowest values for H. *discolor,* and intermediate values for A. *patula* (Figure 4). However, the use of common environmental driving variables clarifies differences among the species by removing the variability derived from temporal differences in environmental conditions between field measurements. Given the same "environment" (i.e., values of the driving variables), the model estimated conductances show clearer differences among the species than do the observed conductances, with increasingly greater separation among species as the season progresses, reinforcing the value of our modeling approach.

Seasonal courses of estimated daily transpiration per unit leaf area (g H_2O cm^{-2} day^{-1}) similarly showed strong separation among the 3 species, with the differences becoming more pronounced as the season progressed (Figure 5). As with estimated leaf conductance, the highest values of daily transpiration per unit leaf area were predicted for C. *sanguineus,* the lowest for *H. discolor,* with intermediate values predicted for A. *patula.*

We believe that use of the multiple factor nonlinear models was a valuable approach for estimating and contrasting soil water removal by the three shrub species. Because of the interdependent nature of the driving variables, the simple relationships between leaf conductance and any of the driving variables were not evident in bivariate plots. Attempts to project and compare leaf conductance and transpiration responses by the three species using bivariate or multiple linear models were unsuccessful,

Table 2. Asymptotic F-statistics for contributions of vapor pressure deficit, plant water potential, leaf temperature, and photosynthetic photon flux density terms to models of stomatal conductance for A. patula, C. sanguineus, and *H. discolor.* * = ***$P < 0.05$; *** = $P < 0.01$; ** * = $P < 0.001$.***

	Model terms			
	Vapor pressure deficit $(1+\eta_1 X_1)$	Plant water potential $(1+(\eta_2 X_2)$	Leaf temperature $(1+\eta_3 X_3+(\eta_4 X_3^2)$	Light intensity $(1-e^{(-\eta_5 X_4)})$
	Asymptotic F-Statistics			
A. patula	20.86***	N. S.	46.40***	8.49*
C. sanguineus	16.88***	18.78***	6.76**	28.96***
H. discolor	6.93*	38.71***	30.26***	57.36***

where:

η_i = model parameters

X_1 = vapor pressure deficit (kPa) -2

X_2 = plant water potential (-MPa) - 10

X_3 = leaf temperature (°C) - 10

X_4 = photosynthetic photon flux density (σEinsteins $m^{-2}s^{-1}$)

NOTE: Constants were subtracted from X_1, X_2, and X_3 to facilitate model convergence.

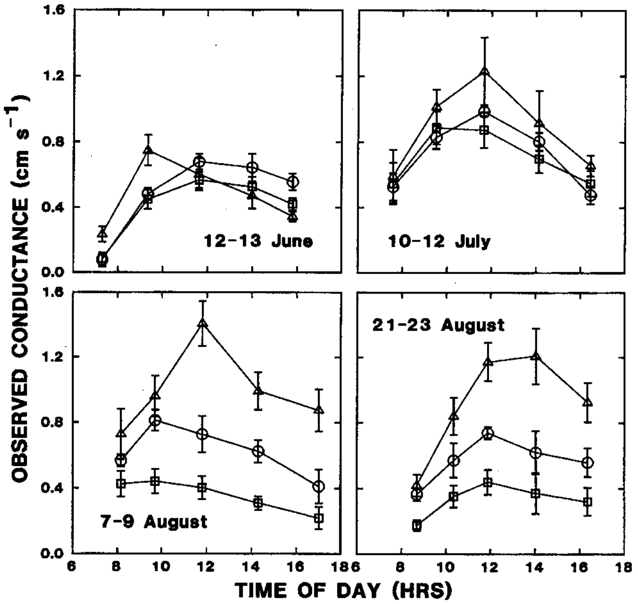

Figure 3. Observed diurnal courses of leaf conductance (cm s^{-1}) for A. *patula* (O), C. *sanguineus* (æ), and *H. discolor* ( ) for four sampling cycles. Values are means (± one SE) of 6 shrubsfor each species for a particular sampling cycle of 2 days (June 12 and 13, July 10 and 12, August 7 and 9, and August 21 and 23).

although such constructions have been employed elsewhere (Hinckley et al. 1975, Pallardy and Kozlowski 1979). In contrast, the nonlinear, multiplicative models we developed show good agreement between estimated and observed leaf conductances (compare Figures 3 and 4), and errors estimated for the estimated mean conductance and transpiration are reasonably low (Figures 4 and 5).

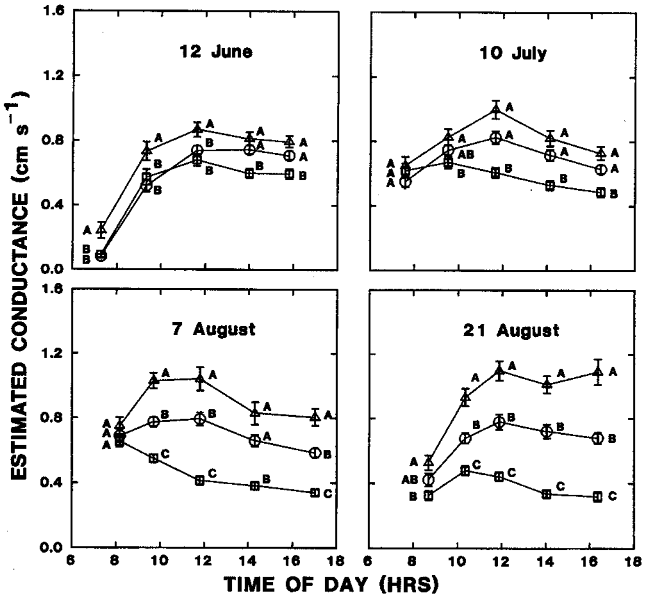

Figure 4. Diurnal courses of model estimated mean (± one SE) leaf conductances (g, cm s^{-1}) based on input environmental variables (shown in Figure 1) and plant water potential (shown in Figure 2) for A. *patula* (O), C. *sanguineus* (æ), and *H. discolor* ( ) for 4 representative dates (June 12, July 10, August 7, and August 21). Different letters adjacent to symbols indicate significant differences among species at each time of day at ζ = 0.05, determined by pairwise asymptotic t-tests with a modified Bonferroni adjustment.

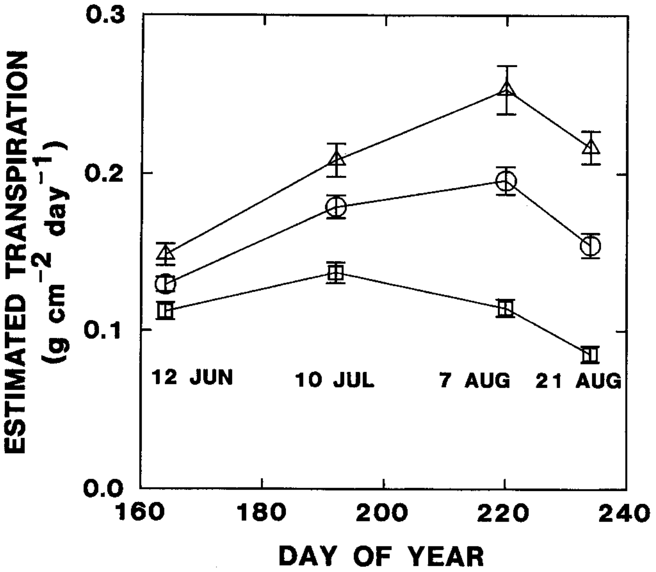

Figure 5. Seasonal courses of estimated transpiration per unit leaf area (g H_2O cm -2 day^{-1}, ± 1 SE) calculated from model estimated leaf conductances and average water vapor concentration gradient (æC_w) A. *patula* (O), C. *sanguineus* (æ), and H. *discolor* ( ) for representative dates (June 12, July 10, August 7, and August 21).

The models also allow predictions of how species would respond in identical environments, thereby facilitating species comparisons and evaluations of potential competitive abilities. Thus, predicted differences in transpiration rates and volumes of water transpired across the season are due to differences in water relations physiology among the species, and not to differences in microclimate among various shrubs or to differences in the day, time of day, or time of season of measurement.

Soil Water Use

Soil water potentials (..$_s$) showed the expected seasonal courses, with the highest values in June, and becoming drier through the season (Figure 6). Soils dried progressively from the shallower to the deeper depths. Presumably plants remove water first from the shallower depths because the internal resistance to transport increases as water is drawn from deeper depths. Soils on July 10 were driest at the 25 cm depth, somewhat wetter at the 50 cm depth, and only slightly decreased from June 12 levels at the 100 cm depth. By the August sampling dates, soils had reached approximately the same values at all 3 depths (< -1.2 MPa). Although the soils were uniformly dry to a depth of 1 m by the August sampling dates, predawn plant water potentials observed on these dates for A. *patula* and C. *sanguineus* were substantially higher than soil water potential in the top meter of soil (Figure 2), indicating that these two species were drawing water from soil deeper in the profile. H. discolor, on the other hand, appeared to be tracking soil water potential at the 1 m depth (Figure 2) indicating a shallower root system. Any plant with roots limited to the top 1 m of soil (for example, conifer seedlings) may thus encounter dry soils as a result of water removal by any of these shrub species.

At the 25 and 50 cm depths, soils beneath A. *patula* shrubs remained significantly wetter on July 10 compared to soils

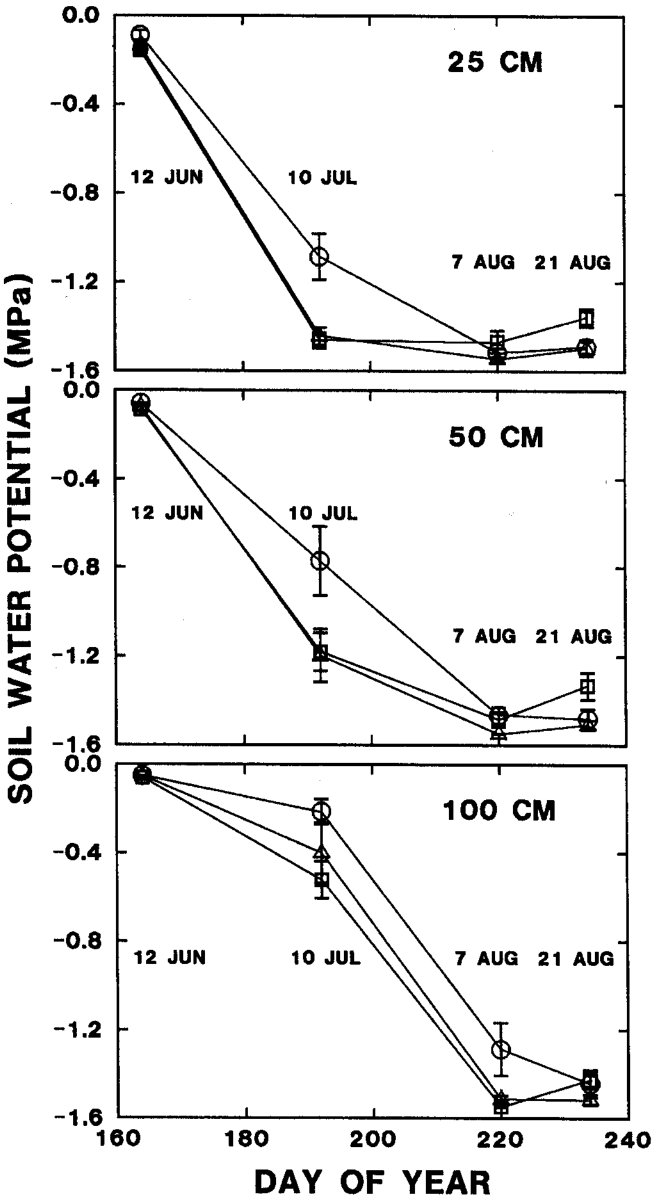

Figure 6. Seasonal courses of soil water potential (MPa) measured at depths of 25 cm, 50 cm, and 100 cm beneath shrubs of A. *patula* (O), C. *sanguineus* (æ), and *H. discolor* ( ). Values are means (± 1 SE) of six soil measurements (one beneath each of six shrubs for each species) for a particular sampling cycle of 2 days (June 12 and 13, July 10 and 12, August 7 and 9, and August 21 and 231. Data from the 2 sampling days were grouped, and only one date is shown on the plots.

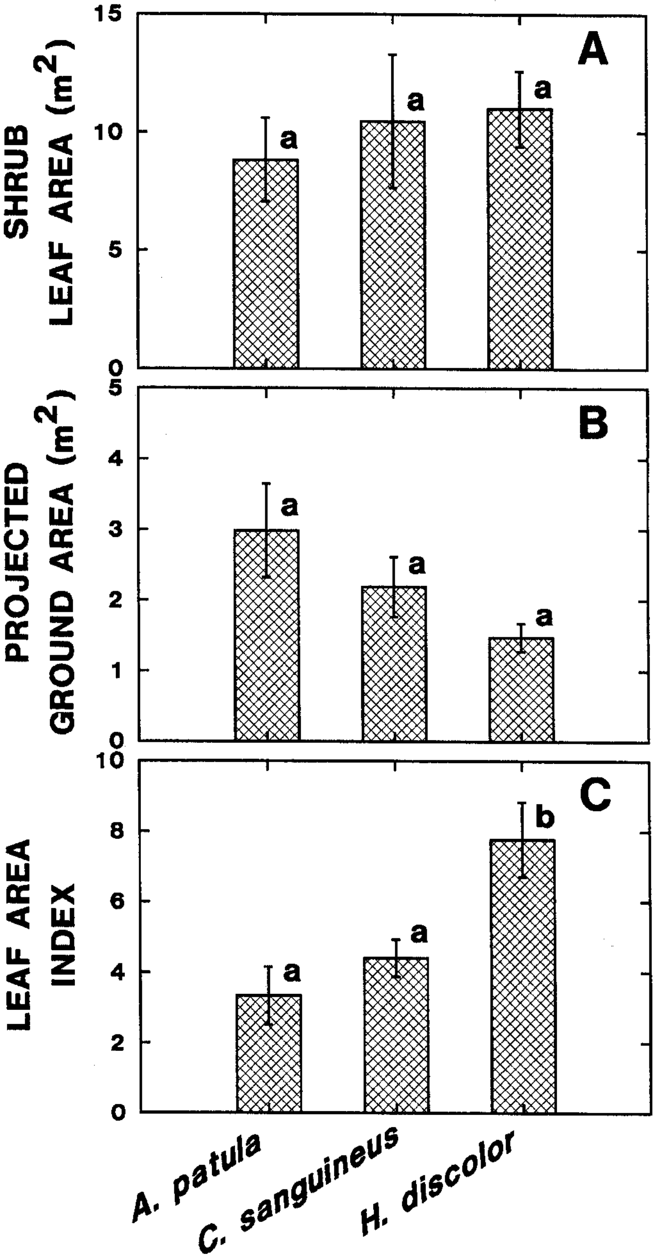

Figure 7. Shrub leaf area (m², AI, projected ground area (m²; B), and leaf area index (m² leaf area / m² ground area; C) for A. patula, C. *sanguineus*, and *H. discolor.* Values are means (± 1 SE) of six shrubs. Different letters indicate significant differences between species at ζ = 0.05.

beneath C. *sanguineus* and *H. discolor* shrubs (Figure 6). Based solely on our estimates of transpiration per unit leaf area (Figure 5), we might expect soils to dry earlier in the season beneath C. *sanguineus* shrubs, followed by A. *patula* soils, and then by soils under *H.* discolor. We would not anticipate similar seasonal soil drying patterns beneath *H.* discolor and *C. sanguineus* shrubs.

Obviously, consideration of total leaf area is critical in predicting soil drying trends (Figure 7). Although total shrub leaf area (Figure 7A) and projected shrub ground area (Figure 713) did not differ significantly among the three species, LAI was significantly greater in *H.* discolorthan in A. *patula* or C. *sanguineus* (Figure 7C; LSD, ζ = 0.05). Mean LAI in *H.* discolor shrubs was nearly twice that in the other two species. Hence, although H. *discolor* transpiration per unit leaf area is much lower compared to the other species, the greater LAI of *H.* discolor shrubs should result in disproportionately large amounts of water being removed from the soils.

Relationships between transpiration per unit leaf area, LAI, and soil water potentials are best appreciated by examining estimated cumulative transpiration per shrub. By the August sampling dates, cumulative transpiration on a wholeshrub basis is estimated to be greatest for C. *sanguineus* shrubs and least for *H. discolor* shrubs, with intermediate values predicted for A. *patula* shrubs (Figure 8A; based on mean leaf areas for each species; Figure 7A). Estimated transpiration per unit of projected shrub ground area, however, is predicted to be similar and high in *H.* discolor and

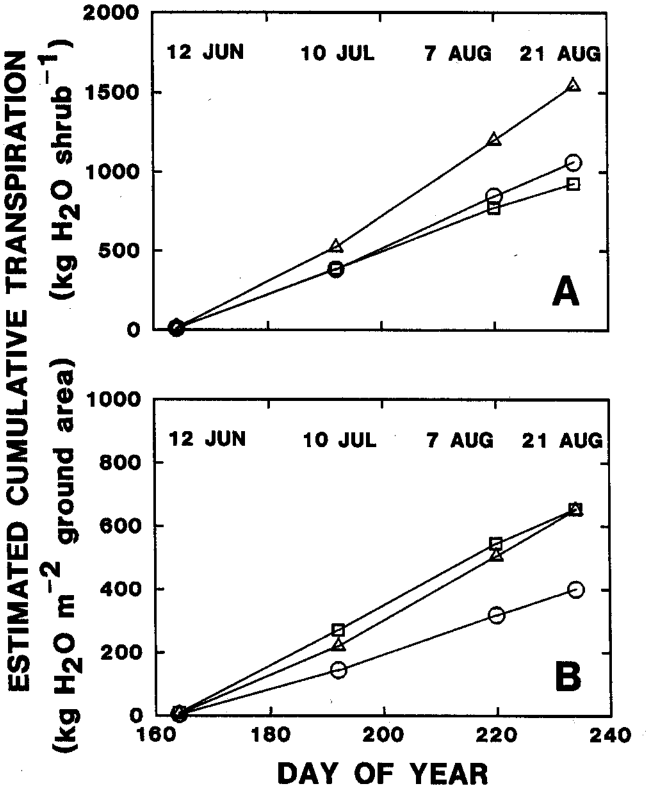

Figure 8. Seasonal courses of estimated cumulative amounts of water transpired by A. *patula* (O), C. *sanguineus* (æ), and H. *discolor* ( ). Values are based on daily transpiration calculated from model estimates of leaf conductance, and mean total leaf area, and mean shrub projected ground area for each species (n; =6 shrubs per species). A. Cumulative water transpired per shrub (kg H_2O shrub^{-1}). B. Cumulative water transpired per unit shrub projected ground area (kg H_2O m^{-2} ground area).

C. sanguineus, and much lower in *A. patula* shrubs (Figure 813; based on mean projected ground areas for each species).

Thus, due to its high LAI, we would predict the rate of water removal from the soils beneath the shrubs to be as high for *H. discolor* shrubs as for C. *sanguineus* shrubs, despite the higher total transpiration per shrub predicted for C. *sanguineus.* High transpiration per unit projected ground area explains the similarity in seasonal patterns of soil water potentials in soils beneath *H. discolor* and C. *sanguineus* shrubs (Figure 6). Densely packed leaves in H. *discolor* shrubs would thus make this species a more significant competitor for water with any nearby tree seedlings or saplings than one would predict based on transpiration rates per unit leaf area alone. Because it is more shallowly rooted, H. *discolor* also draws water from a smaller volume of soil, resulting in more rapid depletion of available water from that portion of the soil. Such high soil water depletion by H. *discolor* despite its relatively low transpiration rates reinforces the dangers of extrapolating results based on physiological responses of leaves to the whole-plant level without consideration of emergent properties such as LAI or root distribution.

Implications for Effects on Conifers

We recognize that the isolation of individual plants necessary for us to compare species responses represents somewhat artificial conditions. However, soil moisture measurements were taken within or near the dripline of individual shrubs, with the expectation that they represent a zone fully occupied by the roots of the target species, with little or no intrusion from other species. Although seasonal transpiration per unit of ground area in a closed canopy stand might be slightly higher due to lateral shading and canopy overlap, we believe that our results should be representative of differences among the 3 species on a stand or landscape level. Our LAI values for individual shrubs are equal to or higher than values reported by Hughes et al. (1987) for 15 to 20 yr old closed canopy stands of *A. patuta* (LAI of 3.5), and of C. *integerrimus* H. & A. (LAI of 2.5), and C. *velutinus* var. *laevigatus* Hook. (LAI of 2.8-5.5) for sites in southwestern Oregon. In intermixed stands, shrub species will be in competition with each other, as well as with conifers. Competitive interactions might be expected to intensify the differences in transpiration and soil moisture we observed here.

Young whiteleaf manzanita (A. *viscida* Parry) stands have been shown to inhibit stem volume growth of both Douglasfir and ponderosa pine seedlings by about 50% over a range in LAI from 0 to 1.4 (White and Newton 1989), well below the values of LAI we report. Shainsky and Radosevich (1986) observed significant decreases in predawn and midday water potentials, and leaf conductance, by late summer in ponderosa pine seedlings grown in various mixtures with *A. patula.* By August, midday water potentials were -2.0 MPa or lower, and leaf conductances were extremely low. This was associated with predawn seedling water potentials of -0.8 to -1.5 MPa and decreased growth of the pines. Pabst et al. (1990) observed a strong linear relationship (r^2 = 0.75) between soil water potential at 30 cm in depth and midday plant water potential for 10 yr old planted Douglas-fir in competition with Pacific madrone *(Arbutus menziesii* Pursh.) on a dry site in southwestern Oregon. Based on their regressions, we would expect young Douglas-fir trees to have midday water potentials less than -2.0 MPa when soil water potential in their rooting zone is below about -0.9 MPa. Radosevich and Conard (1982) observed decreases in photosynthesis to about 50% of maximum at plant water potential less than -1.8 MPa for Douglas-fir seedlings in the Sierra Nevada, and other authors report that both photosynthesis and transpiration are greatly decreased at plant water potentials below -1.8 to -2.0 MPa (Brix 1979, Newton and Preest 1988). By July 10, the soil water potentials we observed under H. *discolor* and C. *sanguineus* were well within the range that might be expected to inhibit photosynthesis of either ponderosa pine or Douglas-fir down to 50 cm (Figure 6). By August 7 soil water potentials down to 1 m were low enough under all species to severely reduce conifer conductance, photosynthesis, and growth.

Conclusions

Nonlinear models of leaf conductance as a function of vapor pressure deficit, leaf temperature, photosynthetic photon flux density, and leaf water potential gave satisfactory estimates of daily courses of leaf conductance. These models were useful for estimating and contrasting water relations of the study species as well as for evaluating potential of the species to compete for soil water. Because of interactions among variables, this type of model is not appropriate for comparing relative effects of particular independent variables among species. We do believe, however, that this type of approach has great potential for standardizing comparisons among species using field data obtained under variable environmental conditions.

Based on measurements of soil water potentials beneath shrubs and model estimates of seasonal transpiration, we predict that both C. *sanguineus* and *H. discolor* will remove water more rapidly from soil in the shrub root zones than will *A. patula*. Although all three species reduced water potential of the top meter of soil enough to cause moisture stress in conifers, C. *sanguineus* and *H. discolor* reduced soil water potential to critical levels earlier in the growing season than did *A. patula*. Thus, despite its potential for year-round water use, we predict that *A. patula* will not compete as strongly for water with conifer seedlings (in the top meter of soil) during the crucial summer drought period as will the two deciduous species.

Rapid soil water removal by C. *sanguineus* results largely from its high rates of transpiration per unit leaf area throughout the season, a pattern that has also been observed for the closely related *C. velutinus* (Conard and Radosevich 1981) on forest sites in California. Soil water removal by H. *discolor* is high primarily because of its high leaf area index and shallow rooting depth, despite relatively low rates of transpiration per unit leaf area. This points out the difficulty of drawing any conclusions about potential competitive interactions from physiological data alone.

Based on late season predawn xylem potentials, we infer that C. *sanguineus* and *A. patula* can draw water from deeper layers in the soil profile than *H. discolor*, where ample water seemed to be available late in the season. These two species may compete more strongly with deeper rooted established saplings or other shrubs than *H. discolor.* Based on the levels of seasonal soil water depletion observed in this study, moisture competition by all three species can be expected to severely retard growth of co-occurring conifers.

Literature Cited

AITCHISON, G.D., P.F. BUTLER, AND C.G. GURR. 1951. Techniques associated with the use of gypsum block soil moisture meters. Aust. J. Appl. Sci. 2:56-75.

BOLSINGER, C.L. 1980. California forests: Trends, problems, and opportunities. USDA For. Serv. Resour. Bull. PNW-89. 138 p.

BRIX, H. 1979. Effects of plant water stress on photosynthesis and survival of four conifers. Can. J. For. Res. 9:160-165.

BURROWS, F.J., AND F.L. MILTHORPE. 1976. Stomatal conductance in the control of gas exchange. P. 103-152 in Water deficits and plant growth, Volume IV, Kozlowski, T.T. (ed.). Academic Press, London, New York.

CARTER, G.A., J.H. MILLER, D.E. DAVIS, AND R. PATTERSON. 1984. Effect of vegetation competition on the moisture and nutrient status of loblolly pine. Can. J. For. Res. 14:1-9.

CONARD, S.G., AND S.R. RADOSEVICH. 1981. Photosynthesis, xylem pressure potential, and leaf conductance of three montane chaparral species in California. For. Sci. 27:627-639.

CONARD, S.G., AND S.R. RADOSEVICH. 1982. Growth responses of white fir to decreased shading and root competition by montane chaparral shrubs. For. Sci. 28:309-320.

CONARD, S G., AND S. R. SPARKS. 1993. Abies concolor growth responses to vegetation changes following shrub removal, northern Sierra Nevada, California. USDA For. Serv. Res. Pap. PSW-RP-218.9 p.

GOLLAN, T., N.C. TURNER, AND E.-D. SCHULZE. 1985. The response of stomata and leaf gas exchange to vapour pressure deficits and soil water content. III. In the sclerophyllous woody species Nerium oleander. Oecologia 65:356-362.

GRATKOWSKI, H., D. HOPKINS, AND O. LAUTERBACH. 1973. The Pacific coast and northern Rocky Mountain region. J. For. 71:138-143.

HALL, A.E. 1982. Mathematical models of plant water loss and plant water relations. P. 231-261 in Encyclopedia of plant physiology, new series, volume 12B, Lange, O.L., et al. (eds.). Physiological plant ecology 11. Water relations and carbon assimilation. Springer-Verlag, Berlin, Heidelberg, New York..

HINCKLEY, T.M., M.O. SCHROEDER, J.E. ROBERTS, AND D.N. BRUCKERHOFF. 1975. Effect of several environmental variables and xylem pressure potential on leaf surface resistance in white oak. For. Sci. 21:201-211.

HITCHCOCK, C.L., AND A. CRONQUIST. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle, WA. 730 p.

HOCHBERG, Y. 1988. A sharper Bonferroni procedure for multiple tests of significance. Biometrika 75:800-802.

HUGHES, T.F., C.R. LATT, J.C. TAPPEINER II, AND M. NEWTON. 1987. Biomass and leaf-area estimates for vamishleaf ceanothus, deerbrush, and whiteleaf manzanita. West. J. Appl. For. 2(4):124-128.

JARVIS, P.G. 1976. The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. Phil. Trans. Roy. Soc. London, Series B 273:593-610.

JONES, M.M., AND H.M. RAWSON. 1979. Influence of rate of development of leaf water deficits upon photosynthesis, leaf conductance, water use efficiency, and osmotic potential in sorghum. Physiol. Plant.45:103-111.

KAUFMANN, M.R., AND Y. LEVY. 1976. Stomatal response of CClruslambhiri to water stress and humidity. Physiol. Plant. 38:105-108.

LANINI, W.T., AND S.R. RADOSEVICH. 1986. Response of three conifer species to site preparation and shrub control. For. Sci. 32:61-77.

NEWTON, M., AND D.S. PREEST. 1988. Growth and water relations of Douglas Fir (Pseudotsuga menziesii) seedlings under different weed control regimes. Weed Sci. 36:653-662.

MOOD, A.M., F.A. GRAYBILL, AND D.C. BOES. 1974. Introduction to the theory of statistics. Ed. 3. McGraw-Hill, New York. 564 p.

PABST, R.J., J.C. TAPPEINER II, AND M. NEWTON. 1990. Varying densities of Pacific madrone in a young stand in Oregon alter soil water potential, plant moisture stress, and growth of Douglas-fir. For. Ecol. Manage. 37:267-283.

PALLARDY, S.G., AND T.T. KOZLOWSKI. 1979. Relationships of leaf diffusion resistance of Populus clones to leaf water potential and environment. Oecologia 40:371-380.

PETERSEN, T.D., M. NEWTON, AND S.M. ZEDAKER. 1988. Influence of Ceariolhus velutinus and associated forbs on the water stress and stemwood production of Douglas-fir. For. Sci. 34:333-343.

RADOSEVICH, S.R., AND S.G. CONARD. 1982. Interactions among weeds, other pests and conifers in forest regeneration. P. 463-486 in Biometeorology in integrated pest management, Hatfield, J.L, and I.J. Thompson (eds.). Academic Press, New York. 491 p.

RASCHKE, K. 1975. Stomatal action. Ann. Rev. Plant Physiol. 26:309-340.

REED, K.L., E.R. HAMMERLY, B.E. DINGER, AND P.G. JARVIS. 1976. An analytical model for field measurement of photosynthesis. J. Appl. Ecol. 13:925-942.

REICH, P.B., AND T.M. HINCKLEY. 1989. Influence of pre-dawn water potential and soil-to-leaf hydraulic conductance on maximum daily diffusive conductance in two oak species. Funct. Ecol. 3:719-726.

SAS INSTITUTE, INC. 1988. SAS / STAT© User's Guide, Release 6.03 Edition. Cary, NC. 1028 p.

SCHULZE, E.-D., O.L. LANGE, M. EVENARI, L. KAPPEN, AND U. BUSCHBOM. 1976. An empirical model of net photosynthesis for the desert plant Hammada scoparia (Pomel) Iljin. 1. Description and test of the model. Oecologia 22:355-372.

SCHULZE, E.-D., AND A.E. HALL. 1982. Stomatal responses, water loss and CO Z assimilation rates of plants in contrasting environments. P. 181-230 in Encyclopedia of plant physiology, new series, volume 12B. Physiological plant ecology 11. Water relations and carbon assimilation, Lange, O.L., et al. (eds.). Springer-Verlag, Berlin, Heidelberg, New York.

SHAINSKY, L.J., AND S.R. RADOSEVICH. 1986. Growth and water relations of Pinus ponderosa seedlings in competitive regimes with Arctostaphylos patula seedlings. J. Appl. Ecol. 23:957-966.

SKAU, C.M., R.O. MEEUWIG, AND T.W. TOWNSEND. 1970. Ecology of eastside Sierra chaparral: A literature review. Report 71, Univ. of Nevada, Max C. Fleischmann Coll. of Agric., Reno, NV. 14 p.

TAKAKURA, T., J. GOUDRIAAN, AND W. LOUWERSE. 1975. A behaviour model to simulate stomatal resistance. Agric. Met. 15:393-404.

TAPPEINER. J.C.11, M. NEWTON, P.M. MCDONALD. AND T.B. HARRINGTON. 1992.
Ecology of hardwoods, shrubs, and herbaceous vegetation: Effects on conifer regeneration. P.136-164 in Reforestation practices in southwest ern Oregon and northern California, Hobbs, S.D. et al. (eds.). For. Res. Lab., Oregon State Univ., Corvallis. 465 p.

THORPE, MR., B. WARRIT, AND J.J. LANDSBERG. 1980. Responses of apple leaf stomata: A model for single leaves and a whole tree. Plant, Cell Environ. 3:23-27.

TURNER, N.C. 1991. Measurement and influence of environmental dnd plant factors on stomatal conductance in the field. Agric. For. Met. 54:137-154.

WALSTAD, J.D., M. NEWTON, AND R.J. BOYD, JR. 1987. Forest vegetation problems in the Northwest. P. 15-53 in Forest vegetation management for conifer production, Walstad, J.D., and P.J. Kuch (eds.). W iley, New York.

WANG, Z.Q., M. NEWTON, AND J.C. TAPPEINER 11. 1995. Competitive relations between Douglas-fir and Pacific madrone on shallow soils in a Mediterranean climate. For. Sci. 41(4) 744-757.

WARRIT, B., J.J. LANDSBERG, AND M. R. THORPE. 1980. Responses of apple leaf stomata to environmental factors. Plant Cell Environ. 3:13-22.

WARTINGER, A., H. HEILMEIER, W. HARTUNG, AND E.-D. SCHULZE. 1990. Dally and seasonal courses of leaf conductance and abscisic acid in the xylem sap of almond trees [Prunus dulcis (Miller) D. A. Webb] under desert conditions. New Phytol. 116, 581-587.

WHITE, D.E., AND M. NEWTON. 1989. Competitive interactions of whiteleaf manzanita, herbs, Douglas-fir, and ponderosa pine in southwest Oregon. Can. J. For. Res. 19:232-238.

ZHANG, J., U. SCHURR, AND W.J. DAVIES. 1987. Control of stomatal behavior by abscisic acid which apparently originates in the roots. J. Exp. Bot. 38:1174-1181.