

BIOMASS ALLOCATION OF MONTANE AND DESERT PONDEROSA PINE: AN ANALOG FOR RESPONSE TO CLIMATE CHANGE¹

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Abstract. We measured aboveground biomass allocation of *Pinus ponderosa* on hydrothermally altered andesite in montane and desert climates. Thus substrate was held constant while climate varied. Trees from montane climates had higher leaf mass per unit cross-sectional area of sapwood (functional conducting xylem) than trees from desert climates, suggesting that a functional response to differences in climate had occurred. Our results also indicate that sapwood mass:leaf mass ratios of *P. ponderosa* may increase $\approx 50\%$ with a 5°C change in mean growing-season temperature, approximately the difference between our montane and desert sites. High proportional allocation of biomass to sapwood may improve water relations of *P. ponderosa*, but because sapwood contains living parenchyma, respiratory costs may be high. Site-specific regression equations were used to calculate aboveground biomass allocation for simulated montane and desert trees with the same diameter at breast height, dbh. Simulated montane trees were 46–52% taller than desert trees, and montane trees 10 cm in dbh had twice the total aboveground mass of desert counterparts. Simulated 50-cm montane and desert trees were almost identical in total mass, even though the montane tree was 46% taller. The predicted proportion of biomass allocated to bole sapwood increased with size for both montane and desert models; however, the 50-cm desert model contained 8% more total sapwood mass than the taller montane model. Total biomass of branches was similar for paired models of all size classes; however, biomass of primary and secondary branches differed considerably. The 50-cm desert model had twice as much biomass in primary branches in comparison to the montane model, whereas the montane model had 3 times more biomass in secondary branches than the desert model. For 10-cm trees of the desert and montane models 29 and 33% of the biomass were leaves, respectively. In larger trees, leaf allocation decreased to 5 and 7% for desert and montane models, respectively. The effects of climate on biomass allocation, such as reported here, and corresponding changes in whole-plant assimilation rates must be incorporated into growth-response models used to predict future fluctuations in forest productivity due to global climate change.

Key words: allocation; allometry; altered andesite; biomass; climate; Great Basin; leaf area; *Pinus ponderosa*; sapwood; Sierra Nevada; temperature.

INTRODUCTION

General circulation models of future climate predict that temperature will increase $1.5^\circ\text{--}4.5^\circ\text{C}$ and precipitation will decrease in much of interior North America in response to a doubling of CO_2 in the atmosphere (Manabe and Wetherald 1987, Mitchell et al. 1990, Rind et al. 1990). In arid ecosystems, where soil moisture is limiting, such a change will decrease plant productivity and may alter current species distributions. These effects of predicted climate change on plant growth may be mitigated by CO_2 "fertilization." Ex-

posure to elevated CO_2 often causes higher leaf-level photosynthetic rates, greater water-use efficiency, and higher growth rates (Long 1991, Mooney et al. 1991).

Plant growth is determined both by rates of net photosynthesis and by allocation of fixed carbon to "autotrophic tissue" (primarily leaves) or "heterotrophic tissue" (branches, stems, roots, and reproductive parts). Although climate change and CO_2 fertilization may affect leaf-level assimilation rates and short-term growth, long-term growth may be influenced more by changes in carbon allocation than by changes in photosynthetic rate (Poorter et al. 1990, Norby et al. 1992).

As in other ecosystems, the net effect of climate change is uncertain in western coniferous forests. Net photosynthetic rates of many western conifers are relatively unresponsive to temperature (Larcher 1980, DeLucia and Smith 1987), but allocation of aboveground bio-

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TABLE 1. Topographical, climate, and soil characteristics for sites used for tree harvests.

Site	Elevation (mm)	Precipitation (mm/yr)	Temperature* (°C)	Aspect
Montane				
Alpine County (<i>n</i> = 10)	2100	≈950	≈11.5	S
Virginia Mts.†	1850	≈450	≈11.5	S
Desert				
Peavine Mt. (<i>n</i> = 7)	1700	242	13.1	SW
DRI‡ (<i>n</i> = 5)	1500	230	13.8	W
Ramsey Mine (<i>n</i> = 5)	1750	≈200	14.0	S

* Temperature is the daily mean for May.

† The Virginia Mts. site for this study was located 250 m higher in elevation than the site described in DeLucia et al. (1988) and Schlesinger et al. (1989).

‡ Desert Research Institute site.

mass varies with site moisture and temperature (Snell and Brown 1978, Pearsons et al. 1984, Waring and Schlesinger 1985). Conifer species native to xeric habitats allocate more biomass to sapwood and roots and less to leaves than species of more mesic habitats. An increase in the sapwood : leaf area ratio may improve the water relations of trees in xeric climates, but because sapwood contains living cells, these changes may increase whole-tree respiration and decrease whole-tree assimilation rates (Ryan 1990, Ryan and Waring 1992). To our knowledge, current predictions of long-term forest growth in response to climate change and CO₂ fertilization do not consider potential shifts in biomass allocation in response to moisture and temperature.

We have used ponderosa pine growing at different elevations, and thus under different temperature and precipitation regimes, to test the hypothesis that trees growing under hotter, drier conditions (desert populations) will allocate proportionally more biomass to sapwood and less biomass to leaves than conspecific trees in cool, moist montane conditions. On the eastern slope of the Sierra Nevada and in the adjacent Great Basin Desert, open stands of *Pinus ponderosa* Laws. (ponderosa pine) and *P. jeffreyi* Grev. & Balf. (jeffrey pine) occur on isolated pockets of soil derived from hydrothermally altered andesite (Billings 1950, Schlesinger et al. 1989). These stands occur in both hot, dry desert and cool, moist montane environments on similar substrate and are surrounded by typical Great Basin sagebrush steppe vegetation at lower elevations and by sagebrush steppe, pinyon-juniper woodland, and conspecific conifers at higher elevations (DeLucia et al. 1988). These open-forest stands provide the opportunity to examine the effects of different precipitation and temperature regimes associated with elevation on biomass allocation without the potentially confounding effects of differences in substrate nutrient availability. We measured aboveground biomass allocation of *P. ponderosa* in desert and montane populations using harvests of whole trees and used regression models based on allometric relationships to compare biomass allocation between desert and montane trees.

METHODS

Sites

To test our hypothesis, we harvested all aboveground biomass of selected *P. ponderosa* trees in montane and desert climates and measured biomass allocation to leaves, branches, sapwood, heartwood, and bark. We selected two montane and three desert populations of *P. ponderosa* growing on soils derived from hydrothermally altered andesite near Reno, Nevada, USA for aboveground harvests in the summer of 1992. Temperature and precipitation for sites in Alpine County and the Virginia Mountains (montane sites), and on Peavine Mountain, at the Desert Research Institute (DRI), and near the Ramsey Mine (desert sites) are summarized in Table 1. All but the site at the Desert Research Institute are described in DeLucia et al. (1988) and Schlesinger et al. (1989). Measurements in the Virginia Mountains were taken ≈250 m higher in elevation than at the site described by DeLucia et al. (1988) and Schlesinger et al. (1989). Soils at each site were typical of those derived from altered andesite with low pH (≈3.7) and low concentrations of HCO₃⁻-extractable phosphorus (≈5.6 μg/g, Schlesinger et al. 1989). Montane and desert sites did not differ significantly in soil pH, SO₄, Ca, P, or N (Schlesinger et al. 1989). For ponderosa pine, the mean foliar concentrations of N (0.096 mg/g), P (0.010 mg/g), and Ca (0.016 mg/g) were not significantly different among populations on altered andesite at different elevations (Schlesinger et al. 1989). A small number of trees (5–10) was harvested at each site and combined into desert or montane groups based on the local temperature and precipitation at the site (Table 1). Total *n* for each climate group was 17.

Allometry and biomass allocation

Sample trees were selected to represent the typical range of diameters at 140 cm above the ground (dbh). Total bole height and the basal diameter of all branches on each bole were measured on trees cut above the swell at the base. Thin disks (3–5 cm transverse sections) were cut at 1-m intervals from each bole and an additional section was cut at the base of the live crown

(BLC). Disks were stained with bromocresol green (Kutscha and Sachs 1962) to delineate sapwood from heartwood, and the cross-sectional areas of sapwood, heartwood, and bark on each disk were traced on clear acetate. The area of each component on the acetate was cut out and weighed. Mass was converted to area by multiplying by the specific area (in square centimetres per gram) of the acetate. The volume (in cubic metres) of each component in each 1-m bole section was calculated using the areas of the disks at each end of the 1-m sections in the following equation: volume = $(A_1 + A_2)/2 \times (1 \text{ m})$, where A_1 = initial area in square metres and A_2 = terminal area in square metres. Bole volume was derived by summing all sections for each tree. Volume of each component was converted to mass using the specific gravity (in kilograms per cubic metre) of wood and bark. Specific gravities were determined using the known dimension and dry mass of wood cores and displacement volume and dry mass of bark subsamples.

Five to six branches were removed from each tree and separated into primary branch (defined as the main axis attached directly to the bole), secondary branches (all other branches), and leaves. Primary branches were cut into 0.5-m sections, and the diameter of heartwood (if present), sapwood, and the total branch was measured at the end of each section. Cross-sectional areas were calculated from these measurements and volumes were estimated using the previous equation modified for 0.5-m sections. Secondary branches were divided into three diameter classes: > 1.5 cm, 0.8–1.5 cm, and < 0.8 cm. The total length of branches in each size class was measured, and the cross-sectional areas of sapwood and bark determined for five subsampled branches from each size class. Volume of secondary branches was estimated by multiplying the total length of each size class by the average cross-sectional area of the sapwood and bark. Pith was included in sapwood estimations and cortex was included in bark estimations. Mass of branches was determined using specific gravity calculated for bole components.

Leaves were removed from each branch, dried at 60°C, and weighed to the nearest gram. Fresh 5–10 g subsamples were collected from one randomly chosen branch from each of the 17 trees in each climate group and measured for one-sided leaf area with a LI-COR 3100 area meter. Specific leaf areas (SLA) of the subsamples were used to convert leaf mass to leaf area.

Statistical analysis

For desert and montane groups, logarithmic least squares regressions ($\log Y = a + b \log X$) were calculated using branch basal area as the independent variable and total sapwood, total bark, primary branch sapwood, primary branch bark, secondary branch sapwood, secondary branch bark, and leaf mass. These regression equations were applied to all branch bases

measured on each tree to estimate total biomass of branch components on whole trees.

Whole-tree leaf mass, bole component masses, and branch component masses were regressed on dbh using logarithmic regressions for each climate group (cf. Whittaker and Woodwell 1968, Chapman and Gower 1991). Leaf area was regressed against cross-sectional sapwood area at BLC, and sapwood mass : leaf mass ratios and sapwood volume : leaf area ratios were regressed against dbh using simple regression models ($Y = a + bX$) for each climate group. For small trees that had branches all the way to the ground, diameter at BLC was substituted for dbh. For individual branches, leaf area was regressed against cross-sectional sapwood area at the base, sapwood mass : leaf : mass ratios were regressed against branch diameter at base, and sapwood volume : leaf area ratios were regressed against branch diameter at base using simple regression models.

Regression models for desert and montane populations were compared using covariance analysis (Steele and Torrie 1980). If slope coefficients were significantly different between the two climate groups, then intercept coefficients were not tested. To compare patterns of aboveground biomass allocation for desert and montane trees of the same diameter, the regression models were used to calculate allocation patterns for hypothetical desert and montane trees with dbh's of 10, 25, and 50 cm.

RESULTS

Aboveground biomass allocation patterns differed among montane and desert populations of *P. ponderosa*. Large trees at montane sites allocated proportionally more biomass to leaves per unit cross-sectional area of sapwood at BLC than large trees at desert sites (Fig. 1). Leaf : sapwood area ratios, measured as the slopes of the regression lines, were 0.201 and 0.104 m^2/cm^2 for montane and desert species, respectively. In an extremely moist forest of western Oregon, the leaf : sapwood area ratio for ponderosa pine increases to 0.25 m^2/cm^2 (Waring et al. 1982). Conversely, sapwood volume : leaf area ratios and sapwood : leaf mass ratios were much higher for large trees in desert climates than for large trees in montane climates (Fig. 2a, b). Sapwood volume : leaf area ratios and sapwood mass : leaf mass ratios are interconvertible by one specific gravity coefficient for sapwood for all trees and two group-specific SLA coefficients. We have presented these data as sapwood volume : leaf area to emphasize potential benefits of these allocation patterns to whole-tree water relations and as sapwood : leaf mass to emphasize potential carbon costs resulting from whole-tree respiration.

Trees in montane populations, regardless of size, had much higher leaf mass per unit dbh than trees in desert populations (Fig. 3a). Total tree sapwood mass was $\approx 65\%$ lower for small trees and saplings in desert cli-

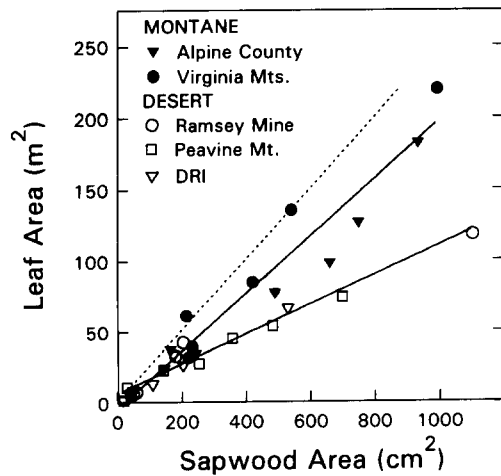


FIG. 1. Whole-tree leaf area (LA) vs. whole-tree cross-sectional sapwood area at the base of the live crown (SA) for *Pinus ponderosa* in montane and desert climates. DRI = Desert Research Institute. For montane trees, $LA = 3.839 + 0.201(SA)$, $r^2 = 0.94$. For desert trees, $LA = 6.646 + 0.104(SA)$, $r^2 = 0.96$. Slopes differed significantly, ANCOVA, $P < 0.001$. --- is from Waring et al. (1982) for *P. ponderosa* from a more mesic climate of western Oregon.

mates than in montane climates, but very similar among large trees in both climate regimes (Fig. 3b). For a given dbh, montane trees were $\approx 50\%$ taller than desert trees (Fig. 3c).

Relationships between cross-sectional sapwood area at the base of branches and leaf area supported on branches paralleled those observed for whole trees (Table 2). As for boles, sapwood : leaf area of small branches did not differ between climates, but large branches from trees in montane climates supported more leaf area per unit basal area of sapwood than large branches in desert climates. Sapwood : leaf mass relationships on individual branches also differed significantly between montane and desert climates; however, sapwood volume : leaf area did not. Mass : mass ratios differed from volume : area ratios because of significant differences in specific leaf area (SLA) between sites. SLA was $2.70 \pm 0.06 \text{ m}^2/\text{kg}$ (mean $\pm 1 \text{ SE}$) for trees from montane populations ($n = 17$ trees) compared to $3.02 \pm 0.06 \text{ m}^2/\text{kg}$ for trees from desert populations ($n = 17$ trees). Unlike tree boles, neither leaf mass per unit branch diameter nor branch length per unit branch diameter differed significantly between the montane and desert sites. However, the regression slope for sapwood mass vs. branch diameter was significantly higher for montane trees, indicating that sapwood mass of large branches was greater on trees from the montane site.

We calculated aboveground biomass allocation for trees with the same dbh from each climate group using regression equations specific to montane and desert trees, respectively (Table 3). Simulated montane trees were 46–52% taller than desert trees, and 10-cm dbh

montane trees had twice the total aboveground mass of their desert counterparts. Simulated 50-cm montane and desert trees were almost identical in total mass, even though the montane tree was predicted to be 46% taller, supporting our general observation that desert trees were more barrel shaped than the cone-shaped montane trees. The predicted proportion of biomass allocated to bole sapwood increased with size for both montane and desert trees; however, the 50-cm desert tree contained 8% more total sapwood mass than the taller montane tree (Table 3). Total biomass of branches was similar for paired simulated trees of all size classes; however, biomass of primary and secondary branches differed considerably. The 50-cm desert tree had twice as much biomass in primary branches in comparison to the montane tree (regression slopes significantly different, $P < 0.01$), whereas the montane

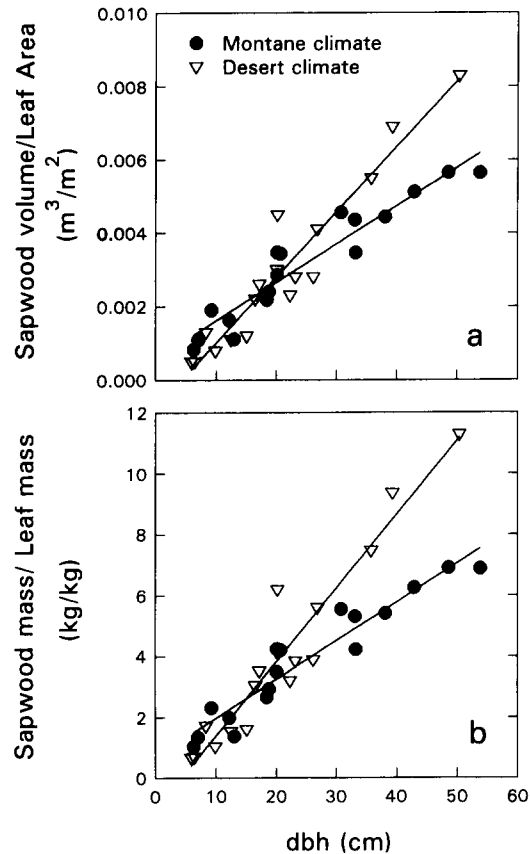


FIG. 2. Whole-tree relationships between sapwood and leaves for *Pinus ponderosa* in montane and desert climates. (a) Whole-tree sapwood volume : leaf area ratios (SLR) vs. dbh for *Pinus ponderosa* in montane and desert climates. For montane trees, $SLR = -0.00057 + 0.00010(\text{dbh})$, $r^2 = 0.90$. For desert trees, $SLR = -0.00077 + 0.00018(\text{dbh})$, $r^2 = 0.92$. Slopes differed significantly, ANCOVA, $P < 0.001$. (b) Whole-tree sapwood mass : leaf mass ratios (SLM) vs. dbh for *Pinus ponderosa* in montane and desert climates. For montane trees, $SLM = 0.701 + 0.127(\text{dbh})$, $r^2 = 0.90$. For desert trees, $SLM = -1.030 + 0.243(\text{dbh})$, $r^2 = 0.92$. Slopes differed significantly, ANCOVA, $P < 0.001$.

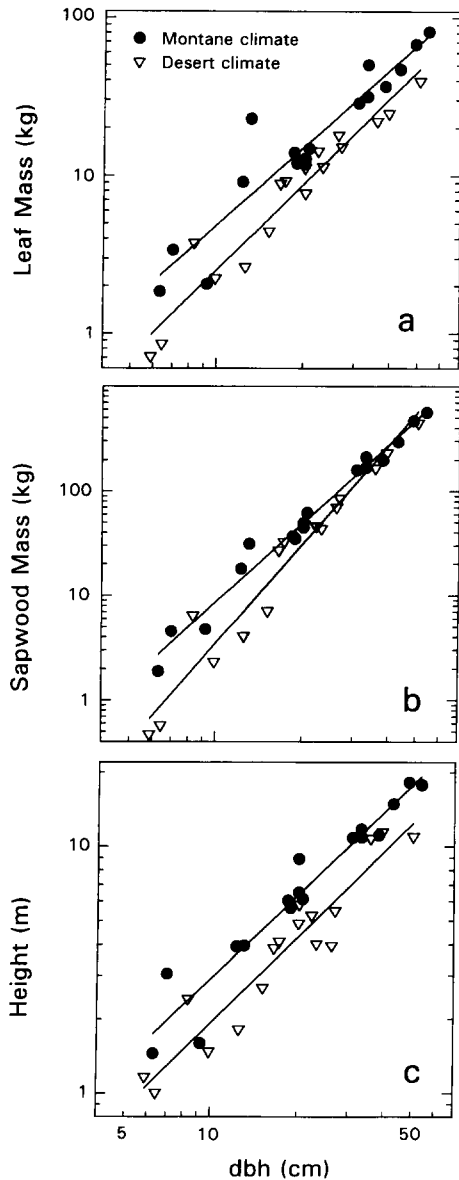


FIG. 3. Relationships between dbh and whole-tree leaf mass, sapwood mass, and tree height for *Pinus ponderosa* in montane and desert climates. (a) Whole-tree leaf mass (LM) vs. dbh for *Pinus ponderosa* in montane and desert climates. For montane trees, $\log LM = -0.939 + 1.631(\log dbh)$, $r^2 = 0.88$. For desert trees, $\log LM = -1.398 + 1.805(\log dbh)$, $r^2 = 0.94$. Slopes did not differ significantly, ANCOVA, $P = 0.227$, y intercepts differed significantly, $P < 0.001$. (b) Whole-tree sapwood mass (SM) vs. dbh for *Pinus ponderosa* in montane and desert climates. For montane trees, $\log SM = -1.559 + 2.499(\log dbh)$, $r^2 = 0.98$. For desert trees, $\log SM = -2.601 + 3.146(\log dbh)$, $r^2 = 0.94$. Slopes differed significantly, ANCOVA, $P = 0.005$. (c) Tree height (H) vs. dbh for *Pinus ponderosa* in montane and desert climates. For montane trees, $\log H = -0.655 + 1.120(\log dbh)$, $r^2 = 0.92$. For desert trees, $\log H = -0.858 + 1.142(\log dbh)$, $r^2 = 0.90$. Slopes did not differ significantly, ANCOVA, $P = 0.805$, y intercepts differed significantly, $P < 0.001$.

tree had 3 times more biomass in secondary branches than the desert tree (regression slopes significantly different, $P < 0.01$). For 10-cm trees of the desert and montane models 29 and 33% of the biomass were leaves, respectively (Table 3). In larger trees, leaf allocation decreased to 5 and 7% for desert and montane models, respectively (Table 3). Regressions for bark mass ($\log bark = -2.26 + 2.54[\log dbh]$ and $\log bark = -2.23 + 2.41[\log dbh]$ for montane and desert trees, respectively) and heartwood mass ($\log heart = -4.63 + 3.78[\log dbh]$ and $\log heart = -4.12 + 3.28[\log dbh]$ for montane and desert trees, respectively) did not differ between montane and desert sites.

DISCUSSION

The finding that large desert *P. ponderosa* trees had higher cross-sectional areas of sapwood at BLC per leaf area displayed, and higher sapwood volume : leaf area ratios than large montane *P. ponderosa* trees indicates that a phenotypic acclimation or genotypic change in response to xeric climate has occurred in the desert populations. High proportional allocation of biomass to sapwood may reduce the impact of xylem cavitations induced by water stress (Tyree and Dixon 1986), mitigate losses in sapwood permeability as water content of the bole decreases (Puritch 1971, Waring and Running 1978), and improve water storage capacity of trees in desert climates. Although portions of functional xylem may become temporarily blocked by cavitations, which can be mitigated by reserve conductive tissue, we do not know whether *P. ponderosa* is more susceptible to cavitations induced by freezing at montane sites or cavitations due to water stress at desert sites. Regardless, water stored in sapwood may provide up to one-third of daily requirements of transpiration in conifers (Waring et al. 1980) and is also thought to help conifers avoid long-term drought (Waring and Running 1978). Large investment in sapwood may also increase carbohydrate storage capacity (Kramer and Kozlowski 1979), potentially improving recovery after stress.

Although high biomass allocation to sapwood appears to have many benefits in hot, dry climates, sapwood contains living ray cells that may increase maintenance respiration, offsetting the potential growth benefits of improved water relations (Ryan 1990). In stands of *Pseudotsuga menziesii*, low cross-sectional sapwood : leaf area ratios were associated with high growth rates (Espinosa Bancalari et al. 1986). A prediction of higher respiratory costs for *P. ponderosa* trees with high sapwood mass : leaf mass ratios assumes no compensatory decreases in tissue-specific respiration rates or acclimation to high temperature in desert climates. Even if respiration rates acclimate to temperature, a net loss of carbon to respiration in desert climates is likely because desert trees allocate proportionally more biomass to sapwood.

We cannot separate phenotypic and genotypic effects

TABLE 2. Regression models for branch-level relationships among sapwood, leaves, and branch physical dimensions for *Pinus ponderosa* at the montane and desert sites.

Relationships		Regression model	r ²
Leaf area (LA) vs. sapwood area at branch base (BA)*	Montane	LA = 0.0012 + 0.0123(BA)	0.92
	Desert	LA = 0.0021 + 0.0064(BA)	0.85
Sapwood volume: leaf area ratios (SLR) vs. branch diameter (BS)†	Montane	SLR = -0.0011 + 0.0020(BD)	0.71
	Desert	SLR = -0.0014 + 0.0023(BD)	0.66
Sapwood mass: leaf area ratios (SMLR) vs. branch diameter (BD)*	Montane	SMLR = -0.0001 + 0.0012(BD)	0.61
	Desert	SMLR = -0.0001 + 0.0016(BD)	0.58
Leaf mass (LM) vs. branch diameter (BD)	Montane	log LM = -1.346 + 1.942(BD)	0.92
	Desert	log LM = -1.387 + 1.697(BD)	0.86
Sapwood mass (SM) vs. branch diameter (BD)*	Montane	log SM = 0.389 + 3.351(log BD)	0.96
	Desert	log SM = 0.570 + 3.026(log BD)	0.96
Branch length (L) vs. branch diameter (BD)†	Montane	log L = -0.0622 + 1.208(log BD)	0.88
	Desert	log L = -0.0560 + 1.024(log BD)	0.85

* Equations with significantly different slopes.

† Equations with significantly different y intercepts.

on biomass allocation differences between desert and montane populations. These populations are likely to differ ecotypically (genetically) because of their spatial isolation (up to 85 km apart) and their probable status as relict populations (Billings 1950). Gene frequencies and physiological characteristics of *P. ponderosa* from disjunct populations may vary substantially (Grant et al. 1989, Monson and Grant 1989). Our regression models show that the sapwood: leaf allocation ratios differ strongly for large trees of different climate groups, whereas there is no difference for small trees (5–10 cm dbh). This indicates that significant differences in biomass allocation develop over time, which may represent phenotypic acclimation rather than ecotypic differences. Phenotypic acclimation was also prominent in controlled laboratory conditions, where 4-mo-old ponderosa pine seedlings from both desert and montane seed sources reallocated significantly more biomass to stems at increased temperature (R. M. Callaway, unpublished data).

Large differences in biomass allocation to primary and secondary branches between desert and montane trees also indicate a functional response to climate. Based on the allometric regression we calculated that a 50-cm dbh desert tree has twice as much biomass in primary branches and considerably less biomass in secondary branches than a montane tree. This allocation pattern could be related to morphological and physiological differences between primary and secondary branches. Sapwood in large primary branches may augment the water storage capacity of desert trees (20% of total sapwood in desert trees), at a carbon cost comparable to bole sapwood. However, most secondary branches had intact cortex occupying a large cross-sectional proportion of what we classified as bark in our allocation measurements. Cortex is composed of living parenchyma and may have high respiration costs for a minimal gain in water storage. High biomass allocation to secondary branches in montane climates also may maximize canopy display and support a larger

TABLE 3. Biomass allocation of simulated trees of *Pinus ponderosa* with 10 cm, 25 cm and 50 cm dbh. Predicted values were derived from regression equations for the montane and desert sites. Regression equations that differed significantly between the two climate types are presented in the Fig. 3 legend. Percentages of total aboveground mass are shown in parentheses.

Measure	10 cm		25 cm		50 cm	
	Montane	Desert	Montane	Desert	Montane	Desert
Height (m)	2.9	1.9	8.2	5.5	17.7	12.1
Aboveground mass (kg)						
Total	27	14	189	137	945	939
Sapwood*	9 (33%)	4 (29%)	86 (46%)	63 (46%)	486 (51%)	556 (59%)
Heartwood	1 (4%)	1 (7%)	7 (4%)	5 (4%)	24 (3%)	17 (2%)
Bark	8 (30%)	5 (36%)	74 (39%)	55 (40%)	367 (39%)	319 (34%)
Leaves†	9 (33%)	4 (29%)	22 (12%)	14 (10%)	68 (7%)	47 (5%)

* Components derived from equations in which the two sites had significantly different slopes.

† Equations in which the sites had significantly different y intercepts.

leaf biomass per branch. Most secondary branch cortex parenchyma contained chlorophyll (R. M. Callaway, *personal observation*), and corticular photosynthesis has been shown by others to be significant for small conifer branches (Sprugel and Benecke 1988). Because respiration increases exponentially with temperature (Fitter and Hay 1981) and corticular photosynthesis is limited by light diffusing through the outer bark (Sprugel and Benecke 1988), the photosynthesis:respiration balance of secondary branches is probably much lower in hot climates.

In summary, the response of trees to future climatic conditions will depend on the combined influence of climatic effects on physiological processes and climate-driven shifts in biomass allocation. The desert populations in this study experienced 2°–3°C higher mean growing season temperature and a twofold reduction in precipitation relative to the montane populations. These climate differences may mimic conditions projected for a doubling of atmospheric CO₂. Our results indicate that growth under warmer, drier desert conditions caused an ≈55% increase in the sapwood:leaf mass ratio of large ponderosa pine trees. This climate-driven shift in biomass allocation from foliage to sapwood will decrease the productivity of large trees and may offset the stimulation of photosynthesis caused by atmospheric CO₂ enrichment (Green and Wright 1977). Biomass allocation responses, such as reported here, and resulting changes in whole-plant assimilation rates must be incorporated into growth-response models used to predict fluctuations in forest productivity and composition with changes in climate and atmospheric CO₂ concentration.

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