

Patterns in water relations of central Himalayan trees

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Abstract: We measured water relations of 11 tree species from tropical to cool-temperate forests at 450-2310 m elevation in the central Himalaya of India, including water potential (ψ), leaf conductance (g_l), osmotic potential (ψ_s), an index of tissue elasticity (ϵ), relative water content at turgor loss (RWC_z), and four aspects of twig xylem conductance. We sought to determine the degree, timing, and distribution of low ψ ; the variation in properties with tree growth form, phylogenetic origin, and distribution of the species; and responses and possible adaptations to drought. Study species represented dominant canopy evergreen angiosperms (*Shorea robusta* Gaertn., *Quercus leucotrichophora* A. Camus, *Q. floribunda* Lindley ex A. Camus), an evergreen canopy oak of limited local importance (*Q. lanata* Smith), undercanopy evergreen angiosperms with a wide (*Rhododendron arboreum* Smith) and restricted (*Machilus duthiei* King) distribution, winter-deciduous angiosperm canopy trees of subordinate importance (*Carpinus viminea* Lindley, *Cornus macrophylla* Wall., *Fraxinus micrantha* Lingelsh.), and canopy conifers with a wide (*Pinus roxburghii* Sarg.) and restricted (*Cupressus torulosa* D. Don) distribution.

The lowest ψ values in our study were moderately severe, compared to trees in other climatic zones and to a subsequent drought year in our region. ψ declined at higher elevations, and was lowest during the hot season before monsoon rains and, for four high elevation species, in winter; secondary lows occurred in early summer. *Shorea robusta*, from the lowest elevation, had the highest ψ ; *Pinus roxburghii* and *Cornus macrophylla* were also usually high. Predawn ψ did not vary consistently with growth form. Widely distributed species had higher ψ , more elastic tissue, and a lower RWC_z than localized species. Canopy species had a higher proportion of active twig xylem than undercanopy species. Oaks had more xylem and higher twig xylem conductance per unit leaf area than other genera. Conifers displayed higher ψ_s , more elastic tissue, and a higher proportion of active twig xylem, but much lower leaf-specific twig xylem conductance, than associated angiosperms. Deciduous species had higher twig xylem conductance than evergreen angiosperms, but often differed from each other. g_l declined with elevation, but did not differ among groups of species.

Resumen: Medimos las relaciones hídricas de 11 especies arbóreas de bosques tropicales y templados frescos, en elevaciones de 450-2310 m, en la porción central de los Himalayas, India, incluyendo el potencial hídrico (ψ), la conductancia foliar (g_l), el potencial osmótico (ψ_s), un índice de elasticidad del tejido (ϵ), el contenido relativo de agua a la pérdida de turgencia (RWC_z) y cuatro aspectos de la conductancia del xilema de las ramillas. Buscamos determinar el grado, la temporalidad y la distribución de valores bajos de ψ , la variación en las propiedades con la forma

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de crecimiento del árbol, el origen filogenético y la distribución de las especies; y las respuestas y posibles adaptaciones a la sequía. Las especies de estudio incluyeron angiospermas perennifolias dominantes del dosel (*Shorea robusta* Gaertn., *Quercus leucotrichophora* A. Camus, *Q. floribunda* Lindley ex A. Camus), un encino perennifolio del dosel de importancia local limitada (*Q. lanata* Smith), angiospermas del subdosel de distribución amplia (*Rhododendron arboretum* Smith) y restringida (*Machilus duthiei* King), angiospermas arbóreas del dosel deciduas de invierno de importancia subordinada (*Carpinus viminea* Lindley, *Cornus macrophylla* Wall., *Fraxinus micrantha* Lingelsh.), y coníferas del dosel de distribución amplia (*Pinus roxburghii* Sarg.) y restringida (*Cupressus torulosa* D. Don).

Los valores más bajos de Ψ en nuestro estudio fueron moderadamente severos en comparación con árboles en otras zonas climáticas y con un año seco subsecuente en nuestra región. Ψ disminuyó hacia las mayores elevaciones y tuvo sus valores más bajos durante la estación caliente antes de las lluvias monzónicas y, para cuatro especies de alta altitud, en el invierno; valores bajos secundarios se presentaron al principio del verano. *Shorea robusta*, presente en el sitio de menor elevación, tuvo el Ψ más alto, *Pinus roxburghii* y *Cornus macrophylla* también fueron inusualmente altos. El valor de Ψ antes del amanecer no varió consistentemente con la forma de crecimiento. Las especies ampliamente distribuidas tuvieron mayores Ψ , un tejido más elástico, y un RWC_z más bajo que las especies de distribución localizada. Las especies del dosel tuvieron una mayor proporción de xilema activo en las ramillas que las especies del subdosel. Los encinos tuvieron más xilema y una mayor conductancia en el xilema de las ramillas por unidad de área foliar que los otros géneros. Las coníferas mostraron mayores Ψ_s , tejido más elástico y una mayor proporción de xilema activo en las ramillas, pero una conductancia específica de la hoja en el xilema de las ramillas mucho más baja que las angiospermas asociadas con ellas. Las especies deciduas tuvieron una mayor conductancia de xilema de las ramillas que las angiospermas perennifolias, pero con frecuencia difirieron entre sí. g_1 disminuyó con la altitud, pero no difirió entre grupos de especies.

Resumo: Mediram-se as relações hídricas em 11 espécies arbóreas de florestas tropicais a temperadas frias num intervalo de altitude entre os 450-2310m nos Himalaias centrais da Índia, incluindo o potencial hídrico (Ψ), condutância foliar (g_1), potencial osmótico (Ψ_s), índice de elasticidade dos tecidos (ϵ), teor relativo em água ao nível de perda de turgescência (RWC_z), e quatro aspectos da condutância do xilema dos ramos. Procurou-se determinar o grau, a altura e distribuição do mais baixo valor de Ψ , a variância nas propriedades com a forma de crescimento da árvore, origem filogenética e distribuição das espécies, bem como respostas e possíveis adaptações à secura. As espécies estudadas representavam as angiospérmicas dominantes no copado sempreverde (*Shorea robusta* Gaertn., *Quercus leucotrichophora* A. Camus, *Q. floribunda* Lindley ex A. Camus), um carvalho sempreverde de importância local limitada (*Q. lanata* Smith), e angiospérmicas sempreverdes do sub-coberto com um distribuição alargada (*Rhododendron arboretum* Smith) e restrita (*Machilus duthiei* King), e angiospérmicas decíduas de Inverno de importância subordinada (*Carpinus viminea* Lindley, *Cornus macrophylla* Wall., *Fraxinus micrantha* Lingelsh.), e coníferas com uma distribuição alargada (*Pinus roxburghii* Sarg.) e restrita (*Cupressus torulosa* D. Don).

Os valores mais baixos de Ψ encontrados no nosso estudo foram moderadamente severos, em comparação com árvores de outras zonas climáticas e a subseqüentes anos secos na nossa região. O valor de Ψ desceu a altas elevações e foi o mais baixo durante a estação quente antes das chuvas de monção, e para quatro espécies de alta altitude no Inverno; valores baixos secundários ocorreram no início do verão. Na elevação mais baixa, a *Shorea robusta* apresentou o valor de Ψ mais elevado, sendo este valor também usualmente elevado para a *Pinus roxburghii* e *Cornus macrophylla*. No início da madrugada o Ψ não variou consistentemente com a forma de crescimento. As espécies com larga distribuição apresentaram um Ψ mais elevado, tecidos mais elásticos, e menor RWC em comparação com as espécies localizadas. O copado das árvores apresentaram uma maior proporção de xilema activo do que o das espécies do sub-coberto. Os carvalhos tinham mais xilema e maior condutância no

xilema dos ramos por unidade de área foliar do que os outros géneros. As coníferas apresentavam elevados valores de Ψ_s , tecidos mais elásticos e mais elevada proporção de xilema activo nos ramos mas uma muito menor condutância dos ramos específica das folhas do que as das angiospérmicas sempre-verdes se bem frequentemente diferindo entre si. O valor de g_1 declinou com a altitude mas não diferiu entre os grupos de espécies.

Key words: Conifers, deciduous trees, leaf conductance, oaks, osmotic potential, tissue elasticity, tree species distribution, water potential, xylem conductance.

Introduction

In many parts of the biosphere, distribution and functioning of plants are controlled by availability of water. Trees in seasonal climates often experience a major water deficiency. Drought at different times of year should produce dissimilar responses and adaptations (for example, Terradas & Save' 1992; Waring & Franklin 1979). Trees in the central Himalaya grow in a strongly seasonal climate (Dhar *et al.* 1987); after three rainy months, fall, winter, spring, and "summer" (the warm period before monsoon rains begin) have little precipitation. This long dry period reduces tree water potential (ψ), modifies tree physiology, and apparently limits tree species distribution (Dhaila 1991; Poudyal *et al.* 2004; Singh *et al.* 2000; Zobel and Singh 1995; Zobel *et al.* 1995; Zobel *et al.* 2001a.). Central Himalayan forests are dominated by evergreen trees with leaf longevity of about one year. Their phenology increases the likelihood that water deficits will limit their performance, as these trees produce most leaves near the end of the months-long hot dry period before the monsoon rains (Negi & Singh 1992; Ralhan *et al.* 1985); drought then may seriously interfere with tree phenology and health (Singh *et al.* 2000). Adjustment of osmotic potential and tissue elasticity, control of water loss, or maintenance of xylem conductance may be required to sustain the water supply for leaf enlargement. In many ways, Himalayan trees and forests differ from those studied elsewhere (Singh *et al.* 1994; Zobel & Singh 1997). Given that their leaf longevity and climate differ from most forests studied previously, the water relations of Himalayan trees may also differ from better known species.

Here we report water relations properties for 11 native tree species; together, they grow from

the base of the central Himalaya, with near-tropical temperatures and tropical taxa, to the mid-elevation forests dominated by cool-temperate taxa, where winter snow pack can accumulate. We sought to determine the intensity and pattern of drought and mechanisms of adaptation to drought for these species. Specific objectives were to determine:

1. How ψ varies among seasons, growth forms, species groups, and species within growth forms;
2. Timing and size of adjustments of osmotic potential, tissue elasticity, leaf conductance, and twig xylem conductance;
3. What generalizations about tree water relations are possible based on a species' habitat, growth form, or relative importance in the forests; and
4. How water relations aid tree performance in the Himalayan monsoon climate.

Study sites and species

Sample trees were selected from intact stands in major forest types across a 1860 m elevational gradient on the southernmost ridge of the outer Himalaya near Naini Tal, Kumaun region, Uttaranchal state, India (29°23' N 79°27' E) (Table 1) (Singh & Singh 1987, 1992; Singh *et al.* 1994). These forests were classified into five types based on which species will apparently be dominant in late seral forests (Zobel *et al.* 2001a): sites 1-3, sal = *Shorea robusta*; sites 4, 7, pine = *Pinus roxburghii*; sites 5, 6, 8, 9, 14, 15, oak = *Quercus leucotrichophora* (banj), *Q. floribunda* (tilonj), or both; sites 12, 13, cypress = *Cupressus torulosa*; and sites 10, 11, 16, mixed, which included at least two oaks and at least one deciduous species per stand.

Table 1. Locations of data collection and characteristics of study sites and trees. Predawn and midday ψ were measured on all species at all sites. Properties: g = leaf conductance, pv = pressure-volume analysis, x = twig xylem conductance. Numbers sampled are for ψ and leaf conductance; 1-5 trees per species were used at each site for pressure-volume analysis and twig xylem conductance.

Location	Site	Elev. (m)	Species	Properties	No. sampled	Height (m)#
Alluvial Sal	1	540	<i>Shorea robusta</i>	g	5	12
Slope Sal	2	450	<i>S. robusta</i>	g	5	10
Mangoli	3	1320	<i>S. robusta</i>	g, pv, x	5	6
			<i>Pinus roxburghii</i>	pv, x	5	6
Bhowali	4	1760	<i>P. roxburghii</i>		5	7
	5		<i>P. roxburghii</i>		3	10
			<i>Quercus leucotrichophora</i>	g	3	8
			<i>Rhododendron arboreum</i>	g	3	7
	6		<i>Q. leucotrichophora</i>	g	5	13
Kailakhan	7	1930	<i>P. roxburghii</i>		5	15
	8		<i>P. roxburghii</i>	pv, x	5	8
			<i>Q. leucotrichophora</i>	pv, x	5	10
	9		<i>Q. leucotrichophora</i>	g	5	14
St. Xavier's E	10	2130	<i>Q. leucotrichophora</i>	g, pv	5	3
			<i>R. arboreum</i>	g, pv, x	5	3
			<i>Quercus floribunda</i>	g, pv	5	3
			<i>Carpinus viminea</i>	g, pv, x	5	2
St. Xavier's W	11		<i>Q. leucotrichophora</i>	g, pv, x	5	4
			<i>Q. floribunda</i>	g, pv, x	3	5
			<i>Machilus duthiei</i>	g, pv, x	4	6
			<i>Fraxinus micrantha</i>	g, pv, x	3	6
China Peak	12	2140	<i>Q. floribunda</i>	g, pv, x	5	8
			<i>Cupressus torulosa</i>	pv, x	5	7
			<i>Cornus macrophylla</i>	g, pv, x	5	10
	13		<i>Q. leucotrichophora</i>	g, pv	5	11
			<i>C. torulosa</i>	pv	5	15
Pre-Kilbury	14	2310	<i>Q. leucotrichophora</i>	g, pv	5	13
			<i>R. arboreum</i>	g, pv	5	5
			<i>Q. floribunda</i>	g, pv	5	11
Kilbury	15	2260	<i>Q. floribunda</i>	g	5	12
	16		<i>Q. leucotrichophora</i>	g, pv, x	3	4
			<i>R. arboreum</i>	g, pv, x	3	6
			<i>Q. floribunda</i>	g, pv, x	3	8
			<i>C. viminea</i>	g, pv, x	3	11
			<i>M. duthiei</i>	g, pv, x	3	5
			<i>F. micrantha</i>	g, pv, x	3	9
			<i>C. macrophylla</i>	g, pv, x	3	19
			<i>Q. lanata</i>	g, pv, x	3	8

= mean of sampled trees.

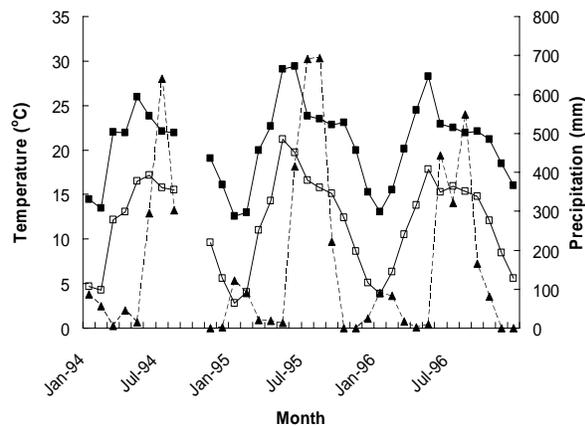


Fig. 1. Precipitation (▲) and temperature (□, ■) at the nearest weather station (Uttar Pradesh State Observatory, 1956 m elevation, 5 km SW of Naini Tal) during 1994-1996. The study began in October, 1994. Values are the monthly precipitation, and the monthly mean of maximum (■) and minimum (□) daily temperatures. No data are available for October and November 1994.

Rainfall in Kumaun varies from 1050-2690 mm annually, concentrated from mid-June to mid-September (Dhar *et al.* 1987), but does not consistently increase with elevation (Singh *et al.* 1994). The 3 calendar years including the study produced a warm, dry premonsoon season in 1995 and a wet one in 1996, as well as contrasting winters (Fig. 1).

Nine sampling locations ranged from 450-2310 m elevation (Table 1). At 16 sites at these nine locations, 1-8 species were measured. Three to five trees per species were selected at each site for measurement of water potential and leaf conductance, and 1-5 per species for pressure-volume analysis and twig xylem conductance. Trees within a stand were selected to be as similar in size among species as feasible (Table 1). Each species was sampled at all study sites where it grew. No species grew across more than 900 m elevation within our sites.

The 11 tree species represent nine plant families: Betulaceae: *Carpinus viminea* Lindley; Cornaceae: *Cornus macrophylla* Wall.; Cupressaceae: *Cupressus torulosa* D. Don; Dipterocarpaceae: *Shorea robusta* Gaertn.; Ericaceae: *Rhododendron arboreum* Smith; Fagaceae: *Quercus floribunda* Lindley ex A. Camus, *Q. lanata* Smith, and *Q. leucotrichophora* A. Camus; Lauraceae: *Machilus duthiei* King;

Oleaceae: *Fraxinus micrantha* Lingelsh.; and Pinaceae: *Pinus roxburghii* Sarg. Nomenclature follows Polunin & Stainton (1984). Species will be referred to by their generic name, except for species of *Quercus*. In tables, species are listed in order from low to high elevation of their lowest occurrence in our plots (Table 1).

Machilus and *Rhododendron* are undercanopy species; others reach the canopy. Mature trees of canopy species are 23-60 m tall, conifers being tallest. Oaks and undercanopy species are sclerophyllous, with specific leaf mass > 130 g m⁻². The oaks (880-970 kg m⁻³) and *Shorea* (800-960 kg m⁻³) have hard, dense wood; *Rhododendron*, *Pinus* and *Cupressus* are lighter (600-700 kg m⁻³) (Jackson 1994). Wood of evergreen angiosperms is generally diffuse-porous or has indistinct rings and vessels ≤ 265 μm diameter.

Leaf longevity of evergreens is about one year (Ralhan *et al.* 1985; Negi & Singh 1992) except for *Cupressus* and *Rhododendron*. All our deciduous species grow at higher elevations and are leafless during the winter and spring. Although *Shorea* lacks leaves for a short period in early summer in some years in some areas, and therefore some authors consider it deciduous, it does not become leafless in our area. Species will be grouped in various ways for discussion: conifers (*Pinus*, *Cupressus*) vs. angiosperms; deciduous (*Carpinus*, *Cornus*, *Fraxinus*) vs. evergreen angiosperms; undercanopy (*Rhododendron*, *Machilus*) vs. canopy trees; *Quercus* (oaks) vs. other genera; and dominant, widespread species (*Shorea*, *Pinus*, *Q. leucotrichophora*, *Rhododendron*, *Q. floribunda*) vs. those of limited importance.

Methods

Water potential (ψ) was sampled during six seasons: *fall*, mid-Sept-mid Nov, after monsoon, with high soil moisture but clear, dry, cooling days; *winter*, mid Nov-mid Jan, after the dry fall, with extended freezing weather at high elevations; *spring*, mid Jan-Feb, with warming temperatures before most new leaf production begins; *early summer*, Mar-Apr, warm, supporting most production of new leaves; *summer*, May-mid June, the hottest season, at the end of the dry months before the monsoon rains, while some leaves are continuing to expand; and the *rainy season*, mid June-mid Sept, hot but wet.

ψ was measured during 12 periods, generally in two years for each season; year 1 = October 1994-September 1995 and year 2 = October 1995-September 1996. A single year (1995) was considered sufficient to describe the rainy season. A third winter sample (December 1996) was required to get two winter data sets at sites 14-16, which were inaccessible due to snowpack in December-February of year 1. Leaf conductance (g_l) was measured for angiosperms except during the rainy season. Samples for pressure-volume analysis (p-v) were collected during four seasons of one year at a given site; a second set of sites was sampled in the second year for widespread species (Table 1). All species were measured for at least one year. Samples for twig xylem conductance measurement were collected during winter, early summer, and the rainy season of one year.

Soil ψ was measured at 60 cm depth in three locations representative of the site, but values cannot be directly related to a given species or tree. Plant ψ was measured at predawn, when tree ψ should be maximal (Pallardy *et al.* 1991), and midday (1300-1400 h), when ψ should be minimal. g_l was measured twice each day, in early morning (during full daylight) and following the midday ψ measurement. Samples for p-v curves and twig xylem conductance were collected after measurement of midday g_l .

Soil ψ was measured with a thermocouple psychrometer (SC-10A sample changer with a NT-3 microvoltmeter, Decagon Devices, Pullman WA USA). Plant ψ was measured for twigs with leaves using a pressure chamber (Model 1000, PMS Instrument Co., Corvallis, OR USA); ψ was calculated as the negative of balance pressure. g_l was measured on the lower (abaxial) side of angiosperm leaves using a diffusion porometer (Model AP-4, Delta-T Devices, Cambridge, UK). P-v curves were developed using a pressure chamber and the free transpiration method (Pallardy *et al.* 1991) for tissue samples rehydrated overnight in the dark in the laboratory; 12-16 measurements taken over 9-10 hours defined each curve. Sample mass was measured after drying at 75°C for 24 hours. Osmotic potentials at full (ψ_{sf}) and zero turgor (ψ_{sz}) and relative water content at zero turgor (RWC_z) were defined by subjectively determining the extent of the linear portion of the p-v curve and following procedures of Pallardy *et*

al. (1991). An index of elasticity (ϵ) was defined as the slope of a linear regression using all non-zero values of pressure potential over RWC, as suggested by Pallardy *et al.* (1991). Curves with plateaus (i.e., no reduction in ψ during the initial loss of RWC) were corrected. We calculated osmotic adjustment as the range of ψ_{sf} values over the seasons (highest – lowest seasonal mean).

Samples for xylem conductance were stored overnight in water. Xylem conductance was measured using gravity flow of a solution of oxalic acid, following suggestions of Sperry *et al.* (1988), Ewers *et al.* (1989), and Cochard & Tyree (1990). Safranin dye infused after measurement of conductance was used to define the percentage of xylem cross-section that was active (% active). Specific conductivity is the conductance per unit of active xylem cross-section; leaf-specific conductivity is the conductance per unit of leaf area supplied by the stem section sampled. Huber value is the ratio of total twig xylem cross-sectional area to the leaf area it supplied.

Before statistical analysis, we tested variables for normality using the Kolmogorov statistic. Variables significantly departing from normality were transformed to produce a normal distribution. Analysis of variance was used to determine significance of differences among species, groups of species, seasons, years, and sites. Means for categories that differed significantly ($P < 0.05$) were separated using Tukey's multiple range test. Comparisons among all species for ψ and g_l were made using site means for each species for each sampling date as the data. Values are presented graphically for individual species and sample dates, and as tables of means by season across both years. Xylem attributes are given as overall means.

Results

Soil water potential

Soil ψ was highly variable; sampling dates differed significantly ($P < 0.0001$) (Fig. 2). Summer and winter means of the two years differed strongly: summer 1, - 3.43 MPa, summer 2, - 1.27; winter 1, - 0.36 MPa; winter 2, - 1.59. Soils were driest in summer and next driest in early summer; other seasons did not differ significantly from the rainy season ($P > 0.05$) (Table 2).

Table 2. Variation in soil water potential (MPa) at 60 cm among five forest types and six seasons. Within the "all types" row, values with the same letters do not differ significantly at $P = 0.05$.

Forest Type	Season					
	Fall	Winter	Spring	Early Summer	Summer	Rainy
Sal	-0.44	-1.19	-0.58	-1.42	-1.81	-0.06
Pine	-0.83	-1.20	-0.55	-1.61	-3.36	-0.76
Oak	-0.81	-1.06	-0.55	-1.43	-3.51	-0.66
Mixed	-0.43	-0.97	-1.05	-1.37	-2.00	-0.34
Cypress	-1.22	-1.26	-0.84	-2.46	-1.79	-0.50
All types	-0.71a	-1.12 ab	-0.68a	-1.57b	-2.60c	-0.48a
<i>P</i> for each season	0.11	0.96	0.18	0.25	0.11	0.45

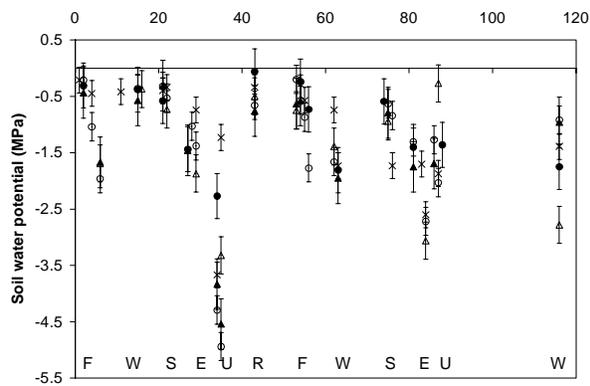


Fig. 2. Soil water potential at 60-cm depth. Each symbol is the mean of three measurements made within a site on that date. Letters on the lower axis designate seasons: F, fall; W, winter; S, spring; E, early summer; U, summer; R, rainy. Symbols represent the types of forest associated with the sites: \blacklozenge = forests with sal (*Shorea robusta*); \blacktriangle = forests of pine (*Pinus roxburghii*) with no angiosperm reproduction; open diamond = forests dominated primarily by oaks (*Quercus leucotrichophora*, *Q. floribunda*, or both); \triangle = forests with significant numbers of winter deciduous tree species; and \blacksquare = forests with cypress (*Cupressus torulosa*).

Plant water potential

Predawn ψ (Fig. 3, Table 3) of evergreen angiosperms did not differ from ψ of deciduous angiosperms (on sites where deciduous species were present) overall or in any season ($P = 0.24$ – 0.98). Deciduous species differed: *Cornus* had high ψ and showed little variation; *Fraxinus* was high in summer; and *Carpinus* had low ψ values during warm, dry seasons. Midday ψ (Fig. 3, Table 4) sometimes differed between evergreen and deciduous angiosperms; the difference was

greatest during early summer (evergreen = -1.65 , deciduous = -1.38 MPa, $P = 0.053$).

Conifer-angiosperm differences varied among species. Predawn ψ of *Pinus* differed significantly from associated angiosperms (all evergreen) only during early summer (*Pinus* = -0.87 MPa, angiosperms = -0.65 , $P = 0.004$); midday values did not differ. Indicators of severity for the driest periods (Table 5), however, show *Pinus*' temperate associates (*Quercus leucotrichophora*, *Rhododendron*) to have lower extreme predawn ψ values and a higher percentage of means < -1.0 MPa. *Pinus*' associate of tropical origin (*Shorea*), in contrast, had the highest ψ of any species. Predawn ψ did not differ between *Cupressus* and co-occurring angiosperm trees, but mean midday values differed (*Cupressus* = -1.62 MPa, angiosperms = -1.33 , $P = 0.027$).

Canopy species of limited importance had lower predawn ψ and a lower $\Delta\psi$ the difference between predawn and midday ψ (-0.85 , 0.52 MPa, respectively) than widespread canopy species (-0.69 , 0.66) ($P = 0.0002$, 0.0003); undercanopy species (-0.74 MPa predawn, 0.58 difference) did not differ from either group of canopy species. Most individual species suffered low water potentials during the year, mostly in the hot, dry months (Fig. 3, Table 5). Winter produced low ψ for four angiosperms at > 2000 m elevation (Tables 3 & 4). Predawn ψ values differed significantly among species ($P < 0.0001$) and sampling dates ($P < 0.0001$). Across all seasons, *Shorea* had higher ψ than other species (Fig. 3). All species except *Shorea* and *Cornus* averaged $\psi < -1.0$ MPa in at least one season (Table 5). Midday ψ varied significantly with species ($P < 0.0001$), season ($P < 0.0001$), and year ($P = 0.0004$) (Fig. 3). *Shorea* usually had the highest midday ψ ; the species

Table 3. Variation in predawn water potential (MPa) among species and seasons. -- = seasons when deciduous species were leafless. Within a column, species with the same a,b,c letter are not significantly different ($P = 0.05$, Tukey's multiple range test). Within the "all species" row, seasons with the same x,y letter are not significantly different.

Species	Season					
	Fall	Winter	Spring*	Early Summer	Summer	Rainy
<i>Shorea</i>	-0.27a	-0.36a	-0.55	-0.52	-0.54	-0.21
<i>Pinus</i>	-0.49ab	-0.64ab	-0.58	-0.87	-1.10	-0.30
<i>Quercus leucotrichophora</i>	-0.53ab	-0.74bc	-0.63	-0.78	-1.20	-0.34
<i>Rhododendron</i>	-0.49ab	-0.93bcd	-0.64	-0.81	-1.25	-0.45
<i>Q. floribunda</i>	-0.75bc	-1.01cd	-0.97	-0.92	-1.14	-0.52
<i>Carpinus!</i>	-0.80bc	--	-0.58	-1.12	-1.36	-0.28
<i>Machilus</i>	-0.56abc	-1.17cd	-0.90	-0.79	-0.69	-0.22
<i>Fraxinus!</i>	--	--	-1.27	-0.85	-1.09	-0.41
<i>Cupressus</i>	-0.79bc	-1.02bcd	-0.59	-0.99	-1.20	-0.46
<i>Cornus!</i>	-0.86c	--	-0.69	-0.71	-0.68	-0.43
<i>Q. lanata</i>	-0.60abc	-1.24bcd	-1.33	-0.96	-1.00	-0.48
All species	-0.60x	-0.85y	-0.75y	-0.83y	-1.06z	-0.37w
<i>P</i> value within season	<0.0001	<0.0001	0.0004	0.24	0.12	0.31

*Significant differences in spring are: *Fraxinus* < *Shorea*, *Pinus*, *Q. leucotrichophora*, and *Rhododendron*.
! Winter-deciduous species

Table 4. Variation in midday water potential (MPa) among species and seasons. -- = seasons when deciduous species were leafless. Within a season, species with the same a,b,c letter are not significantly different ($P = 0.05$, Tukey's multiple range test). Within the "all species" row, seasons with the same x,y letter are not significantly different.

Species	Season					
	Fall*	Winter	Spring	Early Summer#	Summer	Rainy
<i>Shorea</i>	-0.62	-0.64a	-0.94ab	-1.06	-1.15	-0.27
<i>Pinus</i>	-1.13	-1.12ab	-1.20abc	-1.60	-1.84	-0.62
<i>Quercus leucotrichophora</i>	-1.14	-1.29bc	-1.29abc	-1.68	-1.99	-0.53
<i>Rhododendron</i>	-0.93	-1.35bc	-1.22abc	-1.40	-1.77	-0.51
<i>Q. floribunda</i>	-1.23	-1.55bc	-1.43abc	-1.77	-2.00	-0.71
<i>Carpinus!</i>	-0.90	--	-1.05abc	-1.58	-1.94	-0.53
<i>Machilus</i>	-1.06	-1.90c	-1.87c	-1.04	-1.29	-0.39
<i>Fraxinus!</i>	--	--	-1.83c	-1.30	-1.67	-0.53
<i>Cupressus</i>	-1.78	-1.70bc	-1.43abc	-1.94	-1.80	-0.45
<i>Cornus!</i>	-1.26e	--	-0.79a	-1.29	-1.36	-0.42
<i>Q. lanata</i>	-1.19	-1.77bc	-2.01bc	-1.64	-1.64	-0.56
All species	-1.10w	-1.31wx	-1.32x	-1.53y	-1.75z	-0.53v
<i>P</i> value within season	<0.0001	<0.0001	0.0002	0.0009	0.32	0.90

*Fall: Significant differences are: *Cupressus* is < all species except *Cornus* and *Q. lanata*; in addition, *Shorea* is > *Q. leucotrichophora*, *Q. floribunda*, and *Cornus*.

#Early summer: Significant differences are: *Q. floribunda* and *Cupressus* are < *Shorea* and *Machilus*; in addition, *Q. leucotrichophora* < *Shorea*.

! Winter-deciduous species

with lowest ψ varied with season (Table 4). *Machilus*, for example, was low during winter and spring, but among the highest in other seasons. The rainy season was higher than all other

seasons for midday ψ , summer having the lowest values. The daily fluctuation in ψ ($\Delta\psi$) varied significantly among species, seasons, and years (for all factors, $P < 0.0001$) (Fig. 3, Table 6).

Contrasting summers produced different ψ but differing winters did not. During the drier summer 1, mean predawn and midday ψ were lower than in the

wetter summer 2 ($P < 0.0001$) (Fig. 3), and $\Delta\psi$ was larger than in the wetter summer ($P < 0.0003$). Species differed in their responses to the two summers.

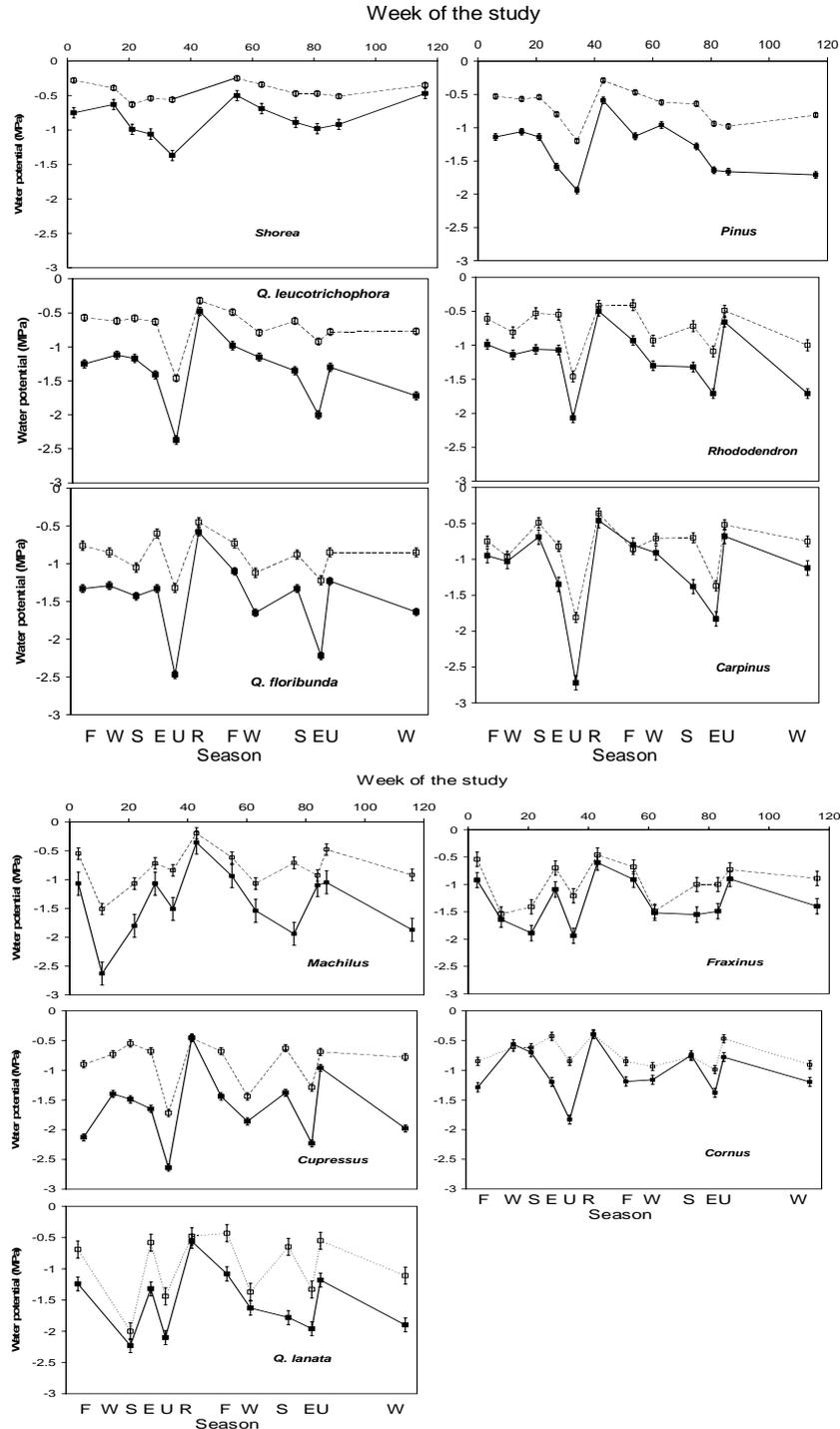


Fig. 3. Predawn (open symbols) and midday (solid symbols) ψ by species. Each value is the mean for one species on one sampling date. Seasons: F, fall; W, winter; S, spring; E, early summer; U, summer; R, rainy.

Table 5. Characteristics of species' predawn ψ that indicate the severity and timing of drought they experienced. "% \leq - 1.0 MPa" is the percent of sample means \leq - 1.0 MPa. Lowest mean values and % of values \leq - 1.0 MPa are based on the set of means for one site at one sampling date. The highest and lowest seasons, and rank of winter, are based on overall seasonal means for all sites and years. Seasons: r = rainy, f = fall, w = winter, s = spring, e = early summer, u = summer.

Species	Lowest mean (MPa)	% \leq - 1.0 MPa	Highest season	Lowest season	Rank of winter#
<i>Shorea</i>	- 0.84	0	r, f	s, e, u	3
<i>Pinus</i>	- 1.71	15	r	u	4
<i>Quercus leucotrichophora</i>	- 2.38	18	r	u	4
<i>Rhododendron</i>	- 2.00	26	r, f	u	5
<i>Q. floribunda</i>	- 1.83	38	r	u	5
<i>Carpinus!</i>	- 1.90	25	r	u	-
<i>Machilus</i>	- 1.51	32	r	w	6
<i>Fraxinus!</i>	- 2.07	46	r, f	w, s	-
<i>Cupressus</i>	- 1.91	29	r	u	5
<i>Cornus!</i>	- 1.14	18	r	f, w	-
<i>Q. lanata</i>	- 2.00	45	r, f	w, s	5

Rank 1 = winter had the highest mean of all seasons, and 6 = winter had the lowest mean of all seasons. Deciduous species were not measured in winter.! Winter-deciduous species

Table 6. Variation in daily change in water potential (MPa) among species and seasons (daily change = predawn ψ - midday ψ). -- = seasons when deciduous species were leafless. Within a season, species with the same a,b,c letter are not significantly different ($P = 0.05$, Tukey's multiple range test). Within the "all species" row, seasons with the same x,y,z letter are not significantly different.

Species	Season					
	Fall	Winter	Spring	Early Summer*	Summer	Rainy
<i>Shorea</i>	0.36ab	0.28a	0.39ab	0.55	0.61	0.06
<i>Pinus</i>	0.64bc	0.48a	0.62ab	0.73	0.73	0.32
<i>Quercus leucotrichophora</i>	0.61bc	0.55a	0.65ab	0.90	0.79	0.19
<i>Rhododendron</i>	0.44abc	0.43a	0.59ab	0.59	0.52	0.06
<i>Q. floribunda</i>	0.47abc	0.54a	0.46ab	0.85	0.85	0.19
<i>Carpinus!</i>	0.10a	--	0.47ab	0.46	0.58	0.25
<i>Machilus</i>	0.50abc	0.73a	0.97b	0.25	0.60	0.17
<i>Fraxinus!</i>	--	--	0.55ab	0.46	0.58	0.13
<i>Cupressus</i>	0.99c	0.68a	0.85ab	0.96	0.60	-0.01
<i>Cornus!</i>	0.40abc	--	0.09a	0.58	0.68	-0.01
<i>Q. lanata</i>	0.59abc	0.52a	0.68ab	0.69	0.65	0.08
All species	0.50xy	0.46x	0.57yz	0.70z	0.70z	0.16w
<i>P</i> value within season	0.001	0.05	0.04	0.0004	0.84	0.60

*Early summer: Significant differences are: *Machilus* < *Q. leucotrichophora*, *Q. floribunda*, *Cupressus*; *Fraxinus* < *Q. leucotrichophora*!. Winter-deciduous species

Leaf conductance

Only for two high elevation oaks did leaf conductance (g_l) differ significantly between morning and afternoon. Therefore, analyses of g_l used mean values ($[\text{morning} + \text{afternoon}]/2$). Leaf conductance varied significantly among species (P

< 0.0001), seasons ($P < 0.0001$), and years ($P = 0.0005$) (Fig. 4, Table 7), but not among any of the species groups for which a contrast was tested. *Shorea* was significantly higher (240 mMol $m^{-2} sec^{-1}$) than other species considering all data, with values substantially higher than other species in

fall, spring, and early summer. *Rhododendron* often had relatively high g_l , and *Carpinus* was often lowest (Fig. 4, Table 7). Overall, g_l was highest during fall and spring, and lowest during

early summer and summer (Table 7). A general decline in g_l of evergreens from fall to summer was clear in year 1, but year 2 and deciduous species showed no clear pattern (Fig. 4).

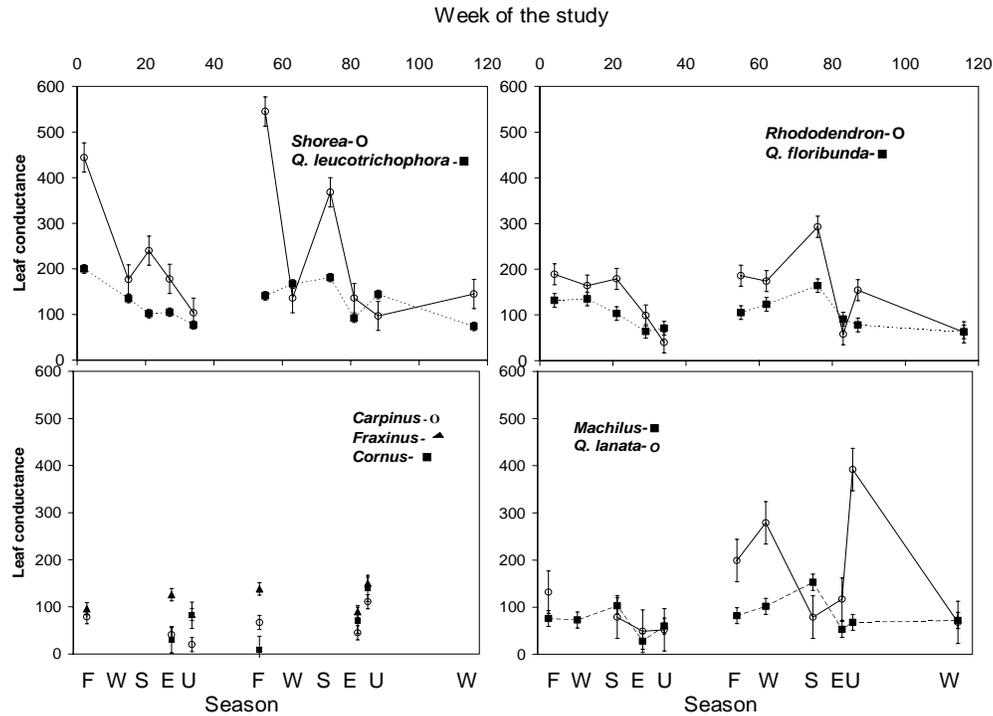


Fig. 4. Mean leaf conductance ($\text{mMol m}^{-2} \text{sec}^{-1}$) by species. Each value is the mean for one species on one sampling date. Seasons: F, fall; W, winter; S, spring; E, early summer; U, summer; R, rainy.

Table 7. Variation in mean leaf conductance (g_l) ($(\text{am} + \text{pm})/2$) ($\text{mMol m}^{-2} \text{sec}^{-1}$) among seasons and species. Within a column, values with the same a,b,c letter are not significantly different ($P = 0.05$, Tukey's multiple range test). Within the "all species" row, seasons with the same x,y,z letter are not significantly different. -- deciduous species lacked leaves during sampling. No measurements were made during the rainy season.

Species	Season				
	Fall	Winter	Spring	Early Summer	Summer *
<i>Shorea</i>	500b	148	308b	157a	101
<i>Quercus leucotrichophora</i>	164a	137	145a	100a	101
<i>Rhododendron</i>	187a	155	222ab	86a	83
<i>Q. floribunda</i>	116a	110	132a	79a	76
<i>Carpinus!</i>	72a	--	--	44a	50
<i>Machilus</i>	88a	90	122a	44a	63
<i>Fraxinus!</i>	--	--	--	61a	101
<i>Cornus!</i>	118a	--	--	93a	119
<i>Q. lanata</i>	155a	174	79a	80a	222
All species	171z	132yz	170z	91x	95xy
<i>P</i> value within season	<0.0001	0.30	<0.0001	0.04	0.05

* In summer, *Q. lanata* was significantly higher than *Q. floribunda* and *Carpinus*.

Osmotic potential

ψ_{sf} differed between conifers and angiosperms (conifers -1.69 MPa, angiosperms -1.86 , $P = 0.038$),

but not among other groups of species. Osmotic potential varied significantly among sampling dates and species ($P < 0.0001$ for both) (Fig. 5, Tables 8-

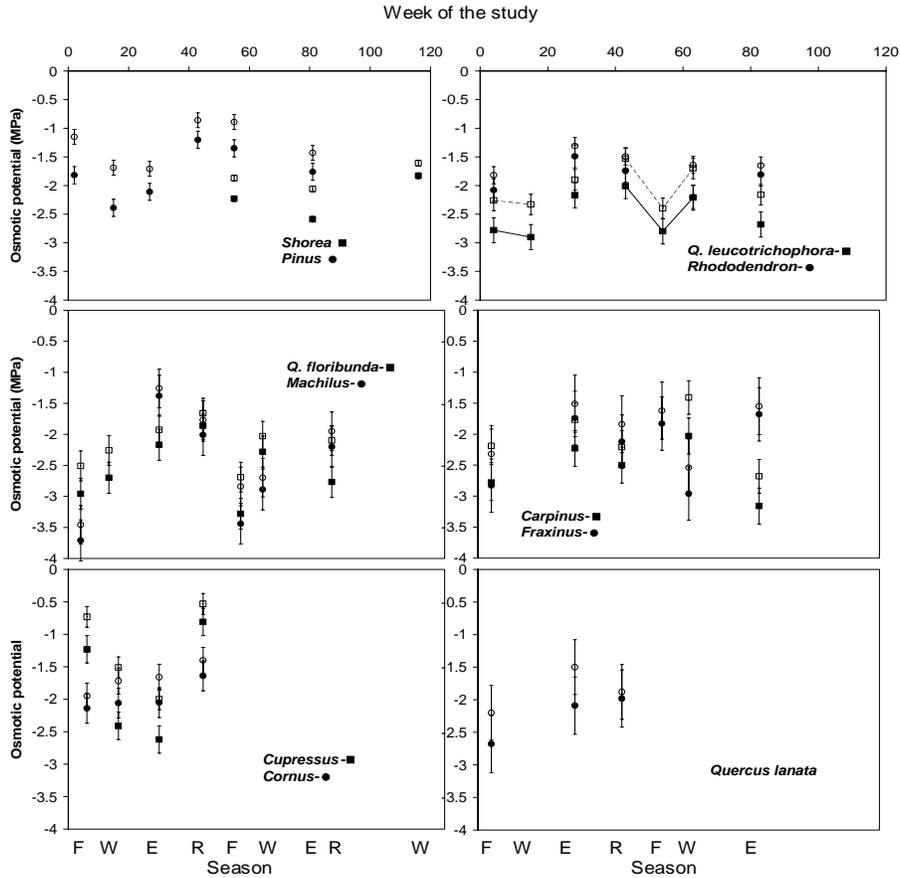


Fig. 5. Osmotic potential (MPa) by species. Each value is the mean for one species on one sampling date. Open symbols are values at full turgor; solid symbols represent zero turgor. Seasons: F, fall; W, winter; S, spring; E, early summer; U, summer; R, rainy.

Table 8. Significance of variation (P -value) among sampling dates in Figs. 5-7 for each species.

Species	ψ_{sf}	ψ_{sz}	ϵ	RWC_z
<i>Shorea</i>	0.41	0.0004	0.02	0.001
<i>Pinus</i>	0.0002	0.0001	0.58	0.06
<i>Q. leucotrichophora</i>	0.005	0.0009	0.18	0.24
<i>Rhododendron</i>	0.04	0.05	0.07	0.09
<i>Q. floribunda</i>	0.02	0.001	0.42	0.09
<i>Carpinus</i>	0.15	0.13	0.12	0.09
<i>Machilus</i>	0.04	0.04	0.003	0.09
<i>Fraxinus</i>	0.37	0.34	0.45	0.43
<i>Cupressus</i>	0.0009	0.0004	0.04	0.007
<i>Cornus</i>	0.18	0.62	0.02	0.02
<i>Q. lanata</i>	0.57	0.61	0.05	0.08
All species	< 0.0001	< 0.0001	< 0.0001	< 0.0001

10), both for ψ_{sf} and ψ_{sz} . ψ_{sf} and ψ_{sz} were closely related: overall, ψ_{sz} (MPa) = - 0.4687 + 0.979 ψ_{sf} (MPa) ($n = 258$, $r^2 = 0.83$, $P < 0.0001$). The two conifers had mean ψ_{sz} (- 1.81 MPa for *Pinus* and - 2.05 MPa for *Cupressus*) (Table 10), significantly higher than that of the angiosperms. The lowest overall means were of *Machilus* (- 2.61 MPa), *Carpinus* (- 2.54 MPa) and two oaks (- 2.52 MPa for *Q. leucotrichophora* and - 2.51 for *Q. floribunda*).

Five individual species (the conifers, two widespread oaks, and *Machilus*) varied significantly with sampling date for both ψ_{sf} and ψ_{sz} (Fig. 5, Table 8); four species (*Q. lanata* and all three deciduous species) did not vary for either measure of ψ_s . ψ_s was highest during the rainy season and lowest during fall (Tables 9, 10). Seasonal values of ψ_{sz} varied similarly to ψ_{sf} , the main exception was that ψ_{sf} of *Shorea* did not vary with season.

Table 9. Variation in osmotic potential at full turgor (MPa) among species and seasons. -- deciduous species lacked leaves during sampling. Species with the same letter within a column did not differ significantly ($P = 0.05$) for that season. All-species values with the same x, y letter do not differ among seasons.

Species	Season			
	Fall	Winter	Early summer	Rainy
<i>Shorea</i> *	-1.87b	-1.61abc	-1.86bcde	-1.58bc
<i>Pinus</i>	-1.15a	-1.51a	-1.57ab	-0.86a
<i>Q. leucotrichophora</i>	-2.30bc	-2.21de	1.96ce	-1.53b
<i>Rhododendron</i>	-1.87b	-1.85abcd	-1.40a	-1.49b
<i>Q. floribunda</i>	-2.60cd	-2.12bcde	-2.00ce	-1.66bc
<i>Carpinus</i> !	-2.07b	--	-2.22e	-2.21c
<i>Machilus</i>	-3.15d	-2.70e	-1.72abcde	-1.77bc
<i>Fraxinus</i> !	--	--	-1.53abd	-1.84bc
<i>Cupressus</i> *	-0.73a	-1.58ab	-2.00cde	-0.53a
<i>Cornus</i> !	-1.95b	--	-1.66abcd	-1.40ab
<i>Q. lanata</i> *	-2.21bc	-1.76abcde	-1.49abcd	-1.88bc
All species	-2.04y	-1.89y	-1.80y	-1.51x
<i>P</i> value within season	<0.0001	0.0003	0.0005	0.002

! Winter-deciduous species * Data available for one year only.

Table 10. Variation in osmotic potential at zero turgor (MPa) among species and seasons. -- deciduous species lacked leaves during sampling. Species with the same letter within a column do not differ significantly ($P = 0.05$) for that season. All-species values with the same x, y letter do not differ among seasons.

Species	Season			
	Fall	Winter	Early summer	Rainy
<i>Shorea</i> *	-2.23bcd	-1.83a	-2.59cd	-2.04cd
<i>Pinus</i>	-1.75ab	-2.27abc	-1.93a	-1.20ab
<i>Q. leucotrichophora</i>	-2.80de	-2.81d	-2.29bcd	-2.01cd
<i>Rhododendron</i>	-2.09bc	-2.20abc	-1.58a	-1.74bc
<i>Q. floribunda</i>	-3.04ef	-2.44abcd	-2.41bcd	-1.86c
<i>Carpinus</i> !	-2.75cde	--	-2.69d	-2.50d
<i>Machilus</i>	-3.58f	-2.89cd	-1.92ab	-2.01cd
<i>Fraxinus</i> !	--	--	-1.71a	-2.12cd
<i>Cupressus</i> *	-1.23a	-2.43abcd	-2.62cd	-0.81a
<i>Cornus</i> !	-2.14bc	--	-2.05abc	-1.64abc
<i>Q. lanata</i> *	-2.68cde	-2.33abcd	-2.09abcd	-1.98bcd
All species	-2.50z	-2.41z	-2.18y	-1.86x
<i>P</i> value within season	<0.0001	0.004	<0.0001	0.002

! Winter-deciduous species * Data available for one year only.

Cupressus (1.47 MPa) and *Machilus* (1.43) showed the greatest osmotic adjustment (defined here as the difference between the lowest and highest seasonal values of ψ_{st}) (Fig. 5, Table 9). *Carpinus* showed the least (0.15 MPa). Osmotic

adjustment occurred primarily from the rainy to fall season; seasonal mean ψ_{st} declined 0.53 MPa then, but rose 0.15 MPa from fall to winter, 0.09 MPa from winter to early summer, and 0.29 MPa from early summer to the rainy season (Table 9).

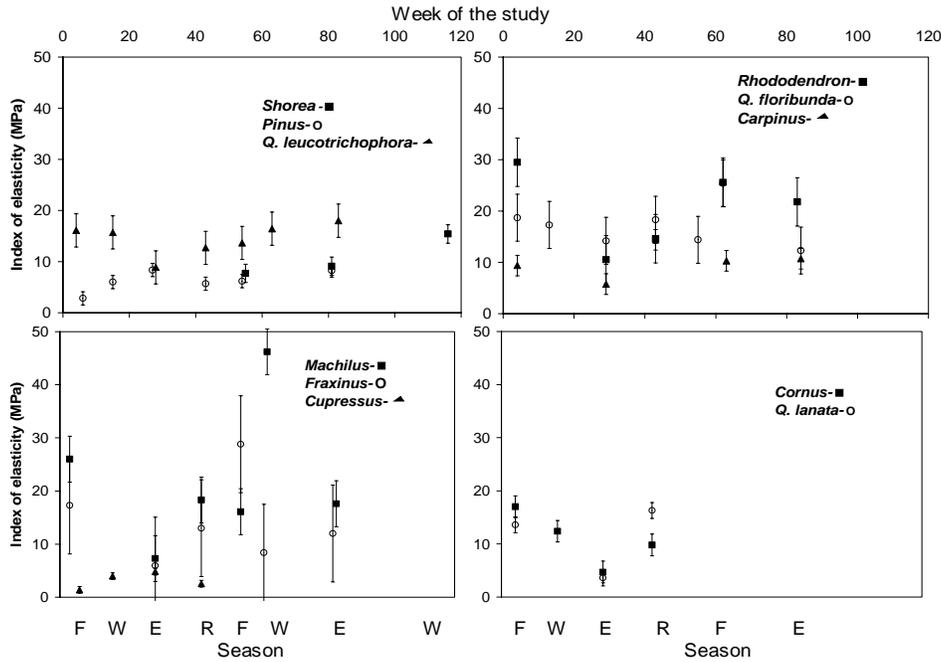


Fig. 6. Index of elasticity (ϵ) (MPa) by species. Each value is the mean for one species on one sampling date. Seasons: F, fall; W, winter; S, spring; E, early summer; U, summer; R, rainy.

Table 11. Variation in index of tissue elasticity (MPa) among species and seasons. -- deciduous species lacked leaves during sampling. Species with the same a, b, c letter within a column do not differ significantly ($P = 0.05$) for that season. All-species values with the same x, y letter do not differ among seasons.

Species	Season			
	Fall	Winter	Early summer	Rainy
<i>Shorea</i> *	7.7ab	15.4cd	8.7	9.9
<i>Pinus</i>	5.2a	6.2ab	8.3	5.7
<i>Q. leucotrichophora</i>	15.9cd	15.1c	11.0	12.7
<i>Rhododendron</i>	27.9e	25.6e	13.7	14.6
<i>Q. floribunda</i>	17.2d	21.9de	13.4	18.3
<i>Carpinus</i> !	9.4abc	--	8.2	14.4
<i>Machilus</i>	21.1de	46.2f	14.2	18.3
<i>Fraxinus</i> !	--	--	9.0	13.0
<i>Cupressus</i> *	1.4a	4.4a	4.8	2.6
<i>Cornus</i> !	17.0bcd	--	4.7	9.8
<i>Q. lanata</i> *	13.5bcd	9.2abc	3.6	16.3
All species	14.5y	14.7y	10.1x	13.1xy
<i>P</i> value within season	<0.0001	<0.0001	0.46	0.08

! Winter deciduous species * Data available for one year only.

The two conifers showed the largest osmotic amplitude (OA) (i.e., the difference between ψ_{sf} and ψ_{sz}) (0.66 MPa for *Cupressus* and 0.54 for *Pinus*); in contrast, undercanopy species had the smallest (0.28 and 0.25 MPa for *Machilus* and *Rhododendron*, respectively). Across all species and sites, OA increased with cooling temperature; the winter and fall mean values (0.54, 0.45 MPa, respectively) were significantly greater than during the rainy season (0.32 MPa). No contrasts among species groups were significant for OA.

Index of elasticity

Conifers had lower ϵ (and thus higher tissue elasticity) ($\epsilon = 4.8$ MPa, $P = 0.003$) than angiosperms (14.7), and widespread species had higher elasticity ($\epsilon = 11.3$ MPa, $P = 0.003$) than those with limited importance (14.0) (Fig. 6, Table 11). The index of elasticity (ϵ) varied significantly among species and among sampling dates for four species (Fig. 6, Table 8). The early summer mean ϵ was significantly lower than means of fall and winter (Table 11). Seasonal patterns of ϵ varied among species (Fig. 6, Table

11); patterns of the two conifers were similar, but there was little consistency among angiosperms. The mean ϵ was significantly higher for *Machilus* (24.2 MPa) than for all other species except *Rhododendron* (20.2 MPa).

Relative water content at zero turgor

Species with wide distribution had significantly lower RWC_z (0.84, $P = 0.0007$) than those of limited distribution (0.86); other contrasts between species groups were not significant. RWC_z varied significantly among species ($P < 0.0001$) (Fig. 7) and among sampling dates for three species. The early summer mean of all species was lower than the other three seasons (Table 12). *Rhododendron* and *Machilus*, undercanopy evergreens, had higher RWC_z than seven other species; conifers, *Carpinus*, and *Q. lanata* had the lowest RWC_z (Table 12).

Conductance of twig xylem

Groups of species differed for all twig conductance variables (Table 13):

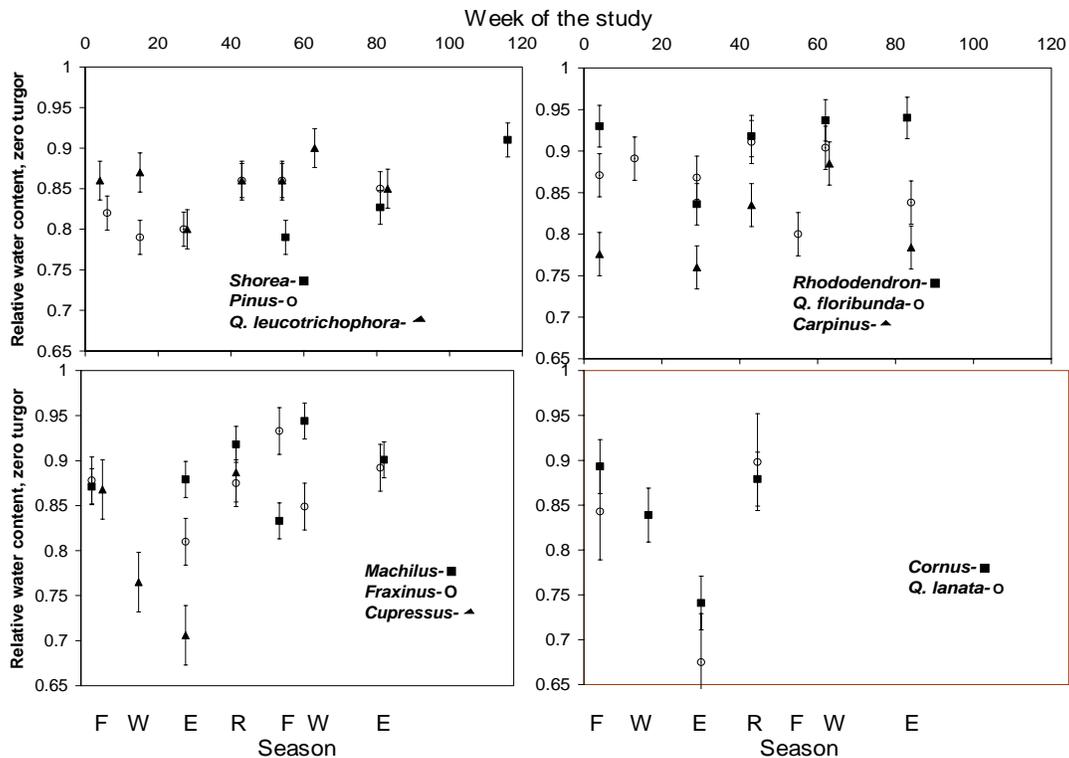


Fig. 7. Relative water content at zero turgor by species. Each value is the mean for one species on one sampling date. Seasons: F, fall; W, winter; S, spring; E, early summer; U, summer; R, rainy.

Table 12. Variation in relative water content at zero turgor among species and seasons. --deciduous species lacked leaves during sampling. Species with the same letter within a column do not differ significantly ($P = 0.05$) for that season. All-species values with the same letter do not differ among seasons.

Species	Season			
	Fall	Winter	Early summer	Rainy
<i>Shorea</i> *	0.789ab	0.909cde	0.827bcde	0.855
<i>Pinus</i>	0.838abc	0.802ab	0.825bcde	0.854
<i>Q. leucotrichophora</i>	0.853c	0.862c	0.810bcd	0.869
<i>Rhododendron</i>	0.925d	0.934e	0.866de	0.918
<i>Q. floribunda</i>	0.850bc	0.909de	0.856de	0.910
<i>Carpinus</i> !	0.786a	--	0.772abc	0.835
<i>Machilus</i>	0.852abcd	0.945e	0.893e	0.918
<i>Fraxinus</i> !	--	--	0.851cde	0.875
<i>Cupressus</i> *	0.868abcd	0.765a	0.706a	0.887
<i>Cornus</i> !	0.893cd	--	0.741ab	0.879
<i>Q. lanata</i> *	0.843abc	0.835abcd	0.675a	0.898
All species	0.852y	0.861y	0.817x	0.879y
<i>P</i> value within season	0.0008	<0.0001	0.003	0.15

! Winter-deciduous species * Data available for one year only.

Table 13. Mean values for parameters related to twig xylem conductance. Active % is the percentage of xylem cross-section that transmitted dye; Specific Conductivity is the hydraulic conductance per unit of active xylem cross-section ($\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$); Huber value is the ratio of total xylem cross-section to leaf area; and Leaf-specific Conductivity is the hydraulic conductance per unit leaf area ($\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$). Species with the same letter within a column do not differ significantly ($P = 0.05$).

Species	Active %	Specific Conductivity	Huber Value ($\times 10^{-4}$)	Leaf-specific Conductivity ($\times 10^{-4}$)
<i>Shorea</i>	65d	1.98a	3.82ab	5.08bcd
<i>Pinus</i>	65d	0.84a	4.87a	1.72a
<i>Q. leucotrichophora</i>	43b	1.00a	6.33cd	2.48bc
<i>Rhododendron</i>	38ab	1.06a	7.61d	1.58bcd
<i>Q. floribunda</i>	46bc	0.81a	26.4d	7.11cd
<i>Carpinus</i> !	35ab	5.60b	4.59bcd	7.70cd
<i>Machilus</i>	29a	0.66a	9.35cd	0.75a
<i>Fraxinus</i> !	37ab	2.33a	4.99abcd	4.29abcd
<i>Cupressus</i>	43ab	0.98a	ND	ND
<i>Cornus</i> !	57cd	1.58a	17.52d	17.8d
<i>Q. lanata</i>	37ab	2.61ab	2.26abc	0.51ab

! Winter-deciduous species, ND = no available data

- Canopy species had higher values than understory species for active % of twig xylem (49, 33, respectively);
- Deciduous species were higher than evergreens for specific conductivity ($3.17 \text{ kg m}^{-1} \text{ s}^{-1} \text{MPa}^{-1}$, 1.21 , respectively) and leaf-specific conductivity ($10.88 \times 10^{-4} \text{ kg m}^{-1} \text{ s}^{-1} \text{MPa}^{-1}$, 3.65×10^{-4} , respectively);
- Oaks were higher than non-oaks for Huber value (i.e., more xylem cross-section per unit leaf area) (13.09×10^{-4} , 8.69×10^{-4} , respectively) and leaf-specific conductivity ($4.29 \times 10^{-4} \text{ kg m}^{-1} \text{ s}^{-1} \text{MPa}^{-1}$, 4.00×10^{-4} , respectively); and,
- Conifers differed from angiosperms in active % (conifer 59, angiosperm 45), Huber value (conifer 5.8×10^{-4} , angiosperm 10.8×10^{-4}), and leaf-specific conductivity (conifer, 2.4×10^{-4} , angiosperm $4.8 \times 10^{-4} \text{ kg m}^{-1} \text{ s}^{-1} \text{MPa}^{-1}$). Species differed significantly ($P < 0.0001$) for all twig xylem properties (Table 13). Only Huber value varied significantly among seasons across all

species ($P = 0.011$), with the rainy season significantly lower than winter and early summer.

Changes in water relations associated with leaf production

ψ declined significantly before leaf initiation in both years for *Pinus*, but no other significant changes in ψ occurred before the usual season of peak leaf formation. Leaf-specific xylem conductivity was highest in early summer, the major season of leaf expansion, for four species (*Cornus*, *Pinus*, *Q. leucotrichophora*, *Rhododendron*).

Correlations of water relations properties with elevation

Some attributes varied significantly ($P < 0.05$) with elevation, although no relationship was strong. Soil ψ at 60 cm declined as elevation increased ($r = -0.20$). Overall predawn ψ , midday ψ and mean g_i also declined as elevation increased ($r = -0.30, -0.21, -0.36$, respectively). Among twig conductance attributes, active % declined with elevation ($r = -0.37$), while Huber value increased ($r = 0.35$). Results from pressure-volume analysis were usually not related to elevation.

Water relations characteristics of species groups

Some species groups based on leaf form, phenology and distribution could be distinguished by their water relations properties (Table 14), as mentioned above. Conifers had high elasticity

(i.e., low ϵ), high ψ_{sf} , and high active % of xylem, but low Huber value and leaf-specific xylem conductivity. Oaks had higher Huber values and leaf-specific xylem conductivity than other genera. Deciduous angiosperms displayed higher xylem conductance than evergreen angiosperms. *Quercus lanata*, however, often had properties more like deciduous species than like other evergreens. The widely-distributed *Pinus*, *Q. floribunda*, *Q. leucotrichophora*, *Rhododendron*, and *Shorea* had lower tissue elasticity and higher RWC_z than less important species. Undercanopy species had lower % active xylem than canopy species.

Discussion

Severity of water deficits in central Himalayan trees

We can judge the severity of drought by the minimal level of ψ . The best indicator may be the most severe site mean of predawn ψ for a species for any sampling date (Table 5). Data from a single year or season would distort the relative severity of ψ among our species, as it would for other forests (e.g., Griffin 1973; Zobel *et al.* 1976; Hinckley *et al.* 1979). A second indicator of drought is how long trees were subjected to limited moisture, here (Table 5) indicated by the percentage of sampling date x site combinations when predawn $\psi < -1$ MPa. This criterion ranks species differently than their lowest ψ value; in particular, *Q. leucotrichophora*, with the lowest ψ ,

Table 14. Characteristics that differentiate species groups ($P < 0.05$), based on comparisons of means for all sites and sample dates. H = the higher group of each pair that differs for that characteristic, L = lower. Cells with no significant differences are blank. Leaf conductance did not distinguish any species groups.

Characteristic	Species group contrast				
	Conifer-Angiosperm	Oaks-Others	Evergreen- Deciduous Angiosperms	Dominant- Less Important	Canopy- Undercanopy
Osmotic potential	H/L				
Elasticity	H/L			H/L	
RWC _z				L/H	
Huber value	L/H	H/L			
% Active xylem	H/L				H/L
Specific conductance of xylem			L/H		
Leaf-specific xylem conductance	L/H	H/L	L/H		

is among the 4 species suffering the least stress by this index. Even though both measures indicate substantial moisture deficit at some season for most species (Table 5), only in *Cupressus* in summer did mid-day ψ repeatedly approach turgor loss (ψ_{sz}).

Species dominating higher elevation communities with more canopy tree species had more severe ψ than species from low elevation, warm sites (*Shorea*, *Pinus*); this pattern also occurred from 1400-2300 m in Nepal (Poudyal *et al.* 2004), but is opposite that in some temperate areas (Zobel *et al.* 2001b). Our two sample years underestimated the potential for moisture stress in this region. The very severe 1999 drought produced predawn ψ for *Q. floribunda* of -5.5 MPa (Singh *et al.* 2000), well below extremes reported during our and other studies near Naini Tal (Dhaila 1991; Garkoti *et al.* 2000, 2003; Zobel *et al.* 1995).

Seasonal patterns of osmotic potential and osmotic adjustment

Osmotic adjustment occurs when ψ_{sf} declines (Ritchie & Shula 1984). Our species had seasonal changes of ψ_{sf} averaging from 0.15 to 1.47 MPa. Adjustment was small for deciduous species, *Shorea*, and *Rhododendron* (<0.6 MPa), intermediate for pine and oaks (0.7-0.9), and large for *Machilus* and *Cupressus* (> 1.4). Most adjustment was from the rainy season to fall, when ψ_s declined in nine species (Table 9), even though predawn ψ remained high, -0.5 to -0.8 MPa, and mid-day ψ was well above turgor loss. Osmotic adjustment depends to a great extent on photosynthesis to supply compatible solutes (Kramer & Boyer 1995). After the monsoon, days are bright, soils moist, and temperature still warm. As fall progresses, soils dry, temperatures decline, and photosynthesis is suppressed, which may curtail osmotic adjustment in winter and spring. Because ψ_{sf} decreased from fall to winter for only the two conifers (Table 9), the fall decline is unlikely to be related to cold acclimation alone.

This pronounced osmotic adjustment when drought was mild should ensure that soil water remains available to maintain fall photosynthesis (R. Thadani & S.P. Singh, unpublished data). The advantage of osmotic adjustment at high ψ would depend on the cost of compatible solutes compared to the carbon gain due to increased water

availability during drought. The metabolic cost appears to be small (Kramer & Boyer 1995).

The relationship among growth, phenology, and osmotic adjustment is variable among dry-tropical (Eamus & Prior 2001) and temperate (Zobel 1996) tree species. Within dry-tropical species, osmotic adjustment was clearly related to the reduction in predawn ψ between the wet and dry seasons (Eamus & Prior 2001), a relationship that did not occur either within all our species or within the evergreens alone. The three deciduous species showed the opposite trend, with more osmotic adjustment when seasonal change in ψ was small.

In a climate with three months of super-abundant water and long, but not severe, drought, osmotic adjustment gives an advantage to species with about one year leaf longevity, like our evergreens (except *Rhododendron* and *Cupressus*). Such species can fix carbon throughout the year and renew their canopy in time to maximize carbon gain during favorable monsoon conditions. In contrast, deciduous species fix little carbon during much of the drought, while evergreen species with leaf longevity > 1 year (*Cupressus* and *Rhododendron* in our study) can fix carbon throughout the year, but their old leaves can take less advantage of the highly productive monsoon months. Some Himalayan evergreen angiosperms suffer considerable leaf damage during the monsoon (Zobel *et al.* 1995, Poudyal *et al.* 2004), making long leaf life of questionable value.

Species that avoid drought by deep rooting or effective water transport often adjust osmotically less than shallow-rooted trees (Abrams 1990). Among our dominant oaks, the shallow-rooted *Q. floribunda* adjusted more than deep-rooted *Q. leucotrichophora* (average = 0.94, 0.77 MPa, respectively). The deep-rooted *Shorea* adjusted little (0.29 MPa).

Tissue elasticity

Niinemets (2001) concluded that changes in ϵ are more significant for adaptation to drought than is osmotic adjustment. However, the role of elasticity in turgor maintenance is not well-defined (Clifford *et al.* 1998, Niinemets 2001). Either low or high elasticity might benefit plant performance, but in different situations. Elastic walls help to maintain turgor during water loss; stiff walls lead to faster reduction of ψ as water is lost, which

increases water uptake and maintains cell volume, thus avoiding toxic concentration of cell solutes (Kramer & Boyer 1995).

Patterns in seasonal change of ϵ varied (Table 11). For all angiosperms, ϵ was lowest in early summer when leaves were young, probably reflecting growing tissue with thin, elastic cell walls (Tyree & Karamanos 1981); the increase after early summer may reflect tissue maturation. High early summer tissue elasticity may enable trees to withstand large changes in cell volume during the late dry season and to maintain higher turgor during leaf development. Because their tissue elasticity declined from early summer to fall (i.e., ϵ rose), our angiosperms appear to maintain turgor during fall and winter droughts primarily by adjusting osmotically. Thus, as soil dries in fall, low elasticity and low ψ_s act together to maintain a steep gradient for water extraction without producing a large decrease in RWC (Abrams 1990).

Their overall high tissue elasticity distinguished our conifers from angiosperms (Table 11). High tissue elasticity of conifers is also reported elsewhere (Anderson & Helms 1994; Bahari *et al.* 1985; Zobel 1996; Zobel *et al.* 2001c, but not by Davis 2005). In contrast to angiosperms, ϵ of conifers was highest in early summer and lowest in fall (Table 11); arguments for the adaptive significance of the pattern for angiosperms do not apply.

Water relations properties of species groups

No single characteristic or related group of characters distinguished among all groups of species that were based on properties other than water relations (Table 14). Groups differed more consistently in twig xylem conductance and tissue elasticity than in ψ_s , as Eamus & Prior (2001) found for evergreen *versus* deciduous dry tropical trees. Elasticity and xylem conductance are measured less frequently than ψ_s , but they are better related to both ecological behavior and phylogenetic origin of our species.

In many situations, little explanation of ecological behavior is provided by p-v analysis alone (Bannister 1986; Duhme & Hinckley 1992; Kubiske & Abrams 1994; Zobel 1996). When xylem properties have also been studied, explanation of species' behavior has improved, both using xylem conductance (Davis 2005; Eamus & Prior 2001; Lo

Gullo & Salleo 1988) and water storage capacity (Borchert 1994b). Even though our xylem conductance data lacked some seasons in which xylem properties may be important, our sample numbers were often small, and our values variable, xylem conductance differentiated four pairs of species groups effectively. Although we lack xylem-water content data, none of our species have the low wood density that allows high wood water content (Borchert 1994b; Santiago *et al.* 2004). Wider study of xylem properties across habitats, seasons, and species should substantially aid comparative interpretation of species behavior, as it has for phenology (Wang *et al.* 1992), and for species in a moister area of the Himalaya (Poudyal *et al.* 2003).

Our evergreen angiosperms had lower xylem conductance than our winter-deciduous species (Table 14), and had a smaller wet-dry season decline in ψ (Fig. 3), similar to dry tropical species (Eamus & Prior 2001). The most successful canopy species, such as *Q. leucotrichophora*, a dominant or co-dominant at 1200 - > 2400 m, had few extremes in any characteristic. Such lack of extremes also occurred in the dominant temperate conifers of western Oregon (Davis 2005). Undercanopy species, *Rhododendron* and *Machilus*, had less active xylem than canopy trees. Their tissue was never very elastic (Table 11). These properties may exclude success outside their usual sheltered position beneath a forest canopy.

Our species with the highest ψ , *Shorea*, *Pinus*, and *Cornus*, had significantly higher % active twig xylem and leaf conductance than others (Tables 7 & 13); both properties may result from high ψ , rather than causing it. The dominance of *Shorea* and *Pinus* in the hot climates of low elevations and on apparently dry topography, and the very high leaf conductance of *Shorea*, suggest that they are well-adapted to drought, rather than consistently growing with moist soil. The only g_l values available for *Pinus*, measured during fall with a different porometer (Zobel *et al.* 2001a), showed a mean of 60 mMol m⁻² s⁻¹, lower than most seasonal values for angiosperms (Table 7). *Cornus*, also with high ψ , grows only > 2000 m, where ψ of other trees is often lower.

Comparison with other tree systems

Compilations of water relations attributes from literature and studies of multiple species (Abrams 1988; Borchert 1994a; Davis 2005; Duhme & Hinckley 1992; Eamus & Prior 2001; Franco 1998; Griffin 1973; Medina & Francisco 1994; Poudyal *et al.* 2003, 2004; Rambal 1992; Zobel 1996; Zobel *et al.* 2001b) allow us to compare the Himalayan species to trees from similar thermal climates elsewhere. As for other ecologically significant attributes (Zobel & Singh 1997) in this monsoon climate, Himalayan trees sometimes differed from similar species elsewhere, especially in osmotic adjustment and tissue elasticity.

Predawn ψ in the low elevation, dense *Shorea* forests was not severe, with levels more similar to tropical savanna than to tropical dry forest. Our conifers had higher ψ than related species, and warm-temperate evergreen angiosperms had predawn ψ values much less severe than oaks in Mediterranean climates. While cool-temperate evergreens had ψ representative of similar forests in North America, our co-occurring deciduous species displayed lower ψ . Our trees suffered lower ψ than the same species farther east in the Himalaya, where the dry season is shorter, even compared to the extreme drought year of 1999 (Poudyal *et al.* 2004). It is worth noting, however, that uncertainty about classification of oaks complicates our comparisons with work in central Nepal; taxonomists there differ in their classification of the major temperate oak species, some calling it *Q. leucotrichophora*, others (including Poudyal *et al.* 2004) *Q. lanata*.

Osmotic potentials of Himalayan trees were not usually extreme, at low elevations again like savanna trees rather than tropical dry forest. Cool temperate species had lower ψ_{st} than most North American species, but they were less extreme than in Mediterranean climates. Osmotic adjustment, however, showed a variable pattern: at low elevations it was higher than savanna trees but less than most in dry forest; for warm-temperate species, adjustment was similar to Mediterranean forests; but for cool temperate species, both evergreen and deciduous, osmotic adjustment was as great or greater than values measured elsewhere.

Based on minimal and maximal values of ϵ among temperate species, our two conifers had

more elastic tissue and less capacity to develop stiff tissue than other published values. In contrast, most Himalayan angiosperms had less capacity to develop highly elastic tissue, and half the species had their maximal elasticity less than did species measured elsewhere.

Huber values (ratio of xylem area to leaf area) were comparatively high for the upper elevation evergreen angiosperms; specific conductivity of active xylem was below to within the range of literature values for evergreens; leaf-specific xylem conductivity was low for undercanopy species and *Q. lanata*, and high for the dominant *Q. floribunda*. Other values were within the ranges published for the appropriate forest type.

To summarize, compared to similar systems elsewhere, our angiosperms suffered only moderate to mild water stress; osmotic potentials were moderate, but osmotic adjustment was high in temperate forests; and our species had relatively inelastic tissue. Conifers, in contrast, maintained elastic tissue with high osmotic potential.

Adaptation to the Himalayan environment

Tree adaptation to the monsoon climate of the Himalaya requires survival of a dry season that is long (usually October to May) but usually not severe; providing turgor for leaf development near the end of the drought; and producing leaves that take maximal advantage of the warm, wet monsoon season. We measured no particular osmotic adjustment or rise in water potential before leafing, in contrast to the rise in water potential during leafing reported farther east in the Himalaya by Poudyal *et al.* (2004); their more frequent measurements and simultaneous phenological assessment on their study trees allowed a more precise judgement than we could make. Leaf conductance was often low during leafing in our trees; likewise, new and aging leaves showed reduced g_i in Nepal (Poudyal *et al.* 2004). The high elasticity of soft, developing leaves should help to maintain their turgor before the monsoon. Transpirational demand during leafing may be reduced by leaf loss that begins well before new leaf expansion, a short period of leaflessness in some years by otherwise evergreen species (Ralhan *et al.* 1985, Negi & Singh 1992, Poudyal *et al.* 2004), or completion of leaf expansion during the monsoon, by *Pinus* (Zobel *et al.* 1995) and one

Quercus sp. (Poudyal *et al.* 2004). Then, all species have fresh leaf tissue available during the warm, wet monsoon season. Substantial post-monsoon osmotic adjustment with a reduction in tissue elasticity should improve water uptake, allowing our trees to extend their season of high photosynthesis into the sunny but dry autumn.

Trees must also be fit for their elevation and local habitat, varying from tropical to cool-temperate, and rocky ridges to seepages. Specific properties may allow trees to succeed widely or limit them to certain habitats. The low-elevation *Shorea* and *Pinus*, with high water potentials, have the highest % of xylem active and are known to be deeply rooted (Troup 1921). *Machilus* in particular differs from other species, and is limited to the undercanopy in high-elevation locations with seepage, as described for members of the Lauraceae elsewhere (Losch 1993). A further distinction is between canopy and undercanopy evergreen angiosperms: *Rhododendron* and *Machilus*, below the canopy, have low tissue elasticity and have less active xylem than canopy species.

We lack much information that would help us to understand Himalayan tree adaptation, important examples being the extremes of rooting depth and the availability of water at depth (emphasized by Eamus & Prior 2001), which probably vary between upper and lower slopes and among rock types. For example, *Shorea* maintains high water potentials despite its very high leaf conductance, even without great xylem conductance or extreme elastic or osmotic properties; perhaps its deep rooting (Troup 1921) and position at the base of the Himalaya near where water outcrops can explain its behavior. Details of wood anatomy and timing of vessel development are sparse or absent. In addition, of course, use of resources besides water varies among Himalayan trees (Singh & Singh 1987, 1992; Zobel & Singh 1997) and may influence some species' success more than water does.

Uncertainty and interpretation of our water relations data

Interpretation of species distribution and importance using our data is subject to some limitations not already discussed:

1. Species distribution and importance are often determined at the seedling stage; we

studied larger trees. Trees of different size differed for three of our species, seedlings having lower ψ than large trees for *Q. floribunda* and *Shorea* (Garkoti *et al.* 2000, 2003); also, leaf types and tree sizes differed in leaf conductance in *Pinus* (Zobel *et al.* 2001a).

2. The aspect of water relations that limits tree survival may vary among species, sites, and years. Some characteristics may be expressed only periodically; for example, some oak populations delay leafing during severe drought (Singh *et al.* 2000).
3. Soil ψ varied differently from tree ψ (Zobel *et al.* 2001b). Soil ψ was measured at 60 cm depth, probably well above the depth from which our trees can extract water.
4. Rooting depth and root growth patterns differ among our species (Troup 1921; Usman *et al.* 1999; S.P. Singh & G.C. Pathak, unpublished data), although details are unavailable for many species. We used only the most general characterization of rooting of a few important species in our interpretations.
5. Some characteristics that are most directly interpretable, according to theory, were less well correlated with species behavior than characteristics for which interpretation is more obscure; examples include the stronger relationships with active % of xylem than with measured xylem conductivity, and with RWC_z than with ψ_s . Perhaps we lack understanding of how our measurements relate to those properties that are really critical to the plant.
6. Our data result from interaction of genotype and environment; species differences might be greater, or less, in a study designed to show genetic differences alone.

Despite such restrictions on interpretation, we developed a description of water relations for species and groups of species that adds substantially to our understanding of the distribution of trees in the central Himalaya. Our extensive sampling in natural conditions, using five seasons replicated over two years, ten species sampled at > 1 site, and characteristics associated with water supply, water loss, and maintenance

of turgor at a given water supply, helped to provide interpretable data. We also showed that many properties are not clearly predictable from the species' morphology, phenology, or anatomy. We believe that a multi-specific, multi-character analysis is necessary to interpret those ecological responses to water availability that affect species importance and distribution.

Conclusions

Predawn ψ became significantly low for most species at some season, the exceptions being the tropical evergreen *Shorea robusta* and the temperate deciduous *Cornus macrophylla*. The lowest ψ reached in our study, however, was not particularly severe, compared to trees in other ecosystems and climatic zones, or to a subsequent drought year in this region. Four high elevation angiosperms reached their lowest ψ in winter; other species usually were lowest in summer. Among our 11 species, we found few overall differences in ψ associated with growth form.

The most common large osmotic adjustment occurred between the rainy season and fall, despite moist soil and warm temperatures. This characteristic feature of some central Himalayan trees should enable them to function more effectively during the long but mild drought. Conifers had higher osmotic potential, higher osmotic amplitude, higher tissue elasticity, more active xylem, but lower xylem conductance than other growth forms. Deciduous species had higher xylem conductance than evergreen angiosperms, and often behaved differently from each other, showing extreme values for some properties. The most important species had higher elasticity and lower relative water content than less widely-distributed species. Understanding the contribution of water relations properties to adaptation will require species-by-species interpretation of information on at least tissue elasticity, xylem conductance, ratio of xylem to leaf area, leaf conductance, and osmotic adjustment.

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