

Climate-driven changes in biomass allocation in pines

EVAN H. DELUCIA,* HAFIZ MAHERALI* and EILEEN V. CAREY†

*Department of Plant Biology, University of Illinois, 265 Morrill Hall, 505 South Goodwin Street, Urbana, IL 61801, USA,

†Department of Forest Resources, University of Minnesota, St. Paul, MN 55108, USA

Abstract

Future increases in air temperature resulting from human activities may increase the water vapour pressure deficit (VPD) of the atmosphere. Understanding the responses of trees to spatial variation in VPD can strengthen our ability to predict how trees will respond to temporal changes in this important variable. Using published values, we tested the theoretical prediction that conifers decrease their investment in photosynthetic tissue (leaves) relative to water-conducting tissue in the stem (sapwood) as VPD increases. The ratio of leaf/sapwood area (A_L/A_S) decreased significantly with increasing VPD in *Pinus* species but not in *Abies*, *Pseudotsuga*, *Tsuga* and *Picea*, and the average A_L/A_S was significantly lower for pines than other conifers (pines: $0.17 \text{ m}^2 \text{ cm}^{-2}$; nonpines: $0.44 \text{ m}^2 \text{ cm}^{-2}$). Thus, pines adjusted to increasing aridity by altering above-ground morphology while nonpine conifers did not. The average water potential causing a 50% loss of hydraulic conductivity was -3.28 MPa for pines and -4.52 MPa for nonpine conifers, suggesting that pines are more vulnerable to xylem embolism than other conifers. For *Pinus ponderosa* the decrease in A_L/A_S with high VPD increases the capacity to provide water to foliage without escalating the risk of xylem embolism. Low A_L/A_S and plasticity in this variable may enhance drought tolerance in pines. However, lower A_L/A_S with increasing VPD and an associated shift in biomass allocation from foliage to stems suggests that pines may expend more photosynthate constructing and supporting structural mass and carry less leaf area as the climate warms.

Keywords: drought, pipe model, sapwood, water relations, water vapour pressure deficit

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Introduction

Industrial activity and reductions in forest area are expected to drive a rapid increase in global temperature and evaporation rate during the next century (Kattenberg *et al.* 1996); mean annual temperature may increase by as much as 4°C or greater. This anticipated warming will occur during the lifetime of many of today's trees and raises the question of how large, long-lived organisms will respond to a warmer future with greater rates of evaporation. Seedlings are not necessarily the best model for large trees, which are not readily amenable to experimentation. We have used data from the literature for large trees to show that individuals in the genus *Pinus* are likely to respond to an increase in water loss

associated with future warmer air temperatures by altering their above-ground allocation patterns.

For an individual tree, total leaf area is closely correlated with the cross-sectional area of the water-conducting portion (sapwood) of the main stem (Waring *et al.* 1982; Enquist *et al.* 1998). This scaling relationship, referred to as the pipe model (Shinozaki *et al.* 1964), reflects coordination between water conducting and transpiring tissues and is expressed as the leaf/sapwood area ratio (A_L/A_S). A_L/A_S provides a functionally relevant metric for describing the above-ground form of trees.

Whitehead and coworkers (Whitehead *et al.* 1984) derived an equation that relates A_L/A_S and the conductivity of sapwood to the evaporative potential of the atmosphere, expressed as the vapour pressure deficit

Correspondence: E.H. DeLucia, fax +1/217-244-7246, e-mail delucia@uiuc.edu

(VPD). By combining Darcy's Law describing water flow through a homogeneous medium with the Penman-Monteith equation describing evapotranspiration from plant canopies, they stated:

$$A_L/A_S = (K * \Delta\Psi) / (VPD * g_s * l * c);$$

where K describes the conductivity of the tracheids to water and $\Delta\Psi$ is the water potential gradient through a stem of length l . Atmospheric evaporative demand is expressed as VPD and g_s is canopy-weighted stomatal conductance. The variable c represents the specific heat and density of air, the latent heat of vaporization and viscosity of water, and the psychrometric constant (Whitehead *et al.* 1984; Mencuccini & Grace 1995).

Anticipated increases in air temperature may increase the vapour pressure deficit of the atmosphere (VPD; Gregory *et al.* 1997), and, along with elevated leaf temperatures, this change will increase water loss from trees. In most conifers the water potential gradient from the soil to the leaves ($\Delta\Psi$) is maintained in a fairly narrow range to ensure positive photosynthetic rates and the continuity of the transpiration stream; the stomata of most species of North American conifers close at a xylem water potential near -2 MPa (Smith *et al.* 1985). From the 'Whitehead equation' we predict that trees will respond to an increase in VPD by decreasing A_L/A_S . Alternatively, trees can support higher transpiration without altering A_L/A_S by increasing the efficiency of the conducting elements expressed as K . To test the prediction that A_L/A_S will decrease as VPD increases, we compared published values for different conifer species growing along environmental gradients.

Materials and methods

Data were compiled from 25 studies published between 1974 and 1998 and one unpublished manuscript (R.M. Callaway), and include observations for 6 genera and 17 species (Table 1). Some studies were not included because sapwood area (A_S) was not measured at 'breast height' (1.35 m), or needle area (A_L) was not expressed as projected leaf area and could not be converted, or the sampling location could not be determined precisely. All-sided A_L for some published reports of *Pinus* and *Abies* were recalculated as projected A_L with conversion factors (Waring *et al.* 1982; Naidu *et al.* 1998).

The mean maximum VPD (June – August) for each published value in North America was calculated from the Vegetation Ecosystem Modelling and Analysis Project (VEMAP) data set (Kittel *et al.* 1995). The Intergovernmental Panel on Climate Change (IPCC) climate dataset (New *et al.* 1999) was used to calculate

VPD for *Pinus sylvestris*, *Picea sitchensis*, *Pinus radiata*, and *Psuedotsuga menzeisii* from the UK, Australia, and Italy.

Results and discussion

The leaf/sapwood area ratio of pines decreased significantly with summer VPD (Fig. 1). Of the 21 observations defining the regression, 15 were for *Pinus contorta* (A_L/A_S : 0.121–0.290 m² cm⁻²) and *P. ponderosa* (A_L/A_S : 0.104–0.201 m² cm⁻²). These North American species dominated the relationship and the A_L/A_S for each of these species individually was negatively correlated with VPD (*P. contorta*: $N=6$, $r^2=0.87$, $P<0.01$; *P. ponderosa*: $N=9$, $r^2=0.80$, $P<0.01$). The large intraspecific variance for these species suggests that there is substantial phenotypic plasticity for A_L/A_S . Some of the variance around the regression is caused by differences in stand density and in height to the base of the live crown among the sample populations (Dean & Long 1986; Mäkelä *et al.* 1995). *Pinus sylvestris* growing in a cool and moist environment in Great Britain (VPD < 1.2 kPa) also showed a negative relationship between A_L/A_S and VPD (Mencuccini & Grace 1995) but was displaced from the other pines.

There was no relationship between A_L/A_S and VPD for the non-*Pinus* conifers (Fig. 1. $P=0.84$), or between A_L/A_S and wind velocity (pines: $P=0.47$; nonpines: $P=0.86$) or precipitation (pines: $P=0.99$; nonpines: $P=0.22$) for the pines or nonpines. The contrasting response of A_L/A_S to VPD between *Pinus* and other genera suggests that evolutionary divergence within the conifers may influence the expected morphological response to rapid changes in climate. We hypothesize that the functional basis of this divergence is related to different mechanisms of drought tolerance among genera.

The flush of leaves and increment of wood each spring is an opportunity for trees to alter structural features that regulate transpiration. The flow of water through stems is controlled by dimensions of the individual conducting elements (tracheids in conifers) and by the total investment in conducting xylem relative to leaves for the whole tree (A_L/A_S). For conifers, larger diameter tracheids and a greater number or size of the bordered pits between them, increases their capacity to transport water (Pallardy *et al.* 1995). Increasing tracheid dimensions, however, elevates the risk of embolism during rapid transpiration when the water column is under extreme tension. Because of this trade-off, a greater investment in sapwood rather than an increase in the dimensions of tracheids may be a safer way of controlling foliage water potential when exposed to a dry atmosphere. In addition to their responsiveness to VPD, pines have, on average, substantially lower A_L/A_S (0.17 m² cm⁻²; $N=8$) than nonpines (0.44 m² cm⁻²; $N=11$; $P<0.01$; two-tailed *t*-test;

Table 1 Leaf:sapwood area ratios (A_L/A_S ; m^2cm^{-2}) 16 conifer species from Europe, North America, and Australia

Species	A_L/A_S	Latitude, longitude	Source
Pines			
<i>Pinus albicaulis</i>	0.310	46°05' N, 114°50' W	R.M. Callaway, unpubl. data
<i>Pinus contorta</i>	0.121	41°30' N, 112°30' W	Dean & Long (1986)
	0.150	41°00' N, 105°00' W	Long & Smith (1988)
	0.150	43°30' N, 122°00' W	Waring <i>et al.</i> (1982)
	0.176	39°30' N, 105°30' W	Kaufmann & Troendle (1981)
	0.228	41°00' N, 106°00' W	Pearson <i>et al.</i> (1984)†
	0.230	54°50' N, 3°40' W	Whitehead <i>et al.</i> (1984)
	0.290	52°07' N, 122°54' W	Keane & Weetman (1987)†
<i>Pinus ponderosa</i>	0.104	39°34' N, 119°50' W	Callaway <i>et al.</i> (1994)
	0.104	39°35' N, 119°47' W	Callaway <i>et al.</i> (1994)
	0.104	39°33' N, 119°22' W	Callaway <i>et al.</i> (1994)
	0.121	35°20' N, 111°48' W	Grier & Waring (1974)
	0.130	46°51' N, 113°29' W	Gower <i>et al.</i> (1993)
	0.158	47°00' N, 114°30' W	O'Hara & Valappil (1995)†
	0.190	43°45' N, 122°00' W	Waring <i>et al.</i> (1982)
	0.201	38°41' N, 119°44' W	Callaway <i>et al.</i> (1994)
	0.201	39°22' N, 119°41' W	Callaway <i>et al.</i> (1994)
<i>Pinus radiata</i>	0.260	37°47' S, 145°26' E	Teskey & Sherriff (1996)
<i>Pinus resinosa</i>	0.112	46°51' N, 113°29' W	Gower <i>et al.</i> (1993)
<i>Pinus sylvestris</i>	0.090	52°25' N, 0°40' E	Mencuccini & Grace (1995)
	0.117	52°00' N, 0°40' E	Whitehead (1978)
	0.150	56°14' N, 4°16' W	Mencuccini & Grace (1995)
	0.105	52°17' N, 5°45' E	VanHees & Bartelink (1993)
<i>Pinus taeda</i>	0.085	35°58' N, 79°05' W	Naidu <i>et al.</i> (1998)
	0.089	34°00' N, 80°30' W	Shelburne <i>et al.</i> (1993)*
Non-pines			
<i>Abies amabilis</i>	0.630	44°10' N, 122°20' W	Waring <i>et al.</i> (1982)
<i>Abies balsamea</i>	0.461	44°54' N, 68°38' W	Gilmore <i>et al.</i> (1996)
	0.673	44°30' N, 72°30' W	Marchand (1984)
<i>Abies grandis</i>	0.400	42°50' N, 122°30' W	Waring <i>et al.</i> (1982)
	0.510	43°45' N, 122°00' W	Waring <i>et al.</i> (1982)
<i>Abies lasiocarpa</i>	0.750	39°30' N, 105°30' W	Kaufmann & Troendle (1981)†
	0.800	46°05' N, 114°50' W	Callaway, unpubl. data
<i>Juniperus occidentalis</i>	0.224	44°00' N, 120°00' W	Gholz (1980)†
<i>Picea engelmannii</i>	0.290	39°30' N, 105°30' W	Kaufmann & Troendle (1981)†
<i>Picea rubens</i>	0.250	44°30' N, 72°30' W	Marchand (1984)
	0.350	43°45' N, 122°0' W	Waring <i>et al.</i> (1982)
<i>Picea sitchensis</i>	0.350	55°50' N, 4°35' W	Whitehead <i>et al.</i> (1984)
<i>Pseudotsuga menziesii</i>	0.370	49°10' N, 123°35' W	Brix & Mitchell (1983)
	0.421	52°00' N, 5°04' E	Bartelink (1996)
	0.458	43°47' N, 11°44' E	Borghetti <i>et al.</i> (1986)
	0.470	42°20' N, 123°00' W	Waring <i>et al.</i> (1982)
	0.480	44°31' N, 123°52' W	St.Clair (1993)
	0.542	44°20' N, 123°21' W	Espinosa Bancalari <i>et al.</i> (1987)
	0.601	49°00' N, 123°55' W	Binkley (1984)
<i>Tsuga heterophylla</i>	0.410	44°30' N, 123°45' W	Waring <i>et al.</i> (1982)

†All-sided leaf area was converted to projected leaf area using a conversion factor from Waring *et al.* (1982).

*All-sided leaf area was converted to projected leaf area using a conversion factor from Naidu *et al.* (1998).

$t = 4.74$, $t_{\text{crit}} = 2.13$). Lower A_L/A_S and the ability to make whole-tree adjustments to VPD may help explain the greater abundance of pines in warmer, drier habitats than other genera of conifers (Farjon 1990).

The importance of plasticity in above-ground allocation relative to changes in tracheid anatomy as a response to aridity is further supported by the non-intuitive observation that drought-adapted pines are

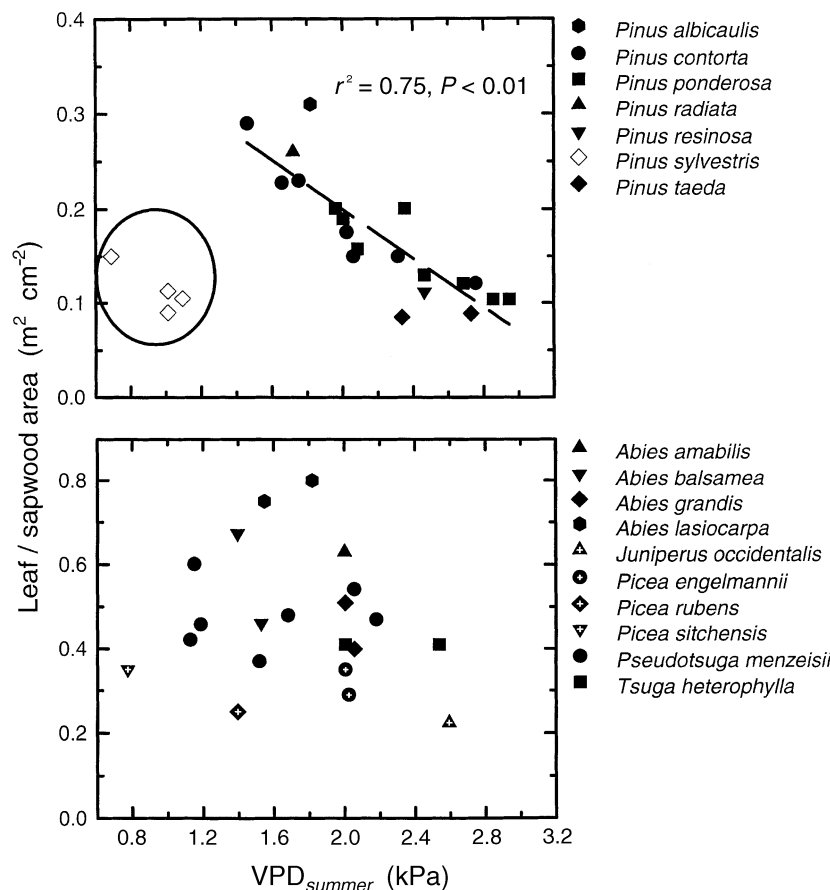


Fig. 1 The relationship between leaf/sapwood area ratio (A_L/A_S) and average maximum summer atmospheric water vapour deficit (VPD) for species in the genus *Pinus* and other nonpine conifer species. Each point is an independent observation and the data were fit by least-squares linear regression. Values for *Pinus sylvestris* were not included in the regression model. There was no statistical relationship between A_L/A_S and VPD for non-*Pinus* species.

more vulnerable to xylem embolism than nonpines. Vulnerability is expressed as the water potential causing a 50% loss of conductivity through a stem segment (LC_{50}). We compiled data from the literature on vulnerability of the xylem to drought-induced embolism for several pine and nonpine conifers (Sperry & Tyree 1990; Cochard 1992; Sperry & Sullivan 1992; Sperry *et al.* 1994; Sperry & Ikeda 1997; Linton *et al.* 1998) and from H. Maherali (unpubl.) and J. Piñol and A. Sala (unpubl.). The mean LC_{50} for *Abies*, *Juniperus*, *Picea*, and *Pseudotsuga* is -4.52 MPa (range: -2.7 to -7.5 MPa, $N = 13$). In contrast, the mean LC_{50} for *Pinus albicaulis*, *P. contorta*, *P. edulis*, *P. ponderosa*, and *P. sylvestris* is -3.28 MPa (range: -2.9 to -4.5 MPa, $N = 6$). This difference (two-tailed t -test, $t_{crit} = 2.11$, $t = 2.55$, $P = 0.02$) in vulnerability provides further evidence that species of *Pinus* overcome the risk of embolism under warm, dry conditions by having lower A_L/A_S than nonpine conifers. The exceptional capacity of pines to acclimate to arid conditions suggests that they may displace nonpine conifer forests as the climate warms.

How will projected changes in A_L/A_S alter the above-ground morphology of pines in the future? As a model system, we compared *Pinus ponderosa* growing on the

same soil substrate and stand density but at high and low elevations on the east slope of the Sierra Nevada and adjacent Great Basin desert (DeLucia *et al.* 1988; DeLucia & Schlesinger 1990). Summer temperature and VPD are approximately $3^\circ C$ warmer and 1 kPa (60%) higher, respectively, in the desert populations; the desert stands therefore provide a reasonable proxy for trees in the future. Desert trees responded to this environmental gradient by having a lower A_L/A_S ($0.1 m^2 cm^{-2}$) compared to montane populations ($0.2 m^2 cm^{-2}$, Callaway *et al.* 1994). Common garden experiments with seedlings indicate that most of this variance is phenotypic (Maherali 1999).

We used allometric descriptions of above-ground form to construct a typical desert and montane tree of the same stem diameter (Carey *et al.* 1997, 1998). Associated with the lower A_L/A_S , the desert pine was considerably shorter than its montane counterpart, had a more open crown, and supported more biomass in sapwood and less biomass in foliage (Fig. 2). This shift in biomass allocation contributes significantly to greater leaf-specific hydraulic conductivity in desert compared with montane trees (Maherali 1999). The combined increase in sapwood mass and decrease in leaf mass means that desert trees,

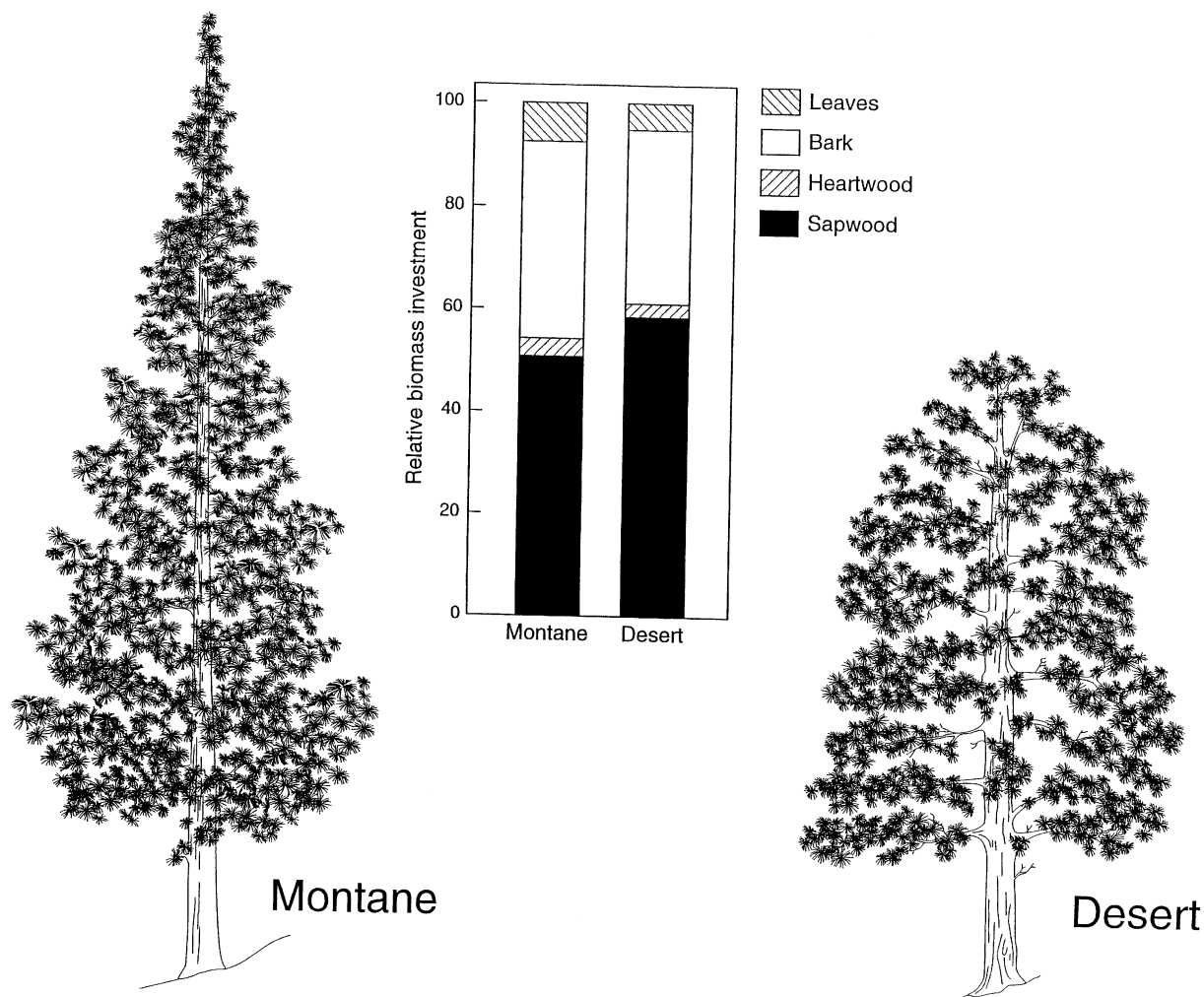


Fig. 2 A representative ponderosa pine tree, derived from allometric equations, from a cool, moist montane environment and from a warm, dry desert environment. Trees are drawn to scale and both have a stem diameter of 50 cm (measured 1.35 m above the ground). The height and total above-ground biomass of the montane and desert trees is 17.7 and 12.1 m and 945 and 939 kg, respectively. The relative investment of biomass in different above-ground components is shown in the bar graph.

and by inference trees in the future, will expend more photosynthate supporting structural mass and have less total leaf area than their contemporary counterparts. A similar shift in above-ground allocation with changing VPD has been reported for *Pinus sylvestris* in the UK (Mäkelä *et al.* 1995). The absence of a substantial stomatal response to growth under elevated CO_2 in pines (Ellsworth *et al.* 1995; Curtis & Wang 1998; Pataki *et al.* 1998), suggests that the increasing concentration of this gas in the atmosphere will not mitigate the effect of higher VPD on A_L/A_S . Elevated CO_2 may, however, provide additional carbon to support sapwood and stems without reducing leaf area. At least for *P. ponderosa* seedlings, elevated CO_2 does not alter the climate-driven change in A_L/A_S (Maherali 1999), but the response of large trees remains unknown.

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Erratum

In the paper by Leclercq *et al.*, CO₂ partial pressure controls the calcification rate of a coral community, **6**, 329–334, some lines in Fig. 2 appeared confused due to

an error in the printing process. We apologise for any inconvenience that this caused and reproduce the figure correctly below.

