ADAPTIVE VARIATION IN THE VULNERABILITY
OF WOODY PLANTS TO XYLEM CAVITATION

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Abstract. The ability of plants to supply water to their leaves is intimately associated with survival. Water supply to leaves depends on maintaining an intact water column in the xylem from the roots to shoots. Because this hydraulic pathway is under tension, it is vulnerable to breakage through the induction of air emboli (cavitation). Although the physiological benefit of resistance to water-stress-induced xylem cavitation for desiccation tolerance is clear, there is considerable interspecific variation within and across climates. To understand the adaptive significance of this variation and the potential trade-off with water transport, we compiled a database of 167 species from 50 seed plant families and examined relationships among resistance to xylem cavitation, water transport capacity (as determined by the specific conductivity of xylem [K_S]), and climate. Relationships were evaluated using standard cross-species correlations (*r*). Because inferences about the adaptive significance of these correlations can be biased by the potential similarity of closely related species, we also analyzed our data using phylogenetically independent contrast correlations (PIC) calculated over a range of alternate seed plant phylogenies. Resistance to cavitation, expressed as the xylem tension at which 50% of hydraulic conductivity was lost (Ψ_{50}), ranged from -0.18 to -9.9 MPa for angiosperms and from -1.5 to -14.1 MPa for conifers. Conifers were most resistant to cavitation, with mean Ψ_{50} 80% more negative than angiosperms. In contrast, K_S was 270% higher in angiosperms than conifers. Across all species, cavitation resistance increased with decreasing mean annual precipitation. However, significant phylogenetically independent contrast correlations between Ψ_{50} and annual precipitation were found within the evergreen angiosperms and conifers but not in the deciduous angiosperms. Thus, the adaptive significance of increased resistance to cavitation as a mechanism of drought tolerance may be of primary importance in evergreen angiosperms and conifers. In contrast, analysis of independent contrasts indicated that K_S increased with decreasing rainfall in deciduous angiosperms, whereas there was no association between K_S and water availability for evergreen angiosperms and conifers. These results suggest that the evolution of increased K_S may be a critical adaptation to water limitation in deciduous angiosperms. Although there was a significant cross-species correlation between Ψ_{50} and K_S, this relationship was not supported by the independent contrast correlation, suggesting that the evolutionary basis for a trade-off between cavitation resistance and water transport capacity is weak.

Key words: adaptation; climate; correlated evolution; hydraulic conductivity; independent contrasts; potential evapotranspiration; precipitation; temperature; vegetation; water-stress-induced xylem cavitation.

INTRODUCTION

A major cost of acquiring CO_2 for photosynthesis is the evaporation of water from plant leaves. Water supply to leaves depends on maintaining an intact water column in the xylem from the roots to shoots. Because this hydraulic pathway is under increasing tension during transpiration, it is vulnerable to cavitation (Zimmermann 1983, Carlquist 1988, Tyree and Sperry 1989). Cavitation induced by water stress occurs

through air seeding, when air bubbles are aspirated into water-filled conduits under tension (Zimmermann 1983, Sperry and Tyree 1988, Tyree and Sperry 1989, Jarbeau et al. 1995). The xylem tension required for air seeding to occur is intimately linked to the anatomy of xylem conduits, specifically the structure of the pit membranes that permit flow between adjacent vessels or tracheids (Jarbeau et al. 1995). Each time cavitation occurs, the resulting vapor-filled conduit no longer carries water, causing a decrease in xylem hydraulic conductivity (Tyree and Ewers 1991, Sperry and Pockman 1993). Without responses to limit transpiration, including stomatal closure (Sperry and Pockman 1993) or leaf shedding (Pataki et al. 1998), decreased hy-

draulic conductivity can drive increased xylem tension and further cavitation (Tyree and Sperry 1989, Tyree and Ewers 1991, Meinzer et al. 2001). Ultimately, if this positive feedback continues, plants may undergo catastrophic hydraulic failure (see Plate 1). Even without hydraulic failure, an immediate consequence of xylem cavitation is reduced photosynthesis and growth (Sperry and Pockman 1993, Meinzer et al. 2001). The direct link between sustained water transport and plant survival and growth suggests that there may be strong selection for the evolution of high resistance to xylem cavitation.

Despite the potential for selection to favor high resistance to cavitation, there is considerable interspecific variation in the resistance of woody plants to water-stress-induced xylem cavitation. Comparative eco-physiological studies indicate that some of this variation is associated with moisture availability (Brodribb and Hill 1999, Kolb and Sperry 1999, Pockman and Sperry 2000). Variation in cavitation resistance could also be driven by evolutionary correlations with other physiological traits (Ackerly and Donoghue 1998). For example, because of the structural changes in pit membranes associated with increased cavitation resistance, there may be a trade-off between resistance to cavitation and xylem conductivity (Sperry 2003). If such a trade-off has an evolutionary basis, low cavitation resistance could be maintained in environments where high conductivity is adaptive. There is evidence for this trade-off in some taxa (Tyree et al. 1994, Piñol and Sala 2000), but not in others (Sperry et al. 1994). The resistance of xylem to cavitation may also be influenced by shared evolutionary history. If phylogenetic history is an important adaptive constraint, interspecific variation in resistance to cavitation would be conserved, occurring only in groups of closely related taxa. In contrast, evidence of adaptive evolution would be provided by trait convergence, with several independent origins of high cavitation resistance observed (Harvey and Pagel 1991, Ackerly 1999).

A limitation of using cross-species comparisons to determine the ecological significance of physiological traits is that these correlations may be biased by the potential similarity of closely related species (Felsenstein 1985, Harvey and Pagel 1991). This shared evolutionary history prevents individual species from being statistically independent data points (Harvey and Pagel 1991). As a result, some observed interspecific correlations among traits or between traits and ecological variables may not reflect true functional or adaptive relationships (Harvey and Pagel 1991, Ackerly and Donoghue 1998). For example, the strong correlation between leaf size and leaf life span observed across species in six biomes was not found when phylogenetic information was included (Ackerly and Reich 1999). In this particular case, the interspecific correlation was driven largely by the ancestral divergence between conifers and angiosperms. It is also equally possible that

PLATE 1. Catastrophic hydraulic failure and branch dieback in *Larrea tridentata* following xylem cavitation. Photo credit: W. T. Pockman.

the lack of statistical independence and the effects of unknown historical events can obscure adaptive relationships (Ackerly and Donoghue 1998, Ackerly 1999). Thus, the inclusion of phylogenetic information can reveal significant adaptive associations between traits that go undetected by traditional cross-species correlation analysis.

Several statistical techniques that incorporate phylogenetic information have been developed to evaluate the evolutionary origin of extant trait variation (e.g., Pagel and Harvey 1991). One of the most powerful is independent contrasts (Felsenstein 1985), which are calculated for each speciation event in the phylogeny (e.g., as the difference in trait values between sister taxa along each branch; Felsenstein 1985, Garland et al. 1992). Trait relationships are then evaluated using correlations among these contrasts. This method identifies adaptive relationships because the strength and sign of the contrast correlation indicates whether evolutionary shifts in a trait are associated with changes in another trait or an ecological variable (Pagel 1993, Ackerly and Reich 1999).

In this study, we analyzed the interspecific relationships between two major components of plant hydraulic architecture (the resistance to water-stress-induced xylem cavitation and hydraulic conductivity) and climate using data from the literature and from global databases. Our goals were to determine the adaptive significance of resistance to xylem cavitation and hydraulic conductivity in contrasting climates and to evaluate the strength of these relationships for different plant functional groups. By using information on phylogenetic relationships among seed plants, we calculated phylogenetically independent contrasts to test for correlated evolutionary change between traits and the environment (Felsenstein 1985, Harvey and Pagel 1991, Ackerly 2000). We examined character evolution by mapping traits onto our phylogeny, and using an index of similarity, we calculated the degree to which hydraulic traits were conserved within taxa or exhibited
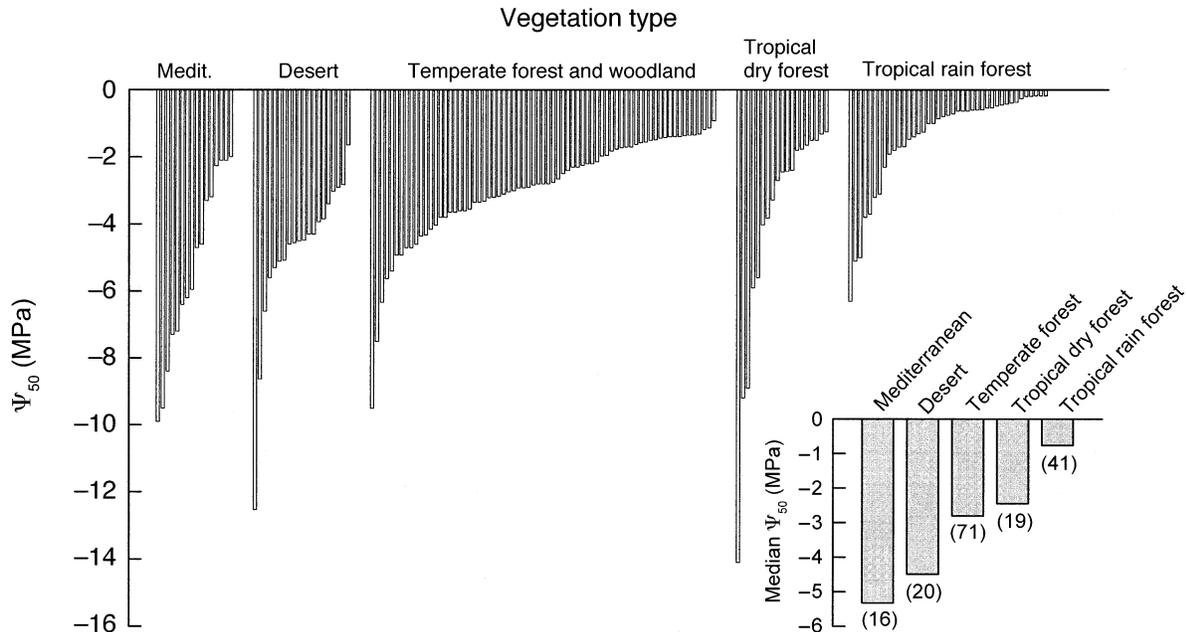
FIG. 1. The distribution of vulnerability to water-stress-induced cavitation (as determined by xylem tension at which 50% cavitation occurred [Ψ_{50}]) for the species used in this database, ranked by magnitude within five vegetation types. The median Ψ_{50} for each vegetation type, along with the sample size for that group, is shown in the inset.

convergent evolution across taxa. We also tested the proposed trade-off between cavitation resistance and water transport capacity (Tyree and Ewers 1991, Tyree et al. 1994, Piñol and Sala 2000) by examining correlated evolution between xylem cavitation resistance and specific conductivity of xylem (K_S).

METHODS

Database of xylem resistance to water-stress-induced cavitation

To examine the relationships between xylem resistance to water-stress-induced cavitation, climate, and water transport, we assembled a database of 60 studies published between 1986 and 2000 and our unpublished data from field sites in North Carolina and Texas, USA. These studies comprised a total of 230 observations for 167 species of woody plants in 50 seed plant families (Appendix A). Only studies that reported vulnerability curves (the response of hydraulic conductivity to changes in xylem tension) of stems or data derived from these curves were used in the analysis. We included vulnerability curves obtained using methods of air dehydration (Sperry et al. 1988), air pressurization (Cochard et al. 1992, Sperry and Saliendra 1994), and centrifugation (Pockman et al. 1995, Alder et al. 1997). We recorded the xylem tension at which 50% cavitation occurred (Ψ_{50}), a parameter commonly used to characterize and interpret interspecific variation in cavitation resistance (Tyree and Ewers 1991). To examine the relationship between water transport efficiency and Ψ_{50}, we also recorded the specific conductivity per unit

xylem area (K_S; in kilograms per meter per megapascal per second) only when it was reported in the same study as Ψ_{50}. Where there were multiple observations for a single species, mean values were used in the analysis. To be able to examine broad patterns of adaptive interspecific variation, we included measurements for adults and saplings, from branches and main stems and from field and greenhouse studies. However, we were unable to assess the influence of intraspecific variation or phenotypic plasticity (Matzner et al. 2001) on our analysis; we note that this limitation may compromise the assumption that trait values were representative for some species.

Geographic coordinates were recorded and used to obtain climate variables. For greenhouse studies, we recorded the geographic coordinates of the site from which seeds were obtained. When unavailable, these coordinates were estimated based on geographic data in the publications. In those cases where geographic coordinates were unobtainable, our analysis was limited to climatic variables provided by the authors.

Climate data

To examine the adaptive relationships between plant hydraulic variables and climate, we gathered data on mean annual precipitation (MAP), temperature (MAT), and potential evapotranspiration (PET) from global databases. We also examined the relationship between hydraulic variables and shorter term indicators of climate, such as growing season precipitation. Growing season precipitation was calculated as the sum of late

TABLE 1. Summary of data and convergent evolution statistics for vulnerability to xylem cavitation (Ψ_{50}) and specific conductivity (K_S).

Comparison	Species values of Ψ_{50} (MPa)				Species values of K_S (kg·m^{-1}·MPa^{-1}·s^{-1})†			
	n	Mean ± 1 SE	Range	QVI‡	n	Mean ± 1 SE	Range	QVI‡
All taxa	167	−3.15 ± 0.19	−0.18, −14.1	0.527	87	1.36 ± 0.15	0.12, 6.7	0.673
Angiosperms	128	−2.65 ± 0.18	−0.18, −9.9	0.563	63	1.70 ± 0.19	0.12, 6.7	0.754
Deciduous	62	−2.64 ± 0.18	−0.92, −8.6	0.651	42	1.50 ± 0.18	0.16, 4.5	0.739
Evergreen	66	−2.65 ± 0.31	−0.18, −9.9	0.523	21	2.11 ± 0.45	0.12, 6.7	0.674
Conifers	39	−4.78 ± 0.44	−1.5, −14.1	0.595	24	0.46 ± 0.05	0.12, 1.1	0.814

† Specific conductivity is measured per unit xylem area.

‡ Quantitative convergence index (scale 0–1, with high values indicating convergent evolution and low values indicating conserved phylogeny).

spring and summer precipitation for each site (May–August for the Northern Hemisphere; November–February for the Southern Hemisphere). Relationships between hydraulic parameters and indices of rainfall were quantitatively similar for both MAP and growing season precipitation across all taxa and within specific functional groups (data not shown). However, annual data were most often included in studies that omitted geographical coordinates (see *Database of xylem resistance...*). Therefore, we chose annual mean data over other representations of climate variation because it allowed us to keep all species in the analysis. Precipitation and temperature data for each study site were obtained from the 0.5° gridded global climate database of the International Institute of Applied Systems Analysis (IIASA; Laxenburg, Austria; Leemans and Cramer 1991). This global database has mean monthly values of precipitation and temperature based on >6000 weather stations (Leemans and Cramer 1991). Values for PET were obtained from the 0.5° gridded global data set of Choudhury (1997) and Choudhury and DiGirolamo (1998) containing mean monthly values of PET calculated from the Penman-Montieth method (Choudhury 1997). We also examined the relationship of hydraulic parameters to a derived moisture index, defined as the ratio of MAP to PET (MAP/PET; Schenk and Jackson 2002).
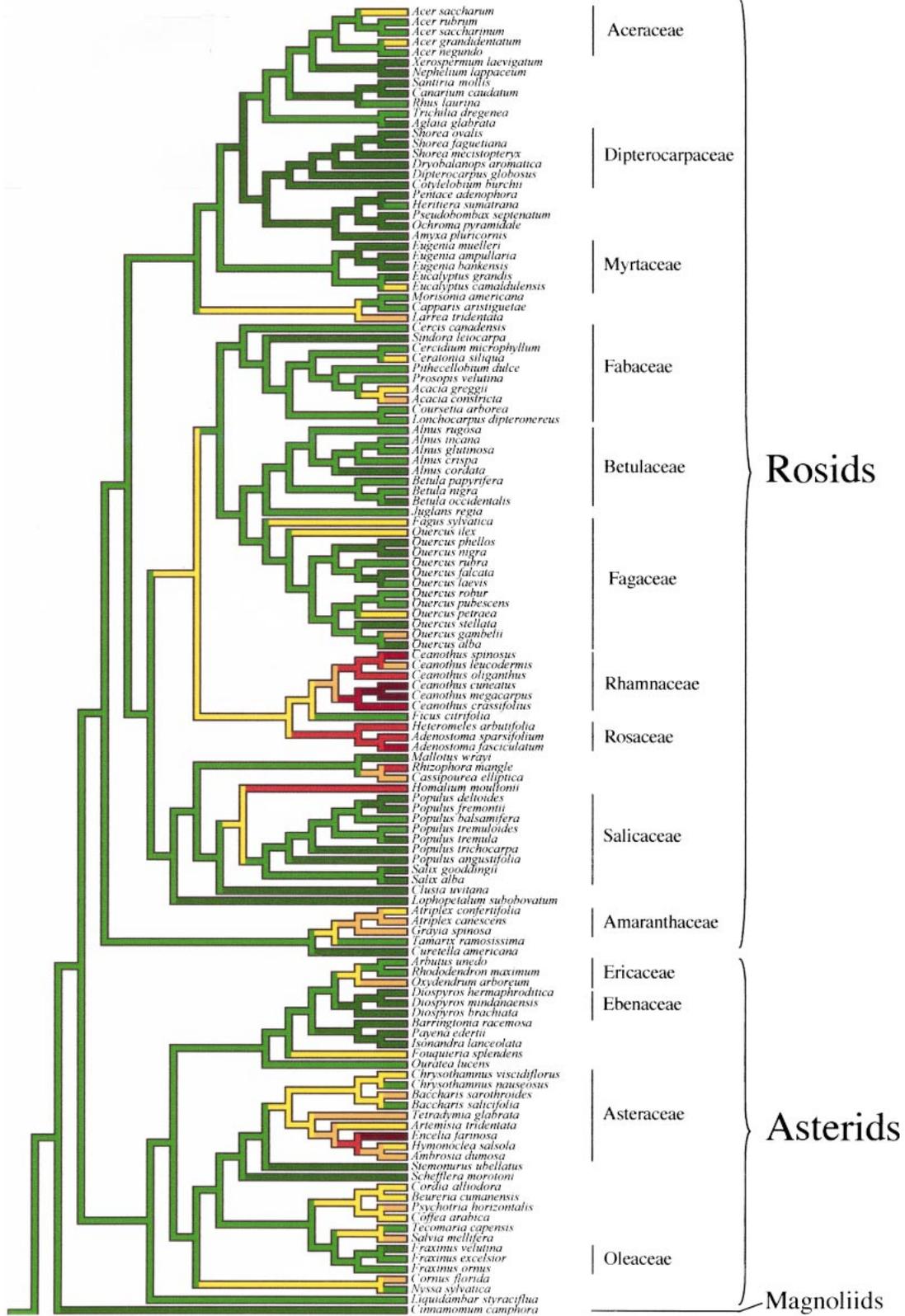
Construction of phylogenetic trees

Because independent contrasts are calculated based on the difference between pairs of sister taxa at each node of a phylogeny, we needed to construct a fully bifurcated tree. To accommodate uncertainties in phylogenetic hypotheses, we constructed alternate fully bifurcated phylogenetic trees, using methods modified from Ackerly and Reich (1999). We started with the strict consensus phylogenies from published analyses of angiosperms (18S rDNA, *rbcL,* and *atpB* gene sequence data; Soltis et al. 1999) and gymnosperms (28S rRNA sequence data; Stefanović et al. 1998). These trees were pruned to show relationships among the families present in our data set, resulting in a fully bifurcated family-level phylogeny. Species within each family were then added, with regions where uncertainties arose (i.e., those having more than two genera or species at a given node) shown as a polytomy. Eleven of these 17 species-level polytomies were resolved by obtaining phylogenetic information on each genus from searches of the primary literature (Appendix B). To generate a fully bifurcated phylogeny for the calculation of independent contrasts, the six remaining polytomies were resolved using the protocol of Donoghue and Ackerly (1996) and Ackerly and Reich (1999). In brief, we generated 553 alternate resolved trees (the

TABLE 2. Vulnerability to xylem cavitation (Ψ_{50}, MPa) and specific conductivity (K_S; kg·m^{-1}·MPa^{-1}·s^{-1}) for the various functional groups included in this study (means ± 1 SE).

Functional group	Cavitation			Conductivity		
	Ψ_{50}	MAP (mm)	n	K_S	MAP (mm)	n
Angiosperms						
Winter deciduous shrubs	−2.66	140	2	1.57	140	2
Winter deciduous trees	−2.34 ± 0.17	768 ± 62	46	1.58 ± 0.22	777 ± 85	30
Drought deciduous shrubs	−4.47 ± 0.64	196 ± 23	9	1.55 ± 0.68	166 ± 26	5
Drought deciduous trees	−2.13 ± 0.48	1383 ± 387	5	0.96 ± 0.22	1383 ± 387	5
Evergreen shrubs	−5.09 ± 0.54	761 ± 175	21	1.75 ± 0.74	434 ± 118	8
Evergreen trees	−1.51 ± 0.23	2610 ± 152	44	2.43 ± 0.62	1539 ± 247	12
Gymnosperms						
Conifer shrubs	−8.95 ± 1.81	511 ± 174	5	0.24	465	2
Conifer trees	−4.17 ± 0.33	984 ± 136	34	0.48 ± 0.05	817 ± 103	22

Notes: Mean (±1 SE) annual precipitation (MAP) and sample size (n) for each group and variable combination are included for comparison. Standard errors were not calculated for those groups with $n < 3$.

Acer saccharum
Acer rubrum
Acer saccharinum
Acer grandidentatum
Acer negundo
Xerospermum laevigatum
Nephelium lappaceum
Santiria mollis
Canarium caudatum
Rhus laurina
Trichilia dregenea
Aglaia glabrata
Shorea ovalis
Shorea faguetiana
Shorea mecistopteryx
Dryobalanops aromatica
Dipterocarpus globosus
Cotylelobium burchii
Pentace adenophora
Heritiera sumatrana
Pseudobombax septenatum
Ochroma pyramidale
Amyxa pluricornis
Eugenia muelleri
Eugenia ampullaria
Eugenia bankensis
Eucalyptus grandis
Eucalyptus camaldulensis
Morisonia americana
Capparis aristiguetae
Larrea tridentata
Cercis canadensis
Sindora leiocarpa
Cercidium microphyllum
Ceratonia siliqua
Pithecellobium dulce
Prosopis velutina
Acacia greggii
Acacia constricta
Coursetia arborea
Lonchocarpus dipteronereus
Alnus rugosa
Alnus incana
Alnus glutinosa
Alnus crispa
Alnus cordata
Betula papyrifera
Betula nigra
Betula occidentalis
Juglans regia
Fagus sylvatica
Quercus ilex
Quercus phellos
Quercus nigra
Quercus rubra
Quercus falcata
Quercus laevis
Quercus robur
Quercus pubescens
Quercus petraea
Quercus stellata
Quercus gambelii
Quercus alba
Ceanothus spinosus
Ceanothus leucodermis
Ceanothus oliganthus
Ceanothus cuneatus
Ceanothus megacarpus
Ceanothus crassifolius
Ficus citrifolia
Heteromeles arbutifolia
Adenostoma sparsifolium
Adenostoma fasciculatum
Mallotus wrayi
Rhizophora mangle
Cassipourea elliptica
Homalium moultonii
Populus deltoides
Populus fremontii
Populus balsamifera
Populus tremuloides
Populus tremula
Populus trichocarpa
Populus angustifolia
Salix gooddingii
Salix alba
Clusia uvitana
Lophopetalum subobovatum
Atriplex confertifolia
Atriplex canescens
Grayia spinosa
Tamarix ramosissima
Curatella americana
Arbutus unedo
Rhododendron maximum
Oxydendrum arboreum
Diospyros hermaphroditica
Diospyros mindanaensis
Diospyros brachiata
Barringtonia racemosa
Payena edertii
Isonandra lanceolata
Fouquieria splendens
Ouratea lucens
Chrysothamnus viscidiflorus
Chrysothamnus nauseosus
Baccharis sarothroides
Baccharis salicifolia
Tetradymia glabrata
Artemisia tridentata
Encelia farinosa
Hymonoclea salsola
Ambrosia dumosa
Stemonurus ubellatus
Schefflera morotoni
Cordia alliodora
Beureria cumanensis
Psychotria horizontalis
Coffea arabica
Tecomaria capensis
Salvia mellifera
Fraxinus velutina
Fraxinus excelsior
Fraxinus ornus
Cornus florida
Nyssa sylvatica
Liquidambar styraciflua
Cinnamomum camphora

Aceraceae

Dipterocarpaceae

Myrtaceae

Fabaceae

Betulaceae

Fagaceae

Rhamnaceae

Rosaceae

Salicaceae

Amaranthaceae

Ericaceae
Ebenaceae

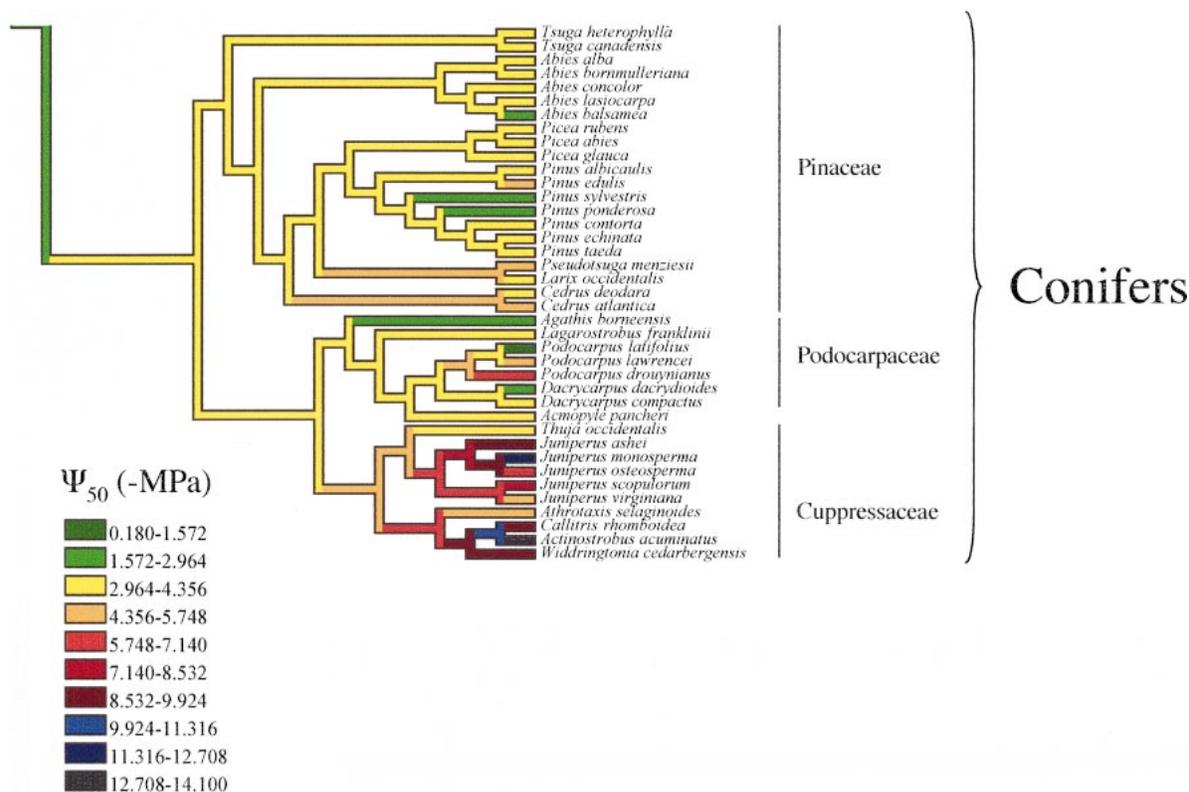Asteraceae

Oleaceae

Rosids

Asterids

Magnoliids

FIG. 2. One of 553 alternate phylogenetic trees showing the evolution of resistance to water-stress-induced xylem cavitation in woody plants (see *Methods* for details). Overlaying of the continuous characters on the tree was done in MacClade 4.0 (Maddison and Maddison 2000). Ancestral state values were determined using squared-change parsimony. However, because taxa were nonrandomly sampled across all seed plants, ancestral state values may be biased (Cunningham et al. 1998). Convergence statistics calculated for all 553 trees are shown in Table 2. To facilitate presentation, continuous Ψ_{50} data were grouped into 10 discrete color-coded categories of equal size.

result of 1000 randomly resolved trees minus duplicates) using the ''randomly resolve current tree'' option in MacClade 4.0 (Maddison and Maddison 2000). This procedure resolves polytomies while preserving the remainder of the topology.

Comparative statistical analyses

To examine the extent to which interspecific variation in hydraulic traits is the result of convergent evolution or constrained by phylogenetic history, we calculated the quantitative convergence index (QVI; Ackerly and Donoghue 1998, Ackerly 1999). QVI values range from 0 to 1, with high values indicating that distantly related species are phenotypically similar (convergent evolution) and low values indicating closely related species are phenotypically similar (phylogenetically conserved).

The strength of the cross-species relationships between hydraulic traits and between hydraulic traits and climate variables without including phylogenetic information were determined using Pearson correlation coefficients (*r*; SPSS 10.0, SPSS, Evanston, Illinois, USA). Statistical differences in hydraulic traits between vegetation types and functional groups were tested with analysis of variance (ANOVA). To meet the assumptions of parametric tests, all data were log transformed prior to analysis.

To examine the strength of correlated evolution among hydraulic traits and between hydraulic traits and climate parameters, we performed a correlation analysis on calculated phylogenetically independent contrasts (PICs; Felsenstein 1985, Harvey and Pagel 1991, Garland et al. 1992, Ackerly and Reich 1999) for each of the 553 fully resolved phylogenies. Independent contrasts are calculated as the difference in trait values between sister taxa and standardized by dividing them by the standard deviation of the expected amount of change along each branch (Garland et al. 1992). However, because trees from various sources were combined to produce our phylogeny, it was impossible to incorporate into our analysis information on branch lengths, which indicate the number of evolutionary changes along each ancestor–descendant pathway (Harvey and Pagel 1991). In the absence of such information, we assumed that branch lengths are equal, a conservative assumption that minimizes type I error rate (Purvis et al. 1994, Ackerly 2000).

Because the sign of an independent contrast is arbitrary (depending on which direction is used to calculate the difference between sister taxa), correlation analysis was done through the origin (Garland et al. 1992). All comparative analyses were done using CACTUS 1.13 (comparative analysis of continuous traits using statistics; Schwilk and Ackerly 2001) and the statistical significance of independent contrast correlations was determined using guidelines and statistical tables for trees with equal branch lengths (Ackerly 2000). To facilitate log transformation and analysis, Ψ_{50} data were converted from negative to positive values.

RESULTS

Variation among species and functional groups

Interspecific variation in Ψ_{50} spanned nearly two orders of magnitude (Fig. 1). The most vulnerable species, in wet tropical forests, reached 50% cavitation at −0.18 MPa, compared with −14.1 MPa for the most resistant species in dry tropical forests. Cavitation resistance also varied substantially within vegetation types, ranging from 35-fold in tropical forests to five-fold in the mediterranean zone. This variation notwithstanding, median Ψ_{50} of species occurring in the most arid vegetation types (e.g., deserts and mediterranean zones) were 6–7 times more negative than those occurring in the wettest types (e.g., tropical rain forest, Fig. 1 inset).

On average, conifers were more resistant to water-stress-induced cavitation (Ψ_{50}) than angiosperms; mean Ψ_{50} was 80% more negative in conifers than angiosperms ($P < 0.0001$, Table 1). We note however, that the range of Ψ_{50} values between angiosperms and conifers largely overlaps (Table 1). In contrast, mean K_S was 270% higher in angiosperms than conifers ($P < 0.0001$, Table 1), although minimum values were similar in both groups (Table 1). Evergreen and deciduous angiosperms had similar mean Ψ_{50} and K_S ($P > 0.75$, Table 1). Shrubs were more resistant to cavitation than trees across winter deciduous, drought deciduous, evergreen, and conifer species and also occurred in drier climates than trees (Table 2). Evergreen angiosperm trees (which were sampled primarily from wet rain forests) were the most vulnerable to cavitation, followed by drought deciduous trees, winter deciduous trees and shrubs, conifer trees, drought deciduous shrubs, evergreen shrubs, and conifer shrubs (Table 2). There were no statistical differences in K_S between shrubs and trees for any group (Table 2).

Quantitative convergence and trait evolution

The impact of variation among the alternate phylogenies (e.g., from different random solutions to polytomies) used in our analysis was quite small. For example, QVIs and phylogenetically independent contrast correlations calculated over 553 alternate phylogenies were similar (range differed by <5%). The mean QVI

was always lower for Ψ_{50} than for K_S across all species (Table 1) suggesting that Ψ_{50} is more conserved than K_S in woody plants. Resistance to cavitation was slightly more conserved in angiosperms than conifers (0.563 vs. 0.595), although the mean QVI for all taxa was >0.5, indicating greater trait convergence than conservation (Table 1). Within angiosperms, Ψ_{50} was more conserved in evergreen than deciduous species (0.523 vs. 0.651). In contrast, K_S was highly convergent in deciduous (0.739) and evergreen (0.674) angiosperms and conifer (0.814) species (Table 1).

The extent to which interspecific variation in cavitation resistance is the result of convergent evolution compared with trait conservation can be illustrated by mapping traits onto a phylogeny (Maddison and Maddison 2000). Because the influence of variation in the phylogenies on quantitative parameters was small, we mapped Ψ_{50} onto one of the 553 phylogenies used in the analysis (Fig. 2). There was qualitative support for convergent evolution in cavitation resistance. Within the angiosperms, high resistance to cavitation ($\Psi_{50} < -3.15$ MPa, the grand mean for all species, Table 1) appeared at least 20 times (Fig. 2). For example, distantly related genera such as *Larrea* (Zygophyllaceae), *Acacia* (Fabaceae), *Ceanothus* (Rhamnaceae), *Adenostoma* (Rosaceae), *Atriplex* (Amaranthaceae), and *Encelia* (Asteraceae) were all highly resistant to cavitation (Fig. 2). Within conifers, resistance to cavitation occurred in distantly related groups such as the Pinaceae (*Pinus edulis* and *Pseudotsuga menziesii*) and Cupressaceae (*Juniperus*, *Callitris*, *Actinostrobus*, and *Widdringtonia*). In many cases, support for convergent evolution on comparatively shorter time scales was also provided by the occurrence of both high and low resistance to cavitation within the same genus (e.g., *Atriplex*, *Baccharis*, *Pinus*, *Podocarpus*).

Cross-species and independent contrast correlations

Our inclusion of phylogenetic information in this study helped identify the adaptive relationship between pairs of traits and between a trait and the environment. We present both cross-species correlations between variables analyzed with Pearson correlation (r) coefficients and phylogenetically independent contrasts (PIC). To facilitate log transformation and subsequent correlation analysis, Ψ_{50} data were converted from negative to positive values. We note, however, that for consistency the data are presented and interpreted with Ψ_{50} as the usual negative values, such that greater resistance to cavitation is indicated by more negative Ψ_{50} values.

Based on interspecific correlations (r), resistance to water-stress-induced xylem cavitation increased (i.e., a more negative Ψ_{50}) with decreasing MAP for all taxa analyzed together (Fig. 3A). These relationships were supported by correlations using phylogenetically independent contrasts (PICs, Table 3). Similar associations were also found for Ψ_{50} and an indicator of mois-
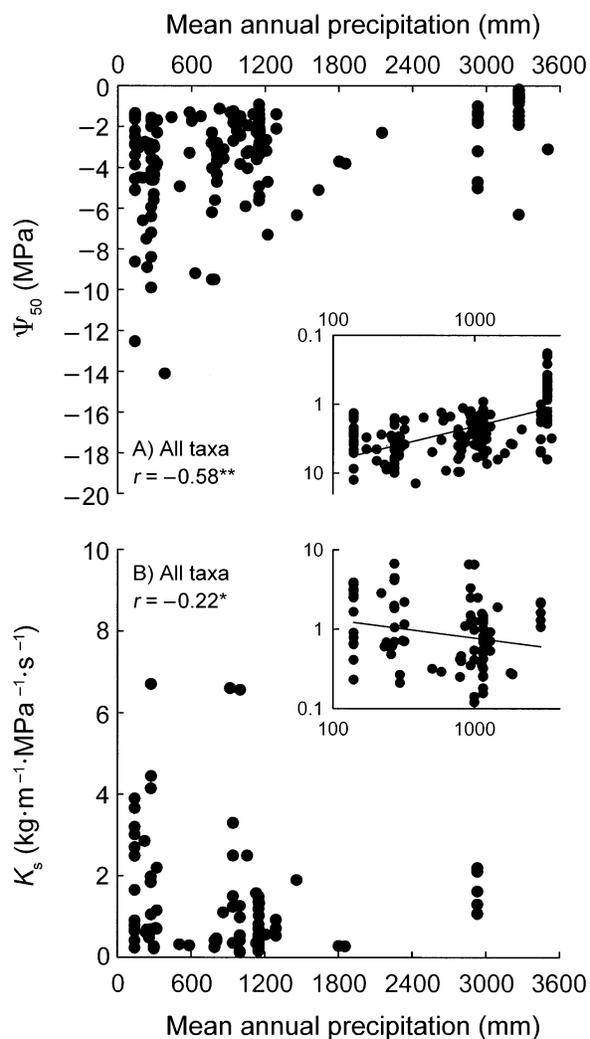
FIG. 3. (A) The relationship between xylem tension at which 50% cavitation occurred (Ψ_{50}) and mean annual precipitation (MAP) and (B) the relationship between specific conductivity of xylem (K_S) and MAP analyzed using Pearson correlation coefficients for all taxa. Log-transformed relationships are shown in the insets. Statistically significant relationships (*$P < 0.05$; **$P < 0.01$) are fitted with least-squares regression lines. To facilitate log transformation for analysis, Ψ_{50} values were converted from negatives to positives. Although data are plotted to reflect the nontransformed relationships, the sign of the correlation coefficient on each plot is based on the log-transformed data (see Table 3).

ture index (MAP/PET, Table 3). Although resistance to water-stress-induced cavitation increased with decreasing PET, this relationship was not supported by PICs (Table 3). However, Ψ_{50} increased with increasing MAT in both cross-species and PIC analyses for all taxa, indicating that species vulnerable to cavitation were found primarily in warm climates. In the traditional cross-species analysis, specific conductivity of xylem (K_S) increased significantly with decreasing MAP for all taxa analyzed together (r, Fig. 3B). The above-de-

scribed associations were also found between K_S and MAP/PET (Table 3). There was no correlation between K_S and MAT or PET across all taxa (Table 3).

The preceding analysis of all taxa pooled together identified overall patterns of trait variation among seed plants, but it has long been recognized that the evolution of xylem characteristics may vary across groups with contrasting life history traits (Zimmermann 1983, Tyree and Ewers 1991, Mencuccini 2003). To accommodate this possibility, we further analyzed relationships between xylem traits and climate variables by subdividing the sampled taxa into deciduous (both winter and drought) angiosperm, evergreen angiosperm, and conifer groups. Our analyses indicated that the adaptive significance of hydraulic characteristics differed among these groups.

Ψ_{50} decreased with decreasing MAP in the cross-species comparison for the deciduous angiosperms (Fig. 4A, Table 3). Subdivided further, we found that the drought deciduous angiosperms appeared to drive this relationship ($r = -0.65$, $P < 0.01$, $n = 14$) when compared to winter deciduous angiosperms ($r = -0.16$, $P > 0.05$, $n = 48$), despite a lower sample size. Nevertheless, there was no association between Ψ_{50} and MAP across all deciduous angiosperms in the independent contrast analysis (Fig. 4D). Independent contrast correlations were not calculated separately for the drought deciduous species because of low sample size (Table 2) and the fact that nine of the 14 species came from only two families. In the cross-species comparison among evergreen angiosperms, Ψ_{50} decreased significantly with decreasing MAP (Fig. 4B) and with other climate variables (MAP/PET, PET, and MAT; Table 3). These relationships were supported by significant phylogenetically independent contrast correlations (Fig. 4E, Table 3). A similar pattern was found for conifers, with Ψ_{50} decreasing significantly with decreasing MAP in both the cross-species and independent contrast correlations (Fig. 4C, F, Table 3).

K_S increased with decreasing MAP and MAP/PET in the cross-species analysis for the deciduous angiosperms (Fig. 5A, Table 3). This relationship was dominated by the winter deciduous species ($r = -0.63$, $P < 0.01$, $n = 32$) when compared to the drought deciduous species ($r = -0.03$, $P > 0.05$, $n = 10$). The overall relationship between K_S and MAP (and MAP/PET) across deciduous angiosperms was nonetheless supported evolutionarily by a significant PIC (Fig. 5D). There was no cross-species association between K_S and PET for deciduous species, but the independent contrast analysis revealed a marginally significant ($P < 0.10$) positive evolutionary association between K_S and PET (Table 3). In evergreen angiosperms, there was no relationship between K_S and any climate variable in either the cross-species or independent contrast analysis (Fig. 5B, E, Table 3). Similarly, there was no relationship between most climate variables (MAP, MAP/PET, MAT) and K_S in the conifers (Fig. 5C, F, Table

TABLE 3. Pearson correlations (r) and phylogenetically independent contrast correlations (PIC) among climate variables and hydraulic traits with vulnerability to xylem cavitation (Ψ_{50}) and specific conductivity (K_S) for all species and for angiosperms, deciduous angiosperms, evergreen angiosperms, and conifers treated separately.

Variable	All taxa		Angiosperms	
	r	PIC	r	PIC
Correlations with Ψ_{50}				
K_S	−0.31**	−0.18	−0.17	−0.12
MAP	−0.58**	−0.40**	−0.60**	−0.40**
PET	−0.26**	−0.13	−0.24**	−0.18
MAP/PET	−0.50**	−0.32**	−0.53**	−0.33**
MAT	−0.47**	−0.28**	−0.45**	−0.39**
Correlations with K_S				
Ψ_{50}	−0.31**	−0.18	−0.17	−0.12
MAP	−0.22*	−0.30**	−0.27*	−0.39**
PET	0.21	0.12	0.14	0.28†
MAP/PET	−0.24*	−0.29**	−0.27*	−0.40**
MAT	−0.19	−0.07	−0.03	−0.08

Notes: To facilitate log transformation for analysis, Ψ_{50} values were converted from negatives to positives. The sign of the correlation coefficients (both r and PIC) therefore reflect that increasing Ψ_{50} values or Ψ_{50} contrasts are indicative of increasing cavitation resistance. Key to abbreviations: MAP, mean annual precipitation; MAT, mean annual temperature; PET, potential evapotranspiration.

* $P < 0.05$; ** $P < 0.01$; † $P < 0.10$.

3). Decreasing K_S was, however, associated with increasing PET in both cross-species and PIC analyses for the conifers (Table 3).

We found little support for an evolutionary relationship between cavitation resistance and water transport. Although Ψ_{50} decreased with decreasing K_S (Fig. 6A, Table 3) among all taxa in the cross-species correlation, this relationship was not supported by a significant independent contrast correlation (Fig. 6D). Among angiosperms, there was no association between Ψ_{50} and K_S as determined by either cross-species correlation or PIC analyses (Fig. 6B, E). Although there was no cross-species correlation between Ψ_{50} and K_S among conifers (r, Fig. 6C), the PIC revealed a marginally significant association between these two variables (Fig. 6F, Table 3).

DISCUSSION

Our evolutionary analyses suggest that there are adaptive associations between resistance to cavitation and water availability. We found that resistance to water-stress-induced cavitation (as indicated by more negative Ψ_{50}) increased significantly with decreasing mean annual precipitation (MAP) and an index of moisture availability (the ratio of MAP to potential evapotranspiration, MAP/PET) (Fig. 3, Table 3). These significant cross-species correlations (r) were supported by significant phylogenetically independent contrast correlations (PIC). In particular, the independent contrast correlations between Ψ_{50} and MAP or MAP/PET were strongest for evergreen angiosperms and conifers (Table 3), suggesting that the evolutionary associations between increasing cavitation resistance and increasing aridity occurred across functional groups, despite considerable differences in xylem anatomy.

Additional support for adaptive variation in resistance to water-stress-induced cavitation was provided by several instances of convergent evolution in Ψ_{50} inferred from traits mapped onto a phylogeny (Fig. 2). Within the angiosperms, high resistance to cavitation ($\Psi_{50} < -3.15$ MPa, the grand mean for all species; Table 1) has evolved independently at least 20 times (Fig. 2). For example, distantly related genera such as *Larrea* (Zygophyllaceae), *Acacia* (Fabaceae), *Ceanothus* (Rhamnaceae), *Adenostoma* (Rosaceae), *Atriplex* (Amaranthaceae), *Encelia* (Asteraceae), and *Juniperus* (Cupressaceae) occur in deserts and mediterranean-type environments and have high resistance to cavitation (Fig. 2). These qualitative inferences of convergent evolution are supported by relatively high quantitative convergence indices for Ψ_{50} (e.g., QVI > 0.5; Table 1). Therefore, our analyses support the conclusion that high cavitation resistance is a key component of drought tolerance.

Support for convergent evolution is also provided by several instances in which species that are more vulnerable to cavitation may have arisen from more resistant ancestors. Within the Asteraceae, both *Chrysothamnus nauseosus* and *Baccharis salicifolia* are more vulnerable to cavitation than their congeners and putative ancestors (Fig. 2). Similarly, within the conifers, relatively vulnerable temperate and tropical species such as *Abies balsamea*, *Podocarpus latifolus*, *Dacrycarpus dacrydiodes*, *Juniperus virginiana*, and *Thuja occidentalis* may have putative ancestors with high resistance to cavitation (Fig. 2). These patterns suggest that high resistance to cavitation may be costly in mesic environments. For example, a biophysical necessity of increased cavitation resistance is increased wood density, which requires greater metabolic construction costs and may therefore reduce growth rate (Hacke et al. 2001). Nevertheless, the observation that relatively high cavitation resistance ($\Psi_{50} < -3.15$ MPa,

TABLE 3. Extended.

Deciduous angiosperms		Evergreen angiosperms		Conifers	
r	PIC	r	PIC	r	PIC
−0.13	0.04	−0.24	−0.19	−0.08	−0.39†
−0.36**	−0.18	−0.71**	−0.56**	−0.46**	−0.41*
0.20	−0.21	−0.58**	−0.29*	0.20	0.27
−0.34	−0.09	−0.65**	−0.51**	−0.49**	−0.33†
−0.02	−0.43**	−0.65**	−0.56**	−0.07	0.12
−0.13	0.04	−0.24	−0.19	−0.08	−0.39†
−0.47**	−0.65**	−0.01	−0.14	−0.04	0.15
0.21	0.40*	−0.19	0.12	−0.52*	−0.54**
−0.45**	−0.65**	0.01	−0.15	0.27	0.32
−0.16	−0.14	0.11	0.21	−0.36	−0.36
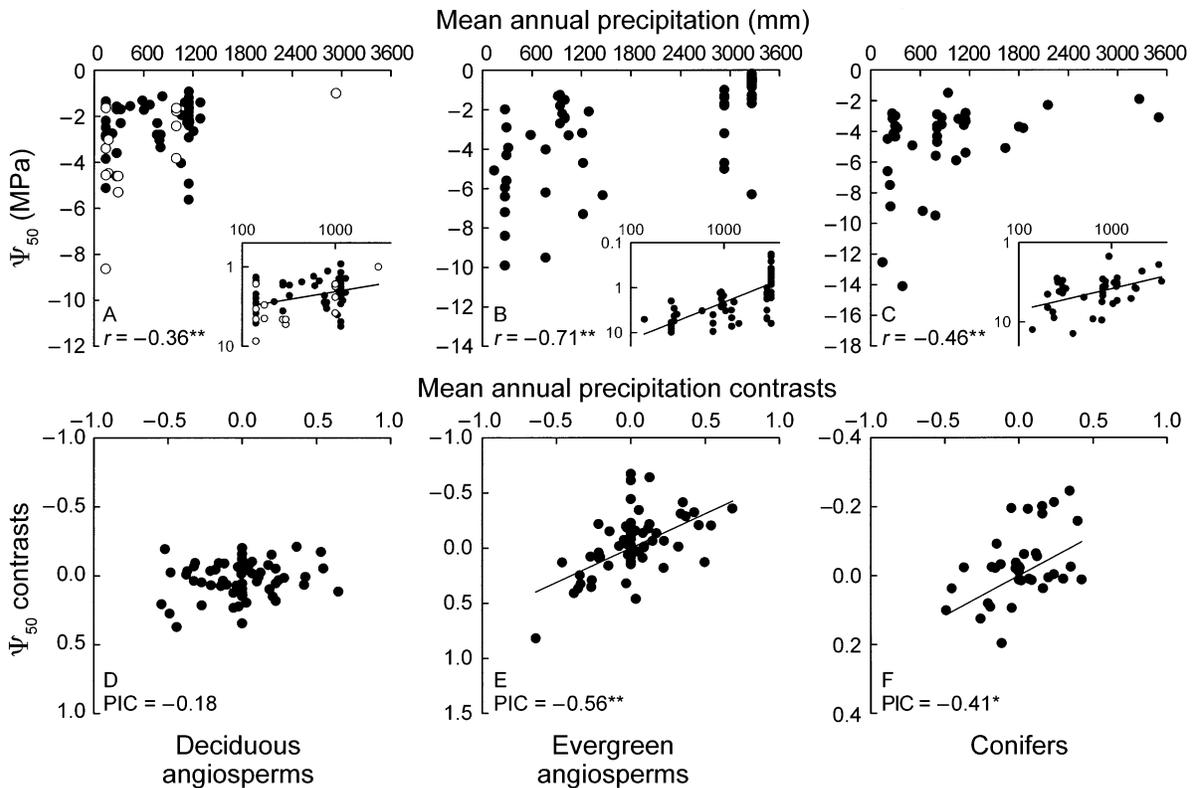
FIG. 4. The relationship between xylem tension at which 50% cavitation occurred (Ψ_{50}) and mean annual precipitation (MAP) analyzed using Pearson correlation coefficients and independent contrast correlations for (A, D) deciduous angiosperms, (B, E) evergreen angiosperms, and (C, F) conifers. Log-transformed relationships are shown in the insets. For descriptive purposes, the relationship between Ψ_{50} and MAP for deciduous angiosperms (panel A) was divided into winter deciduous (solid circles) and drought deciduous (open circles) groups. Statistically significant relationships (*$P < 0.05$, **$P < 0.01$) are fitted with least-squares regression lines. To facilitate log transformation for analysis, Ψ_{50} values were converted from negatives to positives. Although data in panels A–C are plotted to reflect the nontransformed relationships, the sign of the correlation coefficient (both standard cross-species correlations [r] and phylogenetically independent contrast correlations [PIC]) and the independent contrast plots (panels D–F) are based on the log-transformed data (see Table 3).
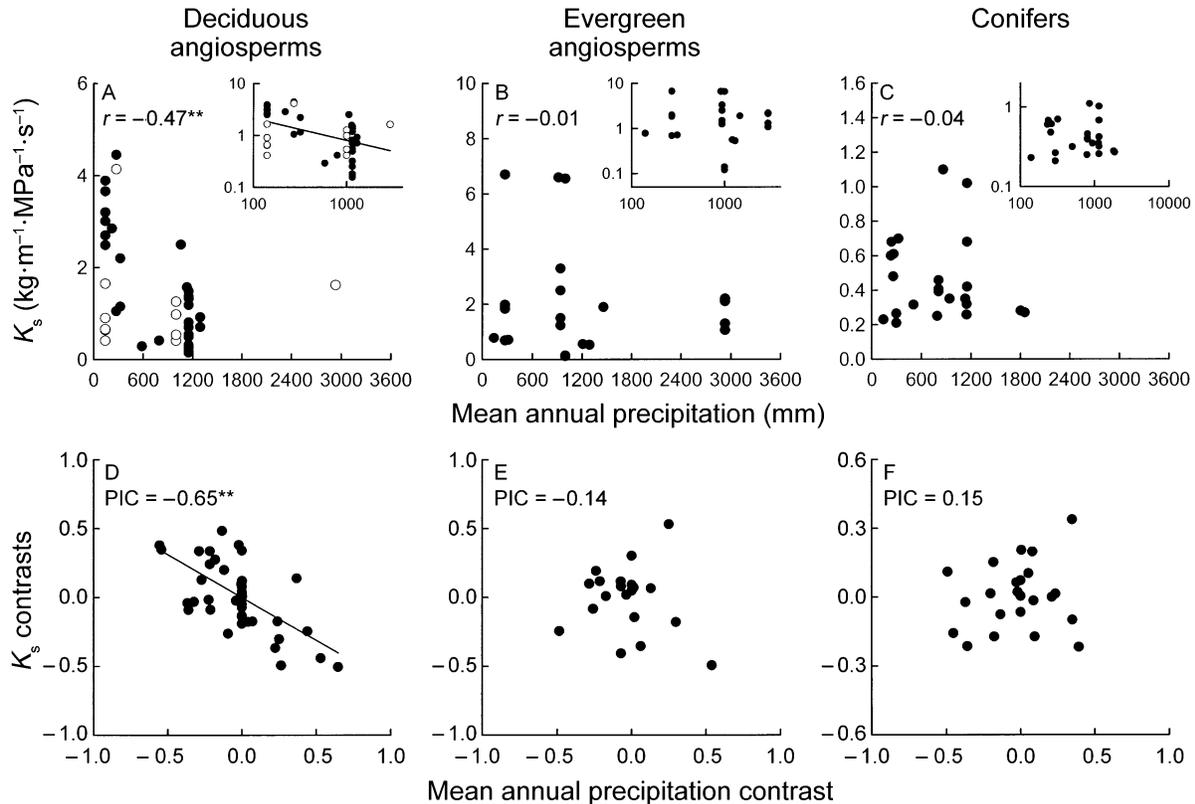
Fig. 5. The relationship between specific conductivity of xylem (K_S) and mean annual precipitation (MAP) analyzed using Pearson correlation coefficients and independent contrast correlations for (A, D) deciduous angiosperms, (B, E) evergreen angiosperms, and (C, F) conifers. Log-transformed relationships are shown in the insets. For descriptive purposes, the relationship between K_S and MAP for deciduous angiosperms (panel A) was divided into winter deciduous groups (solid circles) and drought deciduous groups (open circles). Statistically significant relationships (*$P < 0.05$; **$P < 0.01$) are fitted with least-squares regression lines. Key to abbreviations: PIC, phylogenetically independent contrast correlations; r, standard cross-species correlations.

the mean for all species, Table 1) persists among some of these genera in temperate regions (e.g., *J. virginiana*, *T. occidentalis*) does suggest that phylogenetic history may at least partly constrain the adaptive evolution of cavitation resistance.

Deciduous species may avoid periods of severe water limitation by shedding leaves (both during drought and winter) and, as a result, may experience weaker selection for increased resistance to water-stress-induced cavitation (Sobrado 1997, Eamus and Prior 2001). Our results partially supported this hypothesis. We found no evolutionary correlation (i.e., a nonsignificant PIC) between Ψ_{50} and MAP among deciduous angiosperms (Fig. 4A, D) but we note that the majority (77%) of samples for this comparison was drawn from winter deciduous species. The complete absence of an evolutionary correlation between Ψ_{50} and MAP is somewhat surprising because summer drought stress commonly occurs in habitats where winter deciduous species are found. However, it is possible that selection pressures on xylem that favor increased resistance to freezing-induced cavitation (e.g., Wang et al. 1992)

obscure the relationship between cavitation resistance and rainfall in winter deciduous species. This hypothesis is consistent with the observation that drought deciduous angiosperms, when considered separately, do show increased cavitation resistance with decreased rainfall (Fig. 4A). Nevertheless, further studies are required to determine the relative contributions of cavitation resistance and leaf shedding to the evolution of drought tolerance in the drought deciduous angiosperms. In contrast, we found a strongly significant cross-species and phylogenetically independent contrast correlation between increased resistance to cavitation and decreased MAP in evergreen angiosperms and conifers (Fig. 4B, C, E, F; Table 3). Therefore, the adaptive significance of increased resistance to cavitation as a mechanism of drought tolerance appears to be greatest in evergreen angiosperm and conifer species, largely because they need to preserve a water-conducting pathway for leaves year round.

We found a significant evolutionary correlation between increasing K_S and decreasing annual rainfall in deciduous angiosperms (Fig. 5A, D), but not in ever-
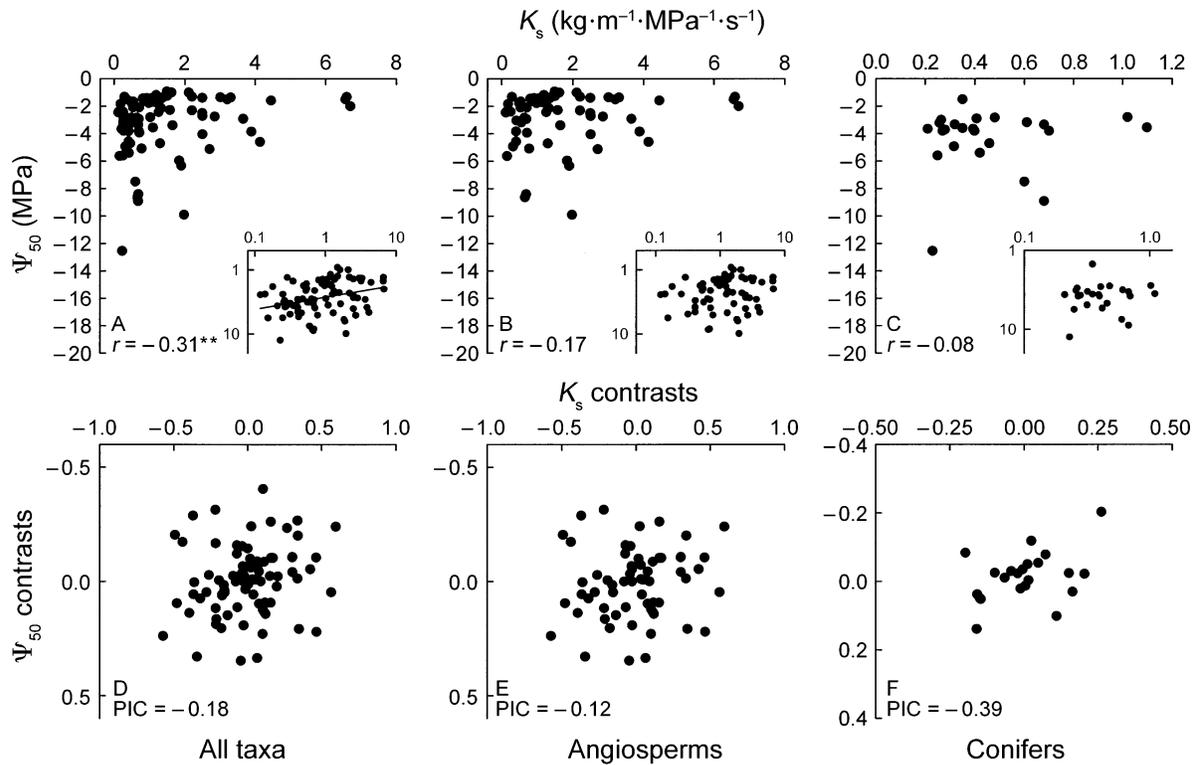
FIG. 6.   The relationship between xylem tension at which 50% cavitation occurred (Ψ_{50}) and specific conductivity of xylem (K_S) analyzed using (A, B, C) Pearson correlation coefficients and (D, E, F) independent contrast correlations for all taxa and for angiosperms and conifers considered separately. Angiosperm data were pooled because there were no differences between deciduous and evergreen groups (Table 3). Log-transformed relationships are shown in the insets. For descriptive purposes, statistically significant relationships (*$P < 0.05$; **$P < 0.01$) are fitted with least-squares regression lines. To facilitate log transformation for analysis, Ψ_{50} values were converted from negatives to positives. Although data are plotted to reflect the nontransformed relationships in panels A–C, the sign of the correlation coefficient (both standard cross-species correlations [r] and phylogenetically independent contrast correlations [PIC]) and the independent contrast plots (panels D–F) are based on the log-transformed data (see Table 3).

green species (Fig. 5B, E) or conifers (Fig. 5C, F). We also observed a significant, positive evolutionary correlation between increased K_S and PET for deciduous angiosperms (Table 3). Winter deciduous species made up the bulk (76%) of deciduous angiosperms analyzed, and our conclusions apply primarily to this group. Nevertheless, our results suggest two non-mutually exclusive interpretations. One interpretation is that high K_S could be adaptive in arid environments with high evaporative demand. Such an adaptation would facilitate increased transpiration without increasing the water potential gradient, permitting the avoidance of cavitation (Maherali and DeLucia 2000, Piñol and Sala 2000). This view is supported by experimental studies showing that increased drought and evaporative demand tend to increase long-term measures of plant hydraulic efficiency (Maherali and DeLucia 2001, Mencuccini 2003). A second interpretation is that the short life span of deciduous leaves necessitates that, for those species in dry climates, water transport must be maximized for carbon fixation during the brief periods when water is available to offset a long dormant period. This hy-

pothesis is consistent with comparative studies showing broad support for an ecophysiological trade-off between leaf life span and leaf CO_2/H_2O flux (e.g., Reich et al. 1999).

Our analyses indicated that high evaporative demand may not be an important selection pressure driving increased resistance to xylem cavitation. Although a weakly significant cross-species correlation was observed between Ψ_{50} and PET for all taxa, these two variables were not correlated evolutionarily (PIC, Table 3). The strongest relationship between Ψ_{50} and PET (for both cross-species and PIC analyses) was in evergreen angiosperms. However, the direction of this relationship was the opposite of expectations; species growing at higher PET were less resistant to water-stress-induced cavitation. This result may have arisen because many species vulnerable to cavitation were often found in the warm and wet tropics or riparian areas in deserts, environments that also had high PET.

We observed a strong evolutionary correlation between increasing cavitation resistance and decreasing MAP in both conifers and evergreen angiosperms (Fig.

4E, F). Despite similar patterns of correlated evolution, and the fact that Ψ_{50} values largely overlapped (Table 1, Fig. 4A, B, C), only 35% of evergreen angiosperms (and 26% of deciduous angiosperms) had Ψ_{50} values more negative than the grand mean for all species (-3.15 MPa), whereas 77% of conifers fell into this category. In consequence, conifers were, on average, 80% more resistant to water-stress-induced cavitation than evergreen angiosperms (Table 1). Although tracheids are not considered to be inherently superior to vessels in resisting water-stress-induced cavitation (Sperry 2003), why are a greater proportion of conifers more resistant to water-stress-induced cavitation than angiosperms? One explanation may be that there are fewer constraints on the evolution of high cavitation resistance in tracheid vs. vessel-bearing wood. For example, resistance to water-stress-induced cavitation via air seeding in a large majority of angiosperms depends on the surface tension of the meniscus in each of the pores of the pit membrane that connects adjacent conduits (Sperry 2003). As a result, increases in resistance to cavitation must be accompanied by presumably costly decreases in pore hydraulic conductivity (Zimmermann 1983, Sperry and Hacke 2004). In conifers, a net-like perimeter (the margo) surrounds a thickened impermeable center (the torus). The large pores of the margo allow high pit hydraulic conductivity but appear to place a weak functional limit on air seeding pressures because the aspiration of the torus is responsible for blocking the spread of air between conduits following cavitation (Sperry 2003, Hacke et al. 2004). Further air seeding depends on the elasticity and mechanical strength of the torus/margo complex (Sperry and Tyree 1990). Because increased air seeding pressure (and thus increased cavitation resistance) is not accompanied by increased pit hydraulic resistance, conifers may more easily respond to selection for increased cavitation resistance than angiosperms.

Given the apparent trade-off between air seeding pressure and pore conductivity, it has long been suggested that increased resistance to water-stress-induced cavitation should be associated with reduced xylem hydraulic transport capacity in the stem (K_S), particularly in angiosperms (Zimmermann 1983, Tyree and Sperry 1989, Tyree and Ewers 1991). This trade-off has been observed within an individual (e.g., Tyree and Sperry 1989, Sperry and Saliendra 1994), but is more difficult to detect across individuals (Kavanagh et al. 1999, Maherali and DeLucia 2000) or species (Tyree et al. 1994, Pockman and Sperry 2000). We found a significant, though weak, cross-species correlation between Ψ_{50} and K_S (Fig. 6A). However, there was no evolutionary correlation between the two traits, suggesting that there may not be an evolutionary trade-off between resistance to cavitation and specific conductivity in woody plants, at least at the broad taxonomic scale of this study. Because angiosperms are on average less resistant to cavitation than conifers and have higher K_S, the significant cross-species correlation may be caused by the ancestral divergence between these two groups (e.g., Ackerly and Reich 1999). The absence of an evolutionary correlation between Ψ_{50} and K_S in angiosperms, despite a trade-off between air seeding pressure and pit conductivity (Sperry and Hacke 2004), may be associated with changes in other traits. For example, increased vessel length and diameter both increase hydraulic conductivity and may compensate for hydraulic limitations in the pit membrane (Comstock and Sperry 2000, Hacke et al. 2004, Sperry and Hacke 2004). Despite the absence of a cross-species correlation between Ψ_{50} and K_S in conifers (Fig. 6C), there was a marginally significant PIC between these two traits (Fig. 6F), suggesting that there may be a weak evolutionary trade-off between Ψ_{50} and K_S in conifers.

Our study, like all meta-analyses with broad interspecific data sets, has limitations. In particular, interspecific relationships analyzed using both traditional cross-species analysis and independent contrasts are limited by the inability to randomly sample taxa (Donoghue and Ackerly 1996, Ackerly 2000). In addition, although our sample was drawn from a broad taxonomic range, several families were represented only by one or two species (e.g., Moraceae, Rhizophoraceae, Zygophyllaceae), whereas others had several species (e.g., Fagaceae, Pinaceae, Cupressaceae). Several ecologically important genera spanning large climate gradients (e.g., *Eucalyptus*, *Nothofagus*, *Ambrosia*) were also not well represented. Finally, our sample only includes woody plants and the Ψ_{50} and K_S values reported here may not necessarily be representative of the distribution of these traits across all seed plants (Ackerly 2000). Simulation analyses suggest that this type of nonrandom sampling could result in the underestimation of true PIC correlation coefficients (Ackerly 2000). Our analysis of correlated evolution was therefore conservative, and the significant PICs we report in this study should be regarded as robust. Nevertheless, weaker relationships may have gone undetected, though this limitation must be balanced against inflated Type I error rates of non-phylogenetically corrected cross-species correlations (Garland et al. 1992, Purvis et al. 1994, Ackerly 2000).

Our study suggests several avenues of future research. First, the cavitation resistance of roots, like that of stems, can limit transpiration (Alder et al. 1996, Jackson et al. 2000). Although root data were too limited to include in our analysis, roots are generally more vulnerable to water-stress-induced cavitation than stems (Jackson et al. 2000), and thus we predict that interspecific variation in root cavitation resistance also has adaptive consequences. Second, our analysis does not specifically incorporate vulnerability to freezing-induced cavitation, which is controlled by the volume of conducting elements in the xylem (Davis et al. 1999). The substantial variation that we observed in K_S indicates that there is large variation in conduit di-

ameter (e.g., 10 μm to >500 μm; Tyree et al. 1994), and therefore conduit volume, among species in our database. However, sufficient data on freezing-induced cavitation were not available for our analysis. Simultaneous consideration of water-stress-induced and freezing-induced cavitation in a phylogenetic framework, particularly among closely related species that span large gradients in precipitation and temperature, will likely be fruitful. Finally, our analysis assumes that embolism formation is largely irreversible in the absence of new growth (Zimmermann 1983) or under conditions of positive root or stem pressure (Ewers et al. 1997, Tyree et al. 1999). However, recent studies suggest that the refilling of emboli may occur during transpiration (McCully 1999, Tyree et al. 1999) causing hydraulic conductivity to vary diurnally (Zwieniecki and Holbrook 1998). The mechanism of cavitation repair under tension is not known, nor is there enough information in the literature to determine whether it is common in many species. Continued research on these processes (Holbrook et al. 2001, Meinzer et al. 2001) across a range of taxa will improve our understanding of the evolutionary and ecological significance of cavitation resistance.

Additional variables such as the leaf-specific conductivity (K_L) and the ratio of leaf area to sapwood area (A_L/A_S) are important in controlling water supply to leaves and are likely associated with variation in resistance to xylem cavitation. These variables were rarely reported in the studies we used to construct our database, preventing us from examining several additional hypotheses that deserve further study. For example, the observation that K_L scales directly with leaf transpiration (Mencuccini 2003) suggests that the hypothesized trade-off between cavitation resistance and water transport could be manifested when leaf level conductivity is taken into account. Alternatively, because increased K_L, like K_S, facilitates increased transpiration without a rise in the water potential gradient, both high K_L and high cavitation resistance (a more negative Ψ_{50}) could represent strategies for coping with prolonged drought (Tyree and Ewers 1991), obscuring a potential trade-off between K_L and cavitation resistance. Observations of a decrease in A_L/A_S, which tends to increase K_L, in response to increasing aridity in many conifer taxa (DeLucia et al. 2000) are consistent with this view. This decline in A_L/A_S with increased drought also suggests that partial leaf shedding could also be an evolutionarily important response to aridity in evergreen angiosperms and conifers.

Our findings highlight the importance of examining functional correlations in a phylogenetic context in order to understand how interspecific variation in plant traits arose. Among other insights, we observed that cavitation resistance likely has different ecological and evolutionary consequences for deciduous vs. evergreen angiosperms and conifers. Our wide taxonomic sample provides evidence of broad patterns, but further studies

at smaller scales (i.e., within specific families or genera) that combine physiological data, molecular phylogenetic hypotheses, and biogeographic information will help provide comprehensive tests of the evolution of functional changes in cavitation resistance. For example, we found no trade-off between cavitation resistance and specific conductivity in a broad sample, but evolutionary associations between these traits may occur within specific groups that have very similar leaf and xylem structure (e.g., Piñol and Sala 2000; Fig. 6F). Resistance to water-stress-induced cavitation is a critical component controlling canopy transpiration and water uptake (Sperry et al. 2002), and interspecific variation in this trait can influence hydrological processes (Jackson et al. 2000, 2001). Further understanding of the evolutionary origins and ecological significance of xylem transport and cavitation resistance is likely to improve predictions of plant and ecosystem water use on both local and global scales and in response to future environmental change.

Literature Cited

Ackerly, D. D. 1999. Phylogeny and the comparative method in plant functional ecology. Pages 391–413 *in* M. C. Press, J. D. Scholes, and M. G. Baker, editors. Plant physiological ecology. Blackwell Scientific Press, Oxford, UK.

Ackerly, D. D. 2000. Taxon sampling, correlated evolution, and independent contrasts. Evolution **54**:1480–1492.

Ackerly, D. D., and M. J. Donoghue. 1998. Leaf size, sapling allometry, and Corner's rules: a phylogenetic study of correlated evolution in maples (*Acer*). American Naturalist **152**:767–791.

Ackerly, D. D., and P. B. Reich. 1999. Convergence and correlations among leaf size and function in seed plants: a comparative test using independent contrasts. American Journal of Botany **86**:1272–1281.

Alder, N. N., W. T. Pockman, J. S. Sperry, and S. Nuismer. 1997. Use of centrifugal force in the study of xylem cavitation. Journal of Experimental Botany **48**:665–674.

Alder, N. N., J. S. Sperry, and W. T. Pockman. 1996. Root and stem xylem embolism, stomatal conductance and leaf turgor in *Acer grandidentatum* populations along a soil moisture gradient. Oecologia **105**:293–301.

Brodribb, T., and R. S. Hill. 1999. The importance of xylem constraints in the distribution of conifer species. New Phytologist **143**:365–372.

Carlquist, S. J. 1988. Comparative wood anatomy: systematic, ecological, and evolutionary aspects of dicotyledon wood. Springer, New York, New York, USA.

Choudhury, B. J. 1997. Global pattern of potential evaporation calculated from the Penman-Monteith equation using satellite and assimilated data. Remote Sensing of Environment **61**:64–81.

Choudhury, B. J., and N. E. DiGirolamo. 1998. A biophysical process-based estimate of global land surface evaporation using satellite and ancillary data—I. Model description and comparison with observations. Journal of Hydrology **205**: 164–185.

Cochard, H., P. Cruiziat, and M. T. Tyree. 1992. Use of positive pressures to establish vulnerability curves. Plant Physiology **100**:205–209.

Comstock, J. P., and J. S. Sperry. 2000. Some theoretical considerations of optimal conduit length for water transport in plants. New Phytologist **148**:195–218.

Cunningham, C. W., K. E. Omland, and T. H. Oakley. 1998. Reconstructing ancestral character states: a critical reappraisal. Trends in Ecology and Evolution **13**:361–366.

Davis, S. D., J. S. Sperry, and U. G. Hacke. 1999. The relationship between xylem conduit diameter and cavitation caused by freezing. American Journal of Botany **86**:1367–1372.

DeLucia, E. H., H. Maherali, and E. V. Carey. 2000. Climate-driven changes in biomass allocation in pines. Global Change Biology **6**:587–593.

Donoghue, M. J., and D. D. Ackerly. 1996. Phylogenetic uncertainties and sensitivity analyses in comparative biology. Philosophical Transactions of the Royal Society of London, Series B **351**:1241–1249.

Eamus, D., and L. Prior. 2001. Ecophysiology of trees of seasonally dry tropics: comparisons among phenologies. Advances in Ecological Research **32**:113–197.

Ewers, F. W., H. Cochard, and M. T. Tyree. 1997. A survey of root pressures in vines of a tropical lowland forest. Oecologia **110**:191–196.

Felsenstein, J. 1985. Phylogenies and the comparative method. American Naturalist **125**:1–15.

Garland, T., Jr., P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. Systematic Biology **41**:18–32.

Hacke, U. G., J. S. Sperry, and J. Pittermann. 2004. Analysis of circular bordered pit function. II. Gymnosperm tracheids with torus-margo pit membranes. American Journal of Botany **91**:386–400.

Hacke, U. G., J. S. Sperry, W. T. Pockman, S. D. Davis, and K. A. McCulloch. 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. Oecologia **126**:457–461.

Harvey, P. H., and M. Pagel. 1991. The comparative method in evolutionary biology. Oxford University Press, Oxford, UK.

Holbrook, N. M., E. T. Ahrens, M. J. Burns, and M. A. Zwieniecki. 2001. In vivo observation of cavitation and embolism repair using magnetic resonance imaging. Plant Physiology **126**:27–31.

Jackson, R. B., S. R. Carpenter, C. N. Dahm, D. M. McKnight, R. J. Naiman, S. L. Postel, and S. W. Running. 2001. Water in a changing world. Ecological Applications **11**:1027–1045.

Jackson, R. B., J. S. Sperry, and T. E. Dawson. 2000. Root water uptake and transport: using physiological processes in global predictions. Trends in Plant Science **5**:482–488.

Jarbeau, J. A., F. W. Ewers, and S. D. Davis. 1995. The mechanism of water stress induced embolism in two species of chaparral shrubs. Plant Cell and Environment **18**:189–196.

Kavanagh, K. L., B. J. Bond, S. N. Aitken, B. L. Gartner, and S. Knowe. 1999. Shoot and root vulnerability to xylem cavitation in four populations of Douglas-fir seedlings. Tree Physiology **19**:31–37.

Kolb, K. J., and J. S. Sperry. 1999. Differences in drought adaptation between subspecies of sagebrush (*Artemisia tridentata*). Ecology **80**:2373–2384.

Leemans, R., and W. Cramer. 1991. The IIASA database for mean monthly values of temperature, precipitation and cloudiness of a global terrestrial grid. Report Number RR-91–18. International Institute for Applied Systems Analysis, Laxenburg, Austria.

Maddison, W. P., and D. R. Maddison. 2000. MacClade 4.0: analysis of phylogeny and character evolution. Sinauer, Sunderland, Massachusetts, USA.

Maherali, H., and E. H. DeLucia. 2000. Xylem conductivity and vulnerability to cavitation of ponderosa pine growing in contrasting climates. Tree Physiology **20**:859–867.

Maherali, H., and E. H. DeLucia. 2001. Influence of climate-driven shifts in biomass allocation on water transport and storage in ponderosa pine. Oecologia **129**:481–491.

Matzner, S. L., K. J. Rice, and J. H. Richards. 2001. Intra-specific variation in xylem cavitation in interior live oak (*Quercus wislizenii*). Journal of Experimental Botany **52**: 783–789.

McCully, M. E. 1999. Root xylem embolisms and refilling. Relation to water potentials of soil, roots, and leaves, and osmotic potentials of root xylem sap. Plant Physiology **119**: 1001–1008.

Meinzer, F. C., M. J. Clearwater, and G. Goldstein. 2001. Water transport in trees: current perspectives, new insights and some controversies. Environmental and Experimental Botany **45**:239–262.

Mencuccini, M. 2003. The ecological significance of long-distance water transport: short term regulation, long term acclimation and the hydraulic costs of stature across plant life forms. Plant Cell and Environment **26**:163–182.

Pagel, M. D. 1993. Seeking the evolutionary regression coefficient: an analysis of what comparative methods measure. Journal of Theoretical Biology **164**:191–205.

Pataki, D. E., R. Oren, and N. Phillips. 1998. Responses of sap flux and stomatal conductance of *Pinus taeda* L. trees to stepwise reductions in leaf area. Journal of Experimental Botany **49**:871–878.

Piñol, J., and A. Sala. 2000. Ecological implications of xylem cavitation for several Pinaceae in the Pacific northern U.S.A. Functional Ecology **14**:538–545.

Pockman, W. T., and J. S. Sperry. 2000. Vulnerability to xylem cavitation and the distribution of Sonoran desert vegetation. American Journal of Botany **87**:1287–1299.

Pockman, W. T., J. S. Sperry, and J. W. O'Leary. 1995. Sustained and significant negative water pressure in xylem. Nature **378**:715–716.

Purvis, A., J. L. Gittleman, and H. K. Luh. 1994. Truth or consequences: effects of phylogenetic accuracy on two comparative methods. Journal of Theoretical Biology **167**: 293–300.

Reich, P. B., D. S. Ellsworth, M. B. Walters, J. Vose, C. Gresham, J. Volin, and W. Bowman. 1999. Generality of leaf traits relationships: a test across six biomes. Ecology **80**:1955–1969.

Schenk, H. J., and R. B. Jackson. 2002. The global biogeography of roots. Ecological Monographs **72**:311–328.

Schwilk, D. W., and D. D. Ackerly. 2001. Flammability and serotiny as strategies: correlated evolution in pines. Oikos **94**:326–336.

Sobrado, M. A. 1997. Embolism vulnerability in drought-deciduous and evergreen species of a tropical dry forest. Acta Œcologica **18**:383–391.

Soltis, P. S., D. E. Soltis, and M. W. Chase. 1999. Angiosperm phylogeny inferred from multiple genes as a tool for comparative biology. Nature **402**:402–404.

Sperry, J. S. 2003. Evolution of water transport and xylem structure. International Journal of Plant Science **164**:S115–S127.

Sperry, J. S., J. R. Donnelly, and M. T. Tyree. 1988. A method for measuring hydraulic conductivity and embolism in xylem. Plant Cell and Environment **11**:35–40.

Sperry, J. S., and U. G. Hacke. 2004. Analysis of circular bordered pit function. I. Angiosperm vessels with homogenous pit membranes. American Journal of Botany, **91**: 369–385.

Sperry, J. S., U. G. Hacke, R. Oren, and J. P. Comstock. 2002. Water deficits and hydraulic limits to leaf water supply. Plant Cell and Environment **25**:251–263.

Sperry, J. S., K. L. Nichols, J. E. M. Sullivan, and S. E. Eastlack. 1994. Xylem embolism in ring-porous, diffuse-porous and coniferous trees of northern Utah and interior Alaska. Ecology **75**:1736–1752.

Sperry, J. S., and W. T. Pockman. 1993. Limitation of transpiration by hydraulic conductance and xylem cavitation in *Betula occidentalis*. Plant, Cell and Environment **16**: 279–287.

Sperry, J. S., and N. Z. Saliendra. 1994. Intra-and inter-plant variation in xylem cavitation in *Betula occidentalis*. Plant, Cell and Environment **17**:1233–1241.

Sperry, J. S., and M. T. Tyree. 1988. Mechanism of water stress-induced xylem embolism. Plant Physiology **88**:581–587.

Sperry, J. S., and M. T. Tyree. 1990. Water-stress-induced xylem embolism in three species of conifers. Plant Cell and Environment **13**:427–436.

Stefanović, S., M. Jager, J. Deutsch, J. Broutin, and M. Masselot. 1998. Phylogenetic relationships of conifers inferred from partial 28S rRNA gene sequences. American Journal of Botany **85**:688–697.

Tyree, M. T., S. D. Davis, and H. Cochard. 1994. Biophysical perspectives of xylem evolution: Is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction? International Association of Wood Anatomists Journal **15**:335–360.

Tyree, M. T., and F. W. Ewers. 1991. The hydraulic architecture of trees and other woody plants. New Phytologist **119**:345–360.

Tyree, M. T., S. Salleo, A. Nardini, M. A. Lo Gullo, and R. Mosca. 1999. Refilling of embolized vessels in young stems of laurel: Do we need a new paradigm? Plant Physiology **120**:11–21.

Tyree, M. T., and J. S. Sperry. 1989. Vulnerability of xylem to cavitation and embolism. Annual Review of Plant Physiology and Plant Molecular Biology **40**:19–38.

Wang, J., N. E. Ives, and M. J. Lechowicz. 1992. The relation of foliar phenology to xylem embolism in trees. Functional Ecology **6**:469–475.

Zimmermann, M. H. 1983. Xylem structure and the ascent of sap. Springer, New York, New York, USA.

Zwieniecki, M. A., and N. M. Holbrook. 1998. Diurnal variation in xylem hydraulic conductivity in white ash (*Fraxinus americana* L.), red maple (*Acer rubrum* L.) and red spruce (*Picea rubens* Sarg.). Plant Cell and Environment **21**:1173–1180.

APPENDIX A

A table presenting species, their geographic locations, and studies used in the database is available in ESA's Electronic Data Archive: *Ecological Archives* E085-067-A1.

APPENDIX B

A table presenting sources of phylogenetic information and polytomy resolutions for selected taxa is available in ESA's Electronic Data Archive: *Ecological Archives* E085-067-A2.