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INCREASED PHOTOSYNTHESIS OFFSETS COSTS OF ALLOCATION TO SAPWOOD IN AN ARID ENVIRONMENT

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Abstract. We assessed the effect that varying patterns of biomass allocation had on growth of ponderosa pine (*Pinus ponderosa*) growing in the desert climate of the Great Basin and the montane climate of the eastern Sierra Nevada. Prior work established that desert trees have lower leaf : sapwood area ratios than montane trees (0.104 and 0.201 m²/cm², respectively) and proportionally greater stem respiration. Sapwood : leaf mass ratios are also greater and increase more as a function stem diameter in desert than in montane trees. We hypothesized that this increased allocation of carbon to stem sapwood and stem respiration in large trees could decrease growth rates in the desert compared to the montane environment, in addition to any growth reduction imposed by drought on physiology and growth processes. Trees of all diameters (dbh) in the desert environment had lower relative growth rates (RGRs) than montane trees (e.g., for a 30 cm dbh tree, RGR = 0.012 vs. 0.021 kg·kg⁻¹·yr⁻¹, respectively). However, growth rates of desert and montane trees declined similarly with increasing dbh and did not reflect diverging sapwood : leaf mass ratios.

Alternatively, we hypothesized that desert trees may increase rates of photosynthetic carbon accumulation (per unit leaf area) with diameter, thereby compensating for increased sapwood respiration. Leaf nitrogen (N) concentration and stable-carbon isotope composition ($\delta^{13}\text{C}$) were measured to examine size-dependent and seasonally integrated photosynthetic capacity within desert and montane environments. Nitrogen concentration was correlated with photosynthetic capacity. Leaf nitrogen (N) concentration and $\delta^{13}\text{C}$ values were greater in the desert (e.g., in 1-yr-old needles, desert = 1.11% and -22.96‰; montane = 0.94% and -24.20‰) and differed between desert and montane trees as a function of dbh. In desert trees, leaf nitrogen concentration in 1-yr-old through 5-yr-old needles increased with dbh, and carbon isotope composition in 1-yr-old needles increased with dbh, suggesting increased photosynthetic capacity and photosynthetic rates with increasing tree size. Needle nitrogen concentration and $\delta^{13}\text{C}$ values decreased or remained constant with dbh in montane trees. Desert trees had greater light extinction coefficients and retained fewer needle cohorts. Our results suggest that increased allocation to heterotrophic stem tissue at the expense of photosynthetic tissue does not always incur a reduction in tree growth as predicted by current models of forest productivity.

Key words: canopy light interception; carbon isotope ratio; forest productivity; forest stand development; leaf age; leaf area index; light extinction coefficient; nitrogen; photosynthetic capacity; *Pinus ponderosa*; relative growth rate.

INTRODUCTION

The balance between biomass allocated to photosynthetic vs. heterotrophic tissue largely determines forest growth and productivity and can be affected by climate (Waring and Schlesinger 1985, Gower et al. 1995). For example, in warm, dry environments trees allocate proportionally more biomass to sapwood and less to foliage than in cooler, moister environments, both among species (Waring and Schlesinger 1985) and within a species (Callaway et al. 1994, Mencuccini and Grace 1995). Proportional changes in leaf : sapwood area ratios within a species may provide a constant

water potential within tree stems in environments with different evaporative demands (Mencuccini and Grace 1995). However, the increase in sapwood biomass at the expense of photosynthetic biomass may decrease growth by increasing the carbon investment in constructing and maintaining proportionally more heterotrophic tissue (Poorter et al. 1990), particularly in warm climates.

Callaway et al. (1994) found that ponderosa pine (*Pinus ponderosa* Laws.) growing in a warm, dry desert allocated proportionally more biomass to sapwood and less to leaf area than trees in a cooler, moister montane environment (0.104 and 0.201 m² leaf area/cm² sapwood area, respectively). Differences in biomass allocation became more pronounced with increasing stem diameter, and for large desert trees (>35 cm dbh) the ratio of leaf mass to sapwood mass was 30–50% less

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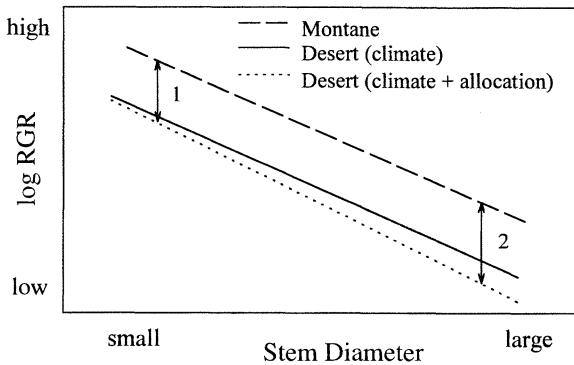


FIG. 1. Prediction of relative growth rate as a function of stem diameter (dbh, bole diameter at 1.4 m above ground level) for ponderosa pine growing in desert and montane environments. The difference in relative growth rate (RGR) between environments attributable to climatic factors (primarily water limitation) is represented by the difference between the montane and desert environments (1). An additional reduction in RGR with increasing dbh was predicted based on the proportional increase in allocation to sapwood and away from foliage for large desert trees (2).

than that for large montane trees (Callaway et al. 1994). Annual stem maintenance respiration for ponderosa pines of comparable foliage mass was greater in the desert and was attributed to higher temperatures and increased biomass allocation to bole sapwood (Carey et al. 1997). Thus, a larger proportion of fixed carbon may have been respired by stems in the desert environment. We hypothesized that greater reductions in leaf : sapwood mass ratios combined with increased allocation of carbon to stem respiration in larger desert trees should decrease growth rates in the desert compared to the montane environment, in addition to any growth reduction imposed by drought.

As part of this study, we measured relative growth rate (RGR) of desert and montane trees to assess the effects of changes in allocation and stem respiration on aboveground productivity. RGR of trees decreases logarithmically with tree age and interspecific comparisons suggest this decline is greatest in warm environments (Waring 1987). Small desert trees, with biomass allocation similar to montane trees of the same diameter, likely have low growth rates because of a direct water limitation. For larger desert trees, which allocate proportionally more biomass to sapwood and less to foliage than montane trees of the same diameter, growth rate may also be lowered by water stress and the costs of building and maintaining sapwood. Therefore, we predicted that RGR would be less in the desert environment for all tree diameters, because of environmental constraints, and that RGR would decline more with increasing stem diameter (Fig. 1).

Alternatively, desert trees may compensate for increasing allocation to sapwood (and proportionally greater stem maintenance respiration) by increased capacity for photosynthetic carbon uptake. We examined

three mechanisms that could contribute to higher carbon gain in large desert trees: (1) a size-dependent increase in photosynthetic rate per unit leaf area, (2) modification of canopy architecture permitting greater light penetration and therefore increased net photosynthesis for older foliage cohorts, and (3) the maintenance of younger, more active needle cohorts through increased needle turnover. To determine if one or more of these mechanisms increase carbon gain with tree size in desert compared to montane trees, we measured photosynthetic capacity, leaf nitrogen concentration, stable-carbon isotope composition, canopy light interception, leaf area index, light extinction coefficients, and leaf demography, and examined changes in these variables as a function of stem diameter.

METHODS

Study area

Our study was conducted in the eastern Sierra Nevada and adjacent Great Basin desert within 100 km of Reno, Nevada. In this region, ponderosa pine and other Sierran conifers can be found growing on patches of soil derived from hydrothermally altered andesite (Billings 1950, DeLucia et al. 1988, Schlesinger et al. 1989). In the warm, dry desert environment, tree islands on these altered soils are surrounded by vegetation characteristic of sagebrush steppe; in the cooler, moister montane environment they are surrounded by Sierran conifers. In both environments, trees are open-grown with nonoverlapping canopies. Soils at these sites are similar across environments with respect to nutrients, organic matter, nitrogen content, and other soil properties (e.g., C, P, pH, Ca^{2+} , HCO_3^- [Schlesinger et al. 1989]). Therefore, these sites provide a unique experimental system for examining the effects of climate, primarily temperature and moisture, on trees without the confounding effect of differing substrates. In addition, they provide an opportunity to test hypotheses regarding conifer growth regulation and forest productivity. Locations and climate data for sites used in the current study are given in Table 1.

Relative growth rate and predicted photosynthetic rate

Relative growth rate of bole sapwood was calculated using sections cut from trees ($n = 17$ trees per environment) for a prior study (Callaway et al. 1994). Sapwood mass 5 yr previous was calculated using allometric equations relating aboveground mass to bole diameter developed from this set of trees (Callaway et al. 1994). Relative growth rate (RGR) was calculated as bole sapwood mass accumulated per unit bole sapwood mass present 5 yr earlier, using the following equation modified from Harper (1977):

$$\text{RGR} = [\ln(\text{biomass}_2) - \ln(\text{biomass}_1)] / (t_2 - t_1). \quad (1)$$

To formulate predictions of net carbon gain as a func-

TABLE 1. Topographic and climatic data for Desert and Montane sites in a study of ponderosa pines. Values given for precipitation and temperature are annual means.

Site	Latitude/longitude	Elevation (m)	Precipitation (mm/yr)	Temperature (°C)
Desert				
Desert Research Institute†	119°48' N, 39°35' W	1500	225	11.4
Ecology Canyon South‡	119°51' N, 39°35' W	1590	262	11.0
Ecology Canyon North‡	119°51' N, 39°35' W	1610	218	11.0
Peavine Mountain†	119°53' N, 39°33' W	1700	250	10.5
Ramsey Mine†	119°24' N, 39°28' W	1750	207	10.5
Montane				
Alpine County 1†‡	119°44' N, 38°41' W	1830	550	7.6
Alpine County 2†‡	119°44' N, 38°41' W	1890	565	7.6
Virginia Mountains†‡	119°41' N, 39°22' W	1860	330	8.4

† Locations for relative growth rate study.

‡ Locations for leaf and canopy study.

tion of stem diameter, we also calculated annual photosynthetic rate (PS_a , in kilograms per square meter per year) for trees of different sizes from desert and montane climates by combining relative growth rate, allometry (Callaway et al. 1994), and wood respiration (Carey et al. 1997) for aboveground components in the following equation adapted from Lambers and Poorter (1992):

$$RGR = (PS_a \times SLA \times LWR) - (SR_w \times SWR) - (LR_w \times LWR) \quad (2)$$

where RGR is relative growth rate (in kilograms of carbon per kilogram of carbon per year), SLA is specific leaf area (in square meters of leaf area per kilogram of leaf carbon), LWR is leaf mass ratio (in kilograms C per kilogram C), SR_w is stem respiration rate (in kilograms C per kilogram sapwood C per year), SWR is stem mass ratio (kilograms C per kilogram C), and LR_w is leaf respiration rate (in kilograms C per kilogram leaf C).

SLA, LWR, and SWR were calculated for trees ranging in size from 5 to 60 cm in diameter (dbh, bole diameter at 1.4 m above ground) using allometric relationships derived from harvested trees spanning this diameter range (Callaway et al. 1994). Sapwood respiration was estimated from in situ gas exchange and calorimetric estimates of construction respiration (Carey et al. 1997). LR_w and PS_a were solved for simultaneously, assuming LR_w was 10% of PS_a (estimated as a percentage of photosynthetic capacity from values in Larcher 1995) multiplied by SLA (to convert to mass-based units).

Leaf nitrogen, carbon isotope composition, and photosynthetic capacity

To examine potential size-dependent differences in canopy gas exchange, we measured leaf nitrogen concentration, stable-carbon isotope composition, light interception, and leaf demography. We sampled 120 trees from three desert and three montane sites (Table 1). Twenty to twenty-five trees per site were divided into

diameter classes (three to four trees per diameter class per site) with dbh class midpoints of: 5, 15, 25, 35, 45, and 55 cm.

Canopies of large trees were inaccessible for instantaneous measurements of photosynthesis. Therefore we measured leaf nitrogen concentration as a proxy for photosynthetic capacity and stable-carbon isotope composition ($\delta^{13}C$) as an indicator of internal CO_2 concentration and water-use efficiency to determine if time-integrated photosynthetic carbon gain may increase with tree diameter. Needle samples were collected by age class from each tree from the tips of sun-exposed branches at each of the four cardinal points. Samples were taken from the lower third of the canopy for all size classes at heights ranging from 0.5–8 m from the ground and grouped by age class and tree ($n \approx 580$ needle samples). Samples were dried and ground to pass a 600- μm mesh screen size in a Wiley mill. Total Kjeldahl nitrogen was determined colorimetrically (Traacs 800, Bran + Luebbe, Elmsford, New York). Stable-carbon isotope composition was determined for 1-yr-old foliage ground to pass a 425- μm mesh ($n = 116$ needle samples). Isotope analyses were performed by Larry Giles at the Duke University Phytotron. Samples were combusted in an elemental analyzer (NA1500, Carlo Erba, Milan, Italy) and the carbon isotope composition of CO_2 derived from combustion of samples was measured with a SIRA Series II isotope mass spectrometer (VG Isotech, Middlewich, UK). The reference CO_2 was calibrated against standard Pee Dee Belemnite; the accuracy was $\pm 0.1\%$.

We measured photosynthetic capacity and leaf nitrogen concentration on a subsample of foliage to verify that leaf nitrogen was correlated with photosynthetic capacity for ponderosa pines growing at these sites. During a 10-d period in August, needles from various age classes were collected from each of the six sites. Samples were collected early in the morning and kept cool and moist ≤ 6 h until measurements were made in the laboratory. Photosynthetic capacity was measured as O_2 evolution by needles under saturating CO_2 (12%

[Day et al. 1991]), irradiance ($2600 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and humidity in a gas-phase oxygen electrode (Hansatech Instruments, Norfolk, UK). The midsections of four to five fascicles were fastened together edge-to-edge forming a rectangle with adaxial side toward the light source ($n = 32$ rectangles from montane trees, $n = 25$ rectangles from desert trees). Temperature inside of the chamber was maintained at 25°C with a chilled water bath. Total Kjeldahl nitrogen content was determined colorimetrically on dried needles (Traacs 800, Bran + Luebbe, Elmsford, New York).

Light interception and leaf demography

Light penetration into crowns of individual trees was measured using diazo paper sensors (Friend 1961), that were calibrated with a quantum sensor (LI-COR, Lincoln, Nebraska, USA) under both sun and shade conditions. Each sensor was composed of 15 layers of diazo paper (Azon #4516 nonerasable diazo sepia paper, Azon, Johnson City, New York, USA) sandwiched between two layers of opaque cardboard. A 5-mm aperture was cut into the top layer to allow sunlight to enter; sensors were protected from the elements by sealing them inside of plastic petri dishes. The amount of photosynthetically active radiation (PPFD, in moles per square meter per second) incident on a sensor was related to the number of diazo paper layers exposed by the relationship: $\log(\text{PPFD}) = 0.358(\text{number of layers exposed}) - 1.922$, $R^2 = 0.99$. One sensor was placed on each of five branches per tree at the base of live crown at the point where the innermost foliage was located; positioning within a tree encompassed all aspects. Sensors were collected after 24 h. Percentage full sunlight reaching the innermost foliage was determined from the ratio of PPFD incident on canopy sensors to reference sensors placed in full sunlight. Parallel measurements of diffuse nonintercepted radiation, a measure of the gap fraction of the crown, were taken for individual trees with a plant canopy analyzer (LAI-2000, LI-COR, Lincoln, Nebraska). A 45° view cap was used to prevent the sensor from seeing the trunk. Measurements were made within a half-hour of sunrise ($n = 80$ trees), and 8–10 readings were taken below the canopy for each reading outside of the canopy. In addition, leaf area index (LAI) of individual trees was estimated as single-sided leaf area (from allometric relationships [Callaway et al. 1994]) per unit projected ground area. The light extinction coefficient (k) was calculated using the Beer-Lambert law ($I = I_0 e^{-kLAI}$) from LAI and the ratio of light incident at base of live crown to total incident irradiance (I/I_0) obtained from diazo paper sensors. Light interception was measured at all montane sites and two of the three desert sites.

To compare leaf demography among diameter classes and between environments, we calculated the percentage contribution by mass of each age class to the total mass of foliage on a sample branch. Current year foliage was excluded to remove any effects related to

differences in needle phenology between sites. In addition, we measured total foliated length on south-facing branches to examine size-dependent differences in foliage display.

Statistical analysis

We tested for a size-dependent relationship for all of the variables using analysis of covariance with diameter class as a covariate. Sites were nested within environments and all components of the model were random effects except for stem diameter class. The diameter class \times site interaction term was not significant in any analysis and was therefore dropped from the model. Values of LAI and k were log transformed to meet assumptions of normality and equal variance. No significant differences between sites, within environments were found for $\delta^{13}\text{C}$, log LAI, log k , or diffuse nonintercept radiation, therefore sites were pooled and results are presented for between-environment comparisons only. One montane site (Virginia Mountains) had lower leaf nitrogen concentrations on average than the other two montane sites. Removing this site did not effect the overall analysis, except that site (within environment) differences were no longer significant. Therefore all six sites were included in the analysis and results are presented for environments. The percentage of foliage within a cohort did not vary with size and between environment differences were tested after eliminating diameter class terms from the model. All data fit assumptions for models used. Analyses were performed using the General Linear Models procedure, Statistical Analysis Software, Version 6.11 (SAS Institute 1996).

RESULTS

Relative growth rate and predicted photosynthetic rate

Trees growing in the desert had significantly lower relative growth rates (RGRs) than montane trees (Fig. 2A, $P < 0.05$). RGRs of small trees (6–8 cm dbh) were $\sim 0.1 \text{ kg}\cdot\text{kg}^{-1}\cdot\text{yr}^{-1}$ in the desert and $\sim 0.3 \text{ kg}\cdot\text{kg}^{-1}\cdot\text{yr}^{-1}$ in the montane environment. RGR decreased to 0.006 and $0.009 \text{ kg}\cdot\text{kg}^{-1}\cdot\text{yr}^{-1}$ for large desert and montane trees, respectively. Contrary to our prediction, there was no difference in the slope of the relationship between RGR and stem diameter between environments ($P = 0.25$).

Estimated annual photosynthetic rate per unit leaf area decreased with diameter more in montane trees than in desert trees. Our calculations of PS_a (in kilograms per square meter per year) suggest there are differences between environments in the relationship of photosynthetic rate as a function of stem diameter (Fig. 2B). If we assume photosynthetic activity averaging 5 h/d for 150–200 d/yr, these annual rates yield estimates of instantaneous PS (in micromoles per square meter per second) ranging between 0.14 and $3.48 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. These rates are low as com-

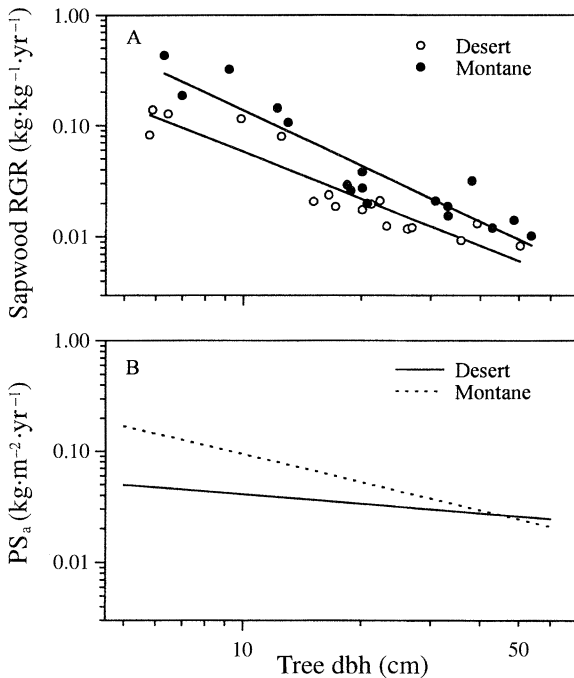


FIG. 2. Two measures of biomass acquisition and allocation for ponderosa pines growing in montane and desert environments. (A) Relative growth rates (RGR) for the 5 yr prior to cutting of bole sapwood, regressed against stem diameter at 1.4 m above ground level (dbh). For montane trees, $\log \text{RGR} = 0.779 - 1.659(\log \text{dbh})$, $R^2 = 0.90$. For desert trees, $\log \text{RGR} = 0.159 - 1.398(\log \text{dbh})$, $R^2 = 0.93$. Environments (intercepts) were significantly different ($P < 0.05$), but slopes did not differ. (B) Calculated annual net photosynthesis per unit leaf area (PS_a , expressed as carbon uptake) as a function of stem diameter (dbh). Values were predicted by growth analysis from measured rates of respiration and growth (see *Methods*).

pared to average maximum values for net photosynthesis in conifers ($3\text{--}6 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ [Larcher 1995: Table 2.4]) and would be lower if belowground allocation was included in our calculations. However, our calculated rates are based on whole canopy leaf area and photosynthesis under less than optimal conditions.

Leaf nitrogen, carbon isotope discrimination, and photosynthetic capacity

Nitrogen content per unit leaf mass increased with increasing tree diameter in the desert environments for all but 6-yr-old needles, which were very few in number (Fig. 3, Table 2). In contrast, nitrogen concentration decreased with tree size or remained constant in montane needles (Fig. 3, Table 2). The intercepts (environment terms) were similar, however the slopes (diameter class \times environment) differed for all but 6-yr-old foliage, indicating that the relationship of foliar nitrogen with diameter class was different in desert vs. montane environments.

The stable-carbon isotope composition ($\delta^{13}\text{C}$) of 1-yr-old needles increased with increasing stem diameter in

desert trees ($P < 0.01$, $R^2 = 0.21$) and was constant with increasing diameter in montane trees (Fig. 4). Environments (intercepts) were significantly different and slopes differed slightly (Table 3). The $\delta^{13}\text{C}$ values for desert and montane trees were -22.96 ± 0.07 and $-24.20 \pm 0.07\%$, respectively (mean ± 1 SE).

Photosynthetic capacity per unit leaf area (in micromoles per square meter per second), measured as O_2 evolution, was positively related to leaf nitrogen concentration ($P < 0.001$, Fig. 5). The slopes and intercepts were not different between environments (slope: $P > 0.40$, intercept: $P > 0.40$). Highest concentrations of leaf nitrogen and values of photosynthetic capacity were found in the desert environment (Fig. 5). Photosynthetic capacity per unit leaf mass (in nanomoles per gram per second) was also related to leaf nitrogen concentration as percentage of dry mass ($A_{\text{max}} = 0.671 + 75.64[\text{N}]$, $R^2 = 0.45$, $P < 0.001$, data not shown).

Light interception and leaf demography

The percentage of full sunlight reaching the innermost needles in the canopy decreased linearly with increasing stem diameter (Fig. 6A, Table 4). Significant differences between sites in the montane environment resulted in greater variability among sites than between environments in the overall model. However, data are presented by environment for simplicity. The range in amount of full sunlight reaching the innermost foliage was greater in the montane (30–86%) than in the desert (45–77%) environment. Diffuse nonintercept radiation did not vary with size or between environments ($P > 0.30$, data not shown).

The relationship of log LAI of individual trees as a function of stem diameter was best described by a third-order polynomial regression for each environment (Fig. 6B, Table 4). Log LAI increased as a function of size before reaching a plateau and then declining, and it was greater for montane trees. Least-squares mean LAI (adjusted for diameter class) was $2.84 \pm 0.88 \text{ cm}^2 \text{ leaf/cm}^2 \text{ ground area}$ (mean ± 1 SE) for desert trees and $6.25 \pm 0.66 \text{ cm}^2/\text{cm}^2$ for montane trees. The relationship between log k and stem diameter was best fit by a second-order polynomial (Fig. 6C, Table 4). Log k of single trees decreased with size in both environments, leveled at larger stem diameters, and was greater for desert trees compared to montane trees. The least-squares mean light extinction coefficient was greater for desert trees ($k = 0.23 \pm 0.03$ vs. 0.11 ± 0.02). Slope coefficients for linear, quadratic, and cubic (log LAI only) terms were the same in both environments for log LAI and log k ($P > 0.20$), and therefore, the diameter \times environment terms were dropped from the model.

The contribution of a single needle cohort to total foliage mass was independent of stem diameter for all age classes, but the percentage of total foliage in each age class differed between environments. Desert trees retained fewer age cohorts of needles than montane trees and the majority of foliage in desert trees was in younger needles

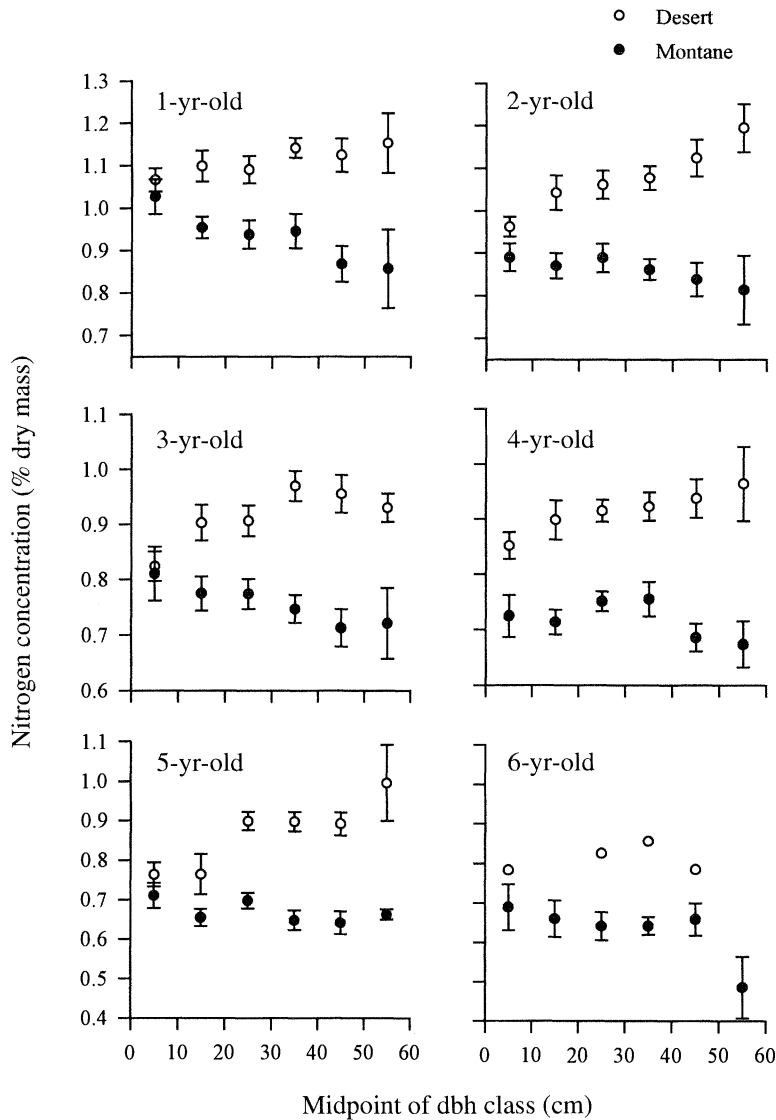


FIG. 3. Leaf nitrogen concentration as a function of stem diameter (dbh) class for 1-yr-old through 6-yr-old ponderosa pines growing in montane and desert environments. (N concentration was used as a surrogate for photosynthetic rate because some needles were physically inaccessible for continuous rate measurement.) Each symbol represents the mean (± 1 SE) of 3–15 trees per diameter class, per environment, with the exception of 6-yr-old desert foliage. Analysis of covariance was performed on raw data rather than means. Leaf nitrogen concentration increased with tree size in all but 6-yr-old desert needles and declined or remained constant with size in montane needles. (Results of covariance analysis are presented in Table 2.)

(Fig. 7). Total foliated length on south-facing branches was the same in both environments (desert, 7.28 ± 0.39 cm [mean ± 1 SE]; montane, 7.39 ± 0.40 cm, $P = 0.53$) and did not vary as a function of tree size ($P = 0.37$, data not shown).

DISCUSSION

The primary factor limiting plant growth in desert environments is water, and the consistently lower relative growth rates (RGRs) in desert compared to montane trees reflect this limitation. We hypothesized that allocation may impose an additional constraint on relative growth

rate of desert trees. In contrast to montane trees, desert trees allocate proportionally more biomass to sapwood and less to leaves as they increase in size (Callaway et al. 1994). In addition, the respiratory cost of maintaining high sapwood mass is greater in the desert environment (Carey et al. 1997). Therefore, we predicted that RGR of desert trees would decrease more with increasing stem diameter (dbh) than RGR of montane trees. However, despite leaf : sapwood mass ratios 30–50% lower for desert trees, RGRs decreased equally with dbh in both environments. Thus, we did not find a growth reduction

TABLE 2. Covariance analysis for leaf nitrogen concentration as a function of stem diameter class (dbh) for 1-yr-old through 6-yr-old ponderosa pine foliage.

Needle age (yr)	<i>n</i>	Environment	Slope	<i>P</i>	dbh × Env	<i>R</i> ²
1	55	desert	+	†	**	0.54
	65	montane	-	**		
2	56	desert	+	**	**	0.63
	63	montane		N.S.		
3	56	desert	+	**	**	0.57
	62	montane	-	†		
4	50	desert	+	*	*	0.68
	57	montane		N.S.		
5	25	desert	+	**	**	0.75
	54	montane		N.S.		
6	4	desert		N.S.	N.S.	0.61
	32	montane		N.S.		

Notes: Slope sign indicates the direction of slope (positive or negative) of foliar nitrogen concentration (percentage of dry mass) as a linear function of diameter class. Asterisks indicate significance (*P* values) of linear slope and differences between environments (dbh × Env interaction) in the relationship of foliar nitrogen with diameter class. Environments (intercepts) were not different (*P* > 0.2 for all needle ages). The *R*² values are for the covariance model.

† *P* < 0.1, * *P* < 0.05, ** *P* < 0.01, N.S. not significant.

associated with increased allocation to sapwood as predicted by current models of forest productivity.

Our analysis of relative growth rates reflects above-ground growth only. Differences in root growth could potentially explain the absence of diverging growth rates of desert and montane trees with increasing size (Fig. 1). If root growth was more rapid in the montane environment, then whole-tree RGRs of montane trees may have actually decreased less with dbh than we report (Fig. 2A).

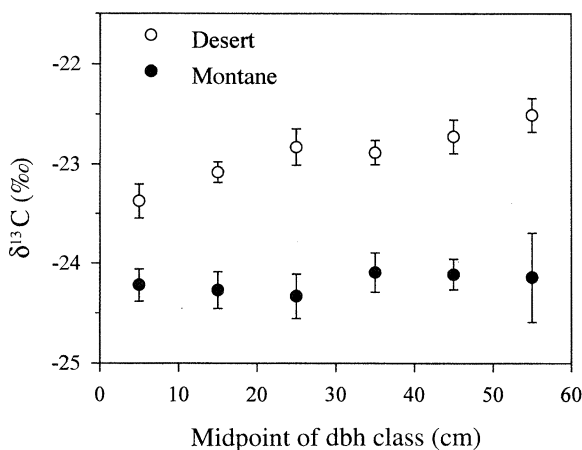


FIG. 4. Stable-carbon isotope composition ($\delta^{13}\text{C}$) as a function of stem diameter (dbh) class for needles of 1-yr-old ponderosa pine growing in montane and desert environments. Each symbol represents the mean (± 1 SE) of 4–14 trees per diameter class in each environment. Analysis of covariance was performed on raw data rather than means; results are presented in Table 3. In desert trees, $\delta^{13}\text{C}$ content increased with increasing dbh (*P* < 0.001).

TABLE 3. Analysis of covariance comparing carbon isotope composition of 1-yr-old foliage from ponderosa pines grown in desert and montane environments.

Source of variation	df	MS	<i>P</i>	Model <i>R</i> ²
Environment (Envt)	1	7.0109	0.0001	0.61
Site within Environment	4	0.4215	0.2313	
Diameter class (dbh)	1	2.2106	0.0074	
Interaction (dbh × Env)	1	0.8031	0.1026	
Error	108	0.2962		

However, biomass allocated to roots generally increases when plants are subjected to water stress (Waring and Schlesinger 1985, Waring 1987, Wilson 1988). Thus, we expect that proportional root productivity would be even higher for desert trees than for montane trees, and it is possible that we have overestimated the difference in RGRs between these two environments (Fig. 2A).

Calculations of photosynthetic rates suggested that size-dependent differences existed between environments and rates declined with tree size (Fig. 2A). However, the decline in photosynthetic rate per unit leaf area estimated in part from observed RGRs was much less in the desert. Based on these calculations, we hypothesized that large desert trees may compensate for increased allocation to sapwood by increasing canopy carbon gain through a size-dependent increase in photosynthetic rate per unit leaf area, modification of canopy architecture, or retention of younger, more active needle cohorts. All of these variables differed between desert and montane trees, but only leaf nitrogen concentration and stable-carbon isotope composition ($\delta^{13}\text{C}$), indicators of photosynthetic capacity (Field and Mooney 1986) and time-integrated CO_2 concentration within the leaf mesophyll (Farquhar et al. 1982), differed as a function of stem diameter between environments.

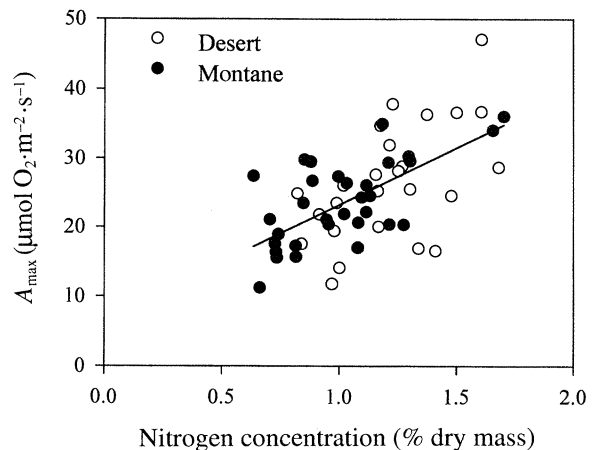


FIG. 5. Photosynthetic capacity (A_{max}), measured as O_2 evolution, as a function of leaf nitrogen concentration in montane (*n* = 32 needle samples) and desert (*n* = 27 needle samples) ponderosa pine populations. For environments combined, $A_{\text{max}} = 2.16 + 19.98(\%N)$, $R^2 = 0.47$, *P* < 0.001.

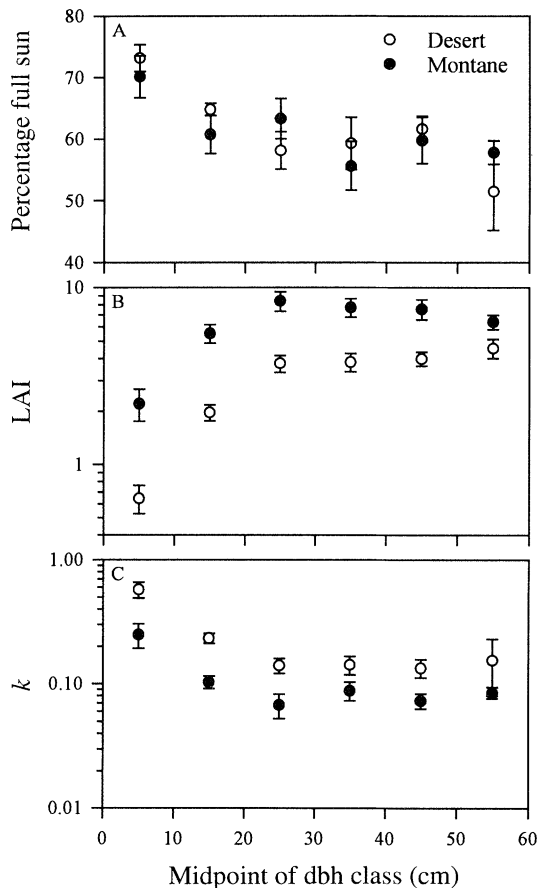


FIG. 6. Three energy-acquisition features as a function of stem diameter (dbh) class, for individual montane and desert ponderosa pines. Data show (A) light penetration into the base of the live crown, (B) leaf area index (LAI), and (C) light extinction coefficient (k) for individual trees. Note log scale on the ordinate. Each symbol represents the mean (± 1 SE) of 3–14 trees per stem diameter (dbh) class, per environment. Analysis of covariance was performed on raw data rather than means; results are presented in Table 4.

Leaf nitrogen concentration and carbon isotope composition were examined to assess differences in seasonally integrated photosynthetic capacity. The slopes of leaf nitrogen concentration as a function of stem diameter were different for desert vs. montane trees (Fig. 3); nitrogen concentration of needles increased with tree size in the desert environment. Trees growing in dry environments may allocate more carbon to root growth (Waring and Schlesinger 1985, Waring 1987, Santantonio 1989), and consequently nitrogen and other minerals taken up by the plant may concentrate in the foliage (Waring and Schlesinger 1985). Large desert trees with proportionally more conducting tissue and less leaf area are more likely to accumulate nutrients in this fashion than small desert trees. The relationship between measured photosynthetic capacity and leaf nitrogen concentration (Fig. 5) suggests that increased leaf nitrogen concentration in large desert trees results in greater photosynthetic capacity.

Needle nitrogen decreased or remained constant across size classes in montane trees, similar to results for bristlecone pine (*Pinus aristata*) and lodgepole pine (*Pinus contorta*) (Shoettle 1994). Age and presumably size-related reductions in photosynthetic capacity have been reported for Norway spruce (*Picea abies*) and *Pinus pumila* (Kull and Koppel 1987, Kajimoto 1990). In contrast to the decrease in leaf nitrogen and photosynthetic capacity in our montane population and these other studies, the increasing photosynthetic capacity in desert trees may partially offset the large investment in sapwood and maximize aboveground growth.

Leaf carbon isotope composition represents discrimination against the heavy isotope of carbon (^{13}C) during photosynthesis, and in C_3 plants it is negatively correlated with time-integrated CO_2 concentration within the leaf mesophyll (c_i) and positively correlated with integrated water-use efficiency (Farquhar et al. 1982, 1989, Ehleringer 1993). Within the desert environment, $\delta^{13}\text{C}$ values increased, thus c_i decreased with increasing stem diameter (Fig. 4). Lower c_i in needles of larger desert trees combined with higher photosynthetic capacity, inferred from higher leaf nitrogen concentrations (Fig. 3), could result from either higher photosynthetic rates or stomatal limitation to photosynthesis. If photosynthetic capacity increases with tree size, and stomatal conductance remains constant (or increases) with size, then higher $\delta^{13}\text{C}$ and lower c_i would result from higher photosynthetic rates. Conversely, if photosynthetic capacity increases and stomatal conductance decreases with tree size, then lower c_i could be interpreted as greater stomatal limitation to photosynthesis in large desert trees. Both the observed relative growth rates and modeled photosynthetic rates (Fig. 2A, B) support the former interpretation.

Comparable patterns of leaf nitrogen concentration and stable isotope composition have been observed in other studies (Donovan and Ehleringer 1994, Rasmuson et al. 1994). Although greater $\delta^{13}\text{C}$ values and, by association, greater water use efficiency are often associated with lower rates of photosynthesis and stomatal conductance, Rasmuson et al. (1994) reported higher nitrogen concentrations, stable isotope compositions and stomatal conductances in southern facing rosettes of Joshua trees (*Yucca brevifolia*) growing in the Mojave desert, indicative of higher rates of carbon gain in these rosettes. Similar to our results for ponderosa pine, Donovan and Ehleringer (1994) found size-dependent differences in leaf nitrogen concentration and stable-carbon isotope composition within a population of rabbitbrush (*Chrysothamnus nauseosus*) in the Great Basin Desert. Juvenile rabbitbrush shrubs had lower leaf nitrogen concentrations (Donovan and Ehleringer 1992) and stable-carbon isotope contents than adults, and water-use efficiency was positively correlated with plant size (Donovan and Ehleringer 1994). These results for Joshua trees, rabbitbrush, and ponderosa pine demonstrate that among individuals (or rosettes) differing in photosynthetic capacity, lower carbon isotope discrimination may be related to greater rates of photo-

TABLE 4. Analysis of covariance comparing three energy-acquisition features of ponderosa pines growing in desert and montane environments.

Source of variation	df	MS	<i>P</i>	Model <i>R</i> ²
Percentage full sunlight†				
Environment (Envt)	1	0.0016	0.6763	0.29
Site within Environment	3	0.0162	0.0004	
Diameter class (dbh)	1	0.1635	0.0001	
Interaction (dbh × Evt)	1	0.0005	0.8162	
Error	88	0.0091		
Log leaf area index				
Environment (Envt)	1	2.5454	0.0001	0.74
Site within Environment	3	0.0821	0.0628	
Diameter class (dbh)	1	1.6366	0.0001	
Interaction (dbh × dbh)	1	0.7608	0.0001	
Interaction (dbh × dbh × dbh)	1	0.4419	0.0004	
Error	88	0.3254		
Log light extinction coefficient				
Environment (Envt)	1	2.2141	0.0001	0.57
Site within Environment	3	0.0647	0.2389	
Diameter class (dbh)	1	1.8069	0.0001	
Interaction (dbh × dbh)	1	1.0942	0.0001	
Error	83	0.0451		

† Percentage of full sunlight reaching the innermost foliage at base of live crown.

synthetic carbon gain. In the desert environment of our study, large trees may have more access to soil water than smaller trees. If water is available to support high rates of transpiration in the hot, high-light desert environment, large trees may maximize water-use efficiency by increasing photosynthesis rather than decreasing water loss through stomatal closure (Mooney and Gulmon 1979).

Foliage from desert trees had higher $\delta^{13}\text{C}$ values and there was a slightly significant diameter class × environment interaction ($P = 0.10$), indicating a differential response of carbon isotope composition as a function of diameter between desert and montane trees. Generally, species at higher elevations have greater (less negative)

carbon isotope ratios and therefore photosynthesize at lower ratios of internal to external CO_2 (Körner 1989, Marshall and Zhang 1993); higher ratios may result from a steeper CO_2 concentration gradient from the atmosphere to the chloroplast in thicker leaves (Marshall and Zhang 1993). In this study, we found the opposite trend. The lower ^{13}C content of montane needles is most likely caused by greater evaporative demand in the desert environment of our study.

Differences in leaf area index (LAI) and light extinction coefficient (k) suggest differences in crown architecture for trees from desert and montane environments. Unlike leaf nitrogen concentration and $\delta^{13}\text{C}$ values, the change in LAI and k as a function of tree size was parallel in the two environments. Leaf area index increased with tree size and was greater in the montane environment. The light extinction coefficient is a measure of the fraction of light absorbed per unit leaf area as light passes through the canopy; with respect to canopy structure, k is influenced by leaf orientation (horizontal to vertical), leaf arrangement (clumped vs. uniform), and leaf optical properties (Nobel et al. 1993). The light extinction coefficient decreased with tree size and leaf area as is common for stands and individual trees (Mencuccini and Grace 1996) and was greater for desert trees. Values for individual open-grown trees were lower than values for a typical canopy (LAI = 0.3–1.3 [Nobel et al. 1993]). Greater k values, in conjunction with similar percentages of full sunlight reaching the innermost foliage (I/I_0) and smaller LAIs, suggest that desert canopies are more efficient at light absorption (more photons absorbed per unit leaf area) and that desert foliage may be less clumped (Stenberg et al. 1995) or less reflective (Waring and Schlesinger 1985). The light extinction coefficients may also reflect a difference between desert and montane trees in the amount of light absorbed by

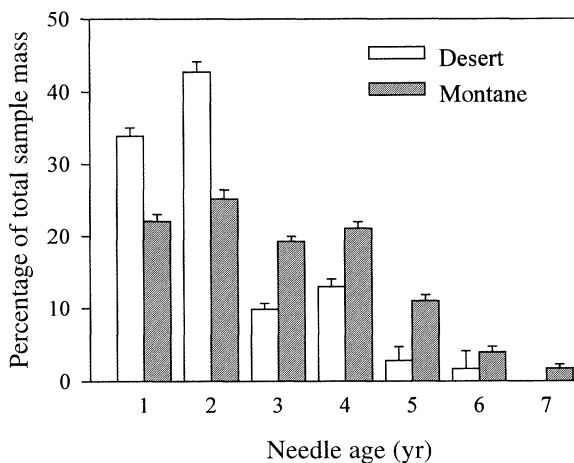


FIG. 7. Percentage of total foliage mass per sample by needle age class of desert and montane ponderosa pines. Each data bar represents the mean (and 1 SE) of 3–14 trees per stem diameter (dbh) class, per environment. Mean percentage foliar mass of needles of all age classes differed significantly between desert and montane environments ($P < 0.05$).

foliage relative to stems and branches. Greater nitrogen concentrations and thus greater chlorophyll content in desert needles (Evans 1989) may also facilitate light absorption. However, these higher nitrogen concentrations in needles also increase the construction cost of foliage (Williams et al. 1987).

Desert trees had fewer needle age classes than montane trees. Retaining young, more efficient foliage may result in maximum stem production for desert trees. However, retention of a greater proportion of older foliage was associated with higher RGRs in montane trees and higher stem biomass production in Scots pine (Kuuluvainen and Kaininen 1992). We found no relationship between needle retention and tree size. Foliage length was also the same between environments and for size classes within an environment. Fewer foliage age classes distributed along a similar length of branch may result in more efficient light use by less self-shaded needles within a branch in desert trees. Our data for leaf demography and canopy structure imply that desert canopies may be more efficient at light capture and utilization, but they do not explain size-dependent differences in canopy carbon gain.

Trees respond to growth environment through changes in biomass allocation and physiology. Within an environment, allocation and physiology can change as a function of tree size (age). As they increase in size, desert-grown ponderosa pines may compensate for the cost of building and maintaining proportionally greater sapwood volume by increasing, or at least maintaining, carbon gain per unit leaf mass. Higher leaf nitrogen concentrations in larger trees, combined with greater light extinction coefficients and less self-shading, contribute to maximum canopy efficiency in the desert environment. Increased photosynthetic capacity in large desert trees as compared to small desert trees may be possible due to the greater water conducting capacity provided by proportionally greater sapwood volumes. Overall, these data demonstrate that increased allocation to heterotrophic stem tissue at the expense of photosynthetic tissue does not always incur a reduction in tree growth as predicted by current models of forest productivity.

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