

Leaf Conductance of Primary and Mature Leaves of *Pinus roxburghii*: A Comparison

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We used a null-balance porometer to measure leaf conductance of mature and primary leaves of natural seedlings, saplings, and trees of *Pinus roxburghii* (chir) during autumn at four sites at 1,320–1,930 m elevation in the central Himalaya of India. Our hypothesis that primary leaves had higher leaf conductance than mature leaves (needles in fascicles), based on measurements in other pines, was rejected. Comparisons on the same saplings and seedlings showed lower leaf conductance for primary leaves than for mature leaves. Primary leaves on seedlings and saplings also did not consistently have higher leaf conductance than mature leaves on nearby trees. Mature leaves on seedlings, however, did often have higher conductance than mature leaves on nearby trees. Mean values for leaf conductance ($\text{mmol m}^{-2} \text{s}^{-1}$, based on total leaf surface area) ranged from 42–82 for mature leaves on trees, 60–121 for mature leaves on seedlings, and 28–67 for primary leaves on seedlings. Compared to published values for other pine species, conductance of mature leaves of *P. roxburghii* is relatively low.

Key words: chir, Himalaya, primary needles, seedling ecology, stomatal response

The earliest phases of seedling growth are critical to a plant's establishment and ecological success, and help to determine a species' distribution (Grubb, 1977). Understanding the responses of a species to environment requires understanding seedling structure and physiology, and how they change as a seedling develops.

Seedlings of conifers have primary leaves that differ from their cotyledons and mature foliage. In pines, primary leaves develop after the cotyledons (Doak, 1935) and comprise most photosynthetic area for the seedling during its early establishment, rapidly exceeding that of the cotyledons and remaining functional well after mature fascicles begin to develop. For example, in well-watered *Pinus taeda* grown in full sun, at 9 weeks all leaves are primary; at 16 weeks, 70% of leaf mass is primary, and by 23 weeks, 32% remains primary (Bormann, 1958). Primary leaves of *P. taeda* continue to be produced, but are reduced to scales during the second or third growing season (Bormann, 1963). Some pine species produce primary leaves for several years, up to a height of 0.5 m, including *P. roxburghii* and the related *P. canariensis*, three Mediterranean pines, and several white pines of southern North America (Troup, 1921; Lester, 1968; Klaus, 1989). Damage to seedlings or changes in environment, either detrimental or growth promoting, may cause older seedlings or trees of several pine species to revert to producing primary leaves (Troup, 1921; Doak, 1935; Stone and Stone, 1954; Mirov, 1967; Wright, 1970).

In pines, primary leaves differ from cotyledons and even more from mature leaves. They are glaucous, flattened with toothed margins, broad at the base, and mature all tissues about the same time (Doak, 1935). In *P. roxburghii* and *P. taeda*, they bear stomata on all surfaces, in contrast to the cotyledons (Konar, 1963; Knauf and Bilan, 1977). Physiology

of primary leaves may also differ from that of cotyledons and mature leaves. Photosynthetic rate/unit leaf dry mass was greater for primary than for mature leaves for three pines in southern California: the difference was $3.1 \times$ for *Pinus attenuata*, $1.8 \times$ for *P. coulteri*, and $2.9 \times$ for *P. lambertiana* (Wright, 1970). In *P. taeda* at 16 weeks, seedlings with mostly primary leaves reached light saturation at one-third the intensity required by those with all mature leaves (Bormann, 1958). Transpiration rates in culture of *P. pungens*, *P. rigida*, and *P. virginiana* with primary leaves were higher than for older seedlings with mature leaves (Zobel, 1969). Conifer seedlings with primary leaves are more sensitive to air pollution than those with mature leaves (Kozłowski *et al.*, 1991). Primary leaves of *P. contorta* block UV radiation more effectively than cotyledons on the same seedlings (Turenen *et al.*, 1999).

Leaf differences can affect seedling success. Among populations of drought resistant *P. taeda*, adaptive differences were present apparently only in seedlings including the primary leaves. Seedlings from a drought tolerant provenance transpired more when water was available but less during drought, compared to a less-tolerant provenance (Van Buijtenen *et al.*, 1976). Drought tolerant genotypes also had primary leaves with smaller surface: volume ratios, thicker cuticle and epidermis, and fewer stomata/volume of mesophyll and area of surface (Knauf and Bilan, 1977). The lower light compensation point is suggested to provide an advantage in competing with weeds during early seedling establishment (Bormann, 1958). Higher rates of photosynthesis for primary leaves provide those species that continue to produce them with an advantage in initial establishment (Wright, 1970). In contrast, treatments that enhance survival of planted *P. roxburghii* also reduce primary leaf number (Dhiman *et al.*, 1997).

The propensity of *Pinus roxburghii* (chir) to produce pri-

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mary leaves over a long period, and to return to their production during later life, makes it useful for the study of differences between primary and mature leaves. Only primary leaves are formed during the first two growing seasons for seedlings, and their production continues into the fourth season (Troup, 1921). Chir is widely distributed in the subtropical and warmer temperate habitats of the central and western Himalaya (Troup, 1921; Singh and Singh, 1992); its importance continues to increase as angiosperm-dominated forests are disturbed for agricultural use and by fire, even where timber harvest has ceased. Chir is widely used for afforestation in Nepal, as it survives poor conditions both in the nursery and after outplanting, and young stands provide habitat for under-planting of species of more use for agriculture (Jackson, 1994). Studies of chir include its seedling growth response to light, water and nutrients in culture (Rao and Singh, 1985; Singh and Singh, 1992; Tewari, 1994; Thadani, 1999), and photosynthetic response to light (Thadani, 1999).

No measurements of leaf conductance appear to be available for either primary or mature leaves of chir. This widespread pine has very short leaf longevity, with year-old needles falling before new needles elongate completely in our study area. Because trees in autumn bear only current-year mature leaves, one might expect that leaf conductance would be high, compared to pines that retain older leaves.

In this paper, we compare the leaf conductance of primary and mature leaves of natural *Pinus roxburghii* Sargent (chir) at three locations in the central Himalaya of India. We test the hypothesis, based on results with other pines, that primary leaves have a higher leaf conductance than mature leaves (*i.e.*, needles in fascicles). We also report the leaf conductance of mature leaves on a larger sample of trees, measured at the same time as the primary leaves, during a season with abundant water and light, and compare leaf conductance of mature leaves of chir with data for better-known pine species.

Methods

Measurements were made in autumn, after the monsoon rains, at each of three sites at three locations in the Kumaun

region in the central Himalaya of India, within 9 km of Naini Tal in Uttar Pradesh state (lat. 29° 23' N, long. 79° 28' E) (Table 1). At all sites, trees were measured for water potential before dawn and in midday, and for leaf conductance (mature leaves on two branches/tree) in morning and midday (Table 2). Trees retained mature leaves only from the current year, which is normal for chir in this region. Sampling of primary leaves varied with site: At Bhowali, in a pure chir stand on a steep SE slope, the tops of the crowns of four seedlings 12–30 cm tall, including only primary leaves, were measured in midday, immediately after measurement of mature leaves on nine trees. At Mangoli, in a mixed stand of chir and *Shorea robusta* on a moderate ESE slope, three sets of comparisons of mature and primary foliage were made in midday: 1) one measurement of primary and two of mature foliage on the same lower branch (not a basal sprout) of a mature tree (this combination of leaf types on a large tree was unusual), 2) on different branches on saplings (1–2 m tall), one branch with each leaf type on one sapling, and one primary and two mature branches on a second individual, and 3) on different branches of the same three seedlings < 1 m tall, a single measurement of each leaf type on each seedling. These comparative measurements followed ten measurements of mature foliage on five trees. At Kailakhan, measurements were made in mid-morning and early afternoon on primary foliage and mature foliage on the same seedlings, for four plants at

Table 1 Location, elevation, tree size, and range of area of leaves/sample.

Location	Elevation (m)	Tree height	Leaf type	Area (cm ²)
Bhowali	1760	3–10 m < 1 m	Mature	8.6–11.9
			Primary	25.1–39.1
Mangoli	1320	3–10 m	Mature	7.1–13.4
			Primary	11.5
		< 3 m	Mature	5.0–8.7
			Primary	13.8–35.8
Kailakhan	1930	3–10 m < 1 m	Mature	9.7–17.7
			Mature	3.6–11.6
		Primary	3.2–14.1	

Table 2 Time, tree water potential (ψ) (pre-dawn and midday), and environmental conditions during measurements of leaf conductance (morning and midday).

Site	Time ¹	ψ (MPa)	Leaf temperature (°C)	Relative humidity (%)	Light ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
Bhowali	7:15–8:20	– 0.39	15–17	43–52	4–131
	12:40–14:00	– 1.09	20–26	35–48	12–1230
Mangoli	7:20–7:45	– 0.36	16–19	56–59	6–25
	12:30–13:46	– 1.07	22–26	46–60	2–1170
Kailakhan 1	8:35–9:45	– 0.70	17–21	38–43	41–470
	12:50–13:30	– 1.36	20–25	35–43	42–1480
Kailakhan 2	10:10–10:55	– 0.50	17–21	33–45	29–1540
	14:10–14:50	– 1.14	18–21	41–50	18–1060

¹ Time for leaf conductance. Pre-dawn water potential measurements began between 5:10 and 6:10.

Discussion

Based on our results, there is no basis for concluding that leaf conductance of primary leaves of *Pinus roxburghii* (chir) is consistently higher than that of mature leaves. Intra-plant comparisons of leaf types on seedlings and saplings, in fact, showed primary leaves to have significantly lower leaf conductance than mature leaves. Comparisons of primary leaves on seedlings and saplings to mature leaves on trees showed no consistent pattern. Only in the single comparison on a mature tree did primary leaves have higher conductance. We reject our hypothesis that primary leaves of chir have higher leaf conductance than mature leaves. In three of five comparisons, leaf conductance of mature leaves on seedlings and saplings exceeded that for mature leaves on trees measured at the same time, suggesting a tree-size effect on conductance of mature leaves.

The origin, anatomy, and morphology of primary and mature leaves differ greatly (Doak, 1935; Konar, 1963; Mirov, 1967; Thompson, 1976). Measurements of photosynthesis and water loss of several pine species in the United States showed that primary leaves had higher rates of gas exchange than mature needles in fascicles (*Pinus pungens*, *P. rigida*, and *P. virginiana*, Zobel, 1969; *P. attenuata*, *P. coulteri*, and *P. lambertiana*, Wright, 1970); this suggested that leaf conductance of primary leaves was higher in these species, and, generalizing from this sample of six species, in pines. The basis for the differences between chir and the earlier studies may reflect different growing or measurement conditions, differences in methods, or real species differences. Even so, sometimes the leaf types do not differ, as for photosynthetic rates (Bormann, 1958) and cold tolerance (Berrang and Steiner, 1986). Explanation of seedling behavior appears to require measurement in the environment in question and an integrated interpretation of performance of all leaf types, as Miller *et al.* (1995) attempted for *Juniperus occidentalis*. Our measurements were made on native plants near the end of the growing season, when most foliage should have reached full size, yet leaves were not so old that senescence could be expected.

Comparisons between leaf types for leaf conductance and rates of gas exchange are influenced by the basis for expressing the values, per unit leaf dry mass or per unit leaf area (Miller *et al.*, 1995). Indeed, our hypothesis, based on results of Wright (1970) and Zobel (1969) expressed per unit dry mass, was rejected using our data expressed per unit area. Unfortunately, we did not weigh our samples, and the earlier reports did not provide information to convert values to an area basis. As mature leaves are thicker than primary leaves and thus weigh more per unit area, their rates would be lower relative to primary leaves if our values had been presented on a per mass basis. Miller *et al.* (1995) recommend expressing rates on a per mass basis for conifers; on the other hand, comparisons with broad-leafed species require area-based data. Another aspect of calculation that differs among workers is the extent of the area used: we used the area of all sides of the leaf (as both primary and mature leaves have

Table 4 A summary of maximal leaf conductance to water vapor ($\text{mmol m}^{-2} \text{s}^{-1}$) for diploxylon (hard or yellow) pines.¹

Species	Number of values	Median	Range	Reference ²
<i>Pinus contorta</i>	6	118	54–152	K1, S
<i>P. resinosa</i>	4	69	25–98	K1
<i>P. sylvestris</i>	6	62	50–155	H, K1, P1, W2
<i>P. taeda</i>	7	150	85–166	D, E, K1, M2, P2, W1, Z
Five others ³	6	118	34–150	K1, K2, M1, W1, W3

¹ All values are the highest mean among a variety of treatments or situations, and are based on total leaf surface area. Values were converted from cm^2/s when necessary if the elevation was given or could be estimated, and assuming a temperature of 20°C, using equation 8–12 in Percy *et al.* (1989). ² D, Dalton and Messina (1995); E, Ellsworth (1999); H, Hari *et al.* (1999); K1, Korner *et al.* (1979); K2, Koskela *et al.* (1999); M1, Morales *et al.* (1999); M2, Murthy *et al.* (1997); P1, Pena and Grace (1986); P2, Peterson *et al.* (1997); S, Smith (1985); W1, Wakamiya *et al.* (1999); W2, Wang and Kellomaki (1997); W3, Weber *et al.* (1993); Z, Zhang *et al.* (1997). ³ *Pinus banksiana*; *P. canariensis*; *P. merkusii*; *P. ponderosa*; and *P. virginiana*.

stomata on all surfaces), rather than projected area or twice projected area. Using projected area would more than double our conductance values (Johnson, 1984).

Even though chir is a common, commercially important species with a large range, few physiological data for it are available (Tewari, 1994; Thadani, 1999). Its behavior may differ from better known pines, as it belongs to a taxonomic group with a single other species (*P. canariensis*) (Price *et al.*, 1998), has the shortest longevity of mature leaves reported among pines (Richardson and Rundel, 1998) (a single year in our study area), and produces more primary leaves than most species. We summarize (Table 4) the values of leaf conductance of mature leaves of hard (diploxylon) pine species (for trees of all sizes), in terms of the maximum observed under a given set of conditions, as compiled by Korner *et al.* (1979) and Smith (1985), and from more recent individual studies. Only values under ambient conditions (*e.g.*, without supplemental CO_2), expressed on the basis of area of all leaf surfaces, were used. Maximal leaf conductance for seedlings of the closely related *P. canariensis* was $150 \text{ mmol m}^{-2} \text{ s}^{-1}$ (Morales *et al.*, 1999), substantially higher than our highest values (Table 3). Our higher means of leaf conductance of current-year mature leaves of chir trees were at the lower end of the range of published values, similar to *P. resinosa* and *P. sylvestris*, but above those of *P. merkusii* (Koskela *et al.*, 1999). Mature leaves on seedlings and primary leaves on the one tree-sample were above the range for the lower species, but not near maximal values for several other species (Table 4). Our measurement of current year leaves in autumn, with bright sun, moist soil, and moderate temperatures, probably produced relatively high leaf conductance for chir. Values from the literature for other species included both current and older needles; often needle age was not specified. Despite its short leaf longevity, chir appears to have lower leaf conductance than some more intensely studied pines such as *P. taeda* and *P. contorta*.

each of two sub-sites in the morning, and for three plants at the same sub-sites in the afternoon. Each set of measurements followed immediately the measurement of mature foliage on five trees at each sub-site. Kailakhan 1 is a mixed stand of chir and *Quercus leucotrichophora* on a steep E slope; Kailakhan 2 is a pure stand of chir on a steep N slope.

All sampling days were dry and primarily clear. Conditions during sampling varied with location, but all conditions were moderate and water potentials of trees were high (Table 2). Seedling water potentials were not measured.

Leaf conductance was measured with a steady-state porometer (Model 1600, with a Model 1600-07 cylindrical sampling chamber, Li-Cor, Lincoln, Nebraska, USA). Tufts of primary leaves were completely enclosed within the chamber, and held so that they were well separated in the chamber. Mature leaves were measured by stretching the 12 needles from four fascicles, in a single layer and separated from each other, across the opening of the sampling chamber, thus sampling about a 5-cm length from the center of the leaves. Fascicles were chosen from the middle of the current year's growth. Leaves in a sample were collected immediately after sampling and measured while fresh. Leaf area (Table 1) was calculated for all surfaces of primary and mature leaves; stomata occur on all surfaces of both leaf types (Konar, 1963). For primary leaves, the length and width were measured and used to calculate the area of the triangular leaf; the area was doubled to account for both surfaces and adjusted to account for the thickening along the center of the leaf. Area of mature leaves was calculated based on the length sampled and the diameter of the cylinder formed by the three leaves in the fascicle. The surface of the cylinder and the width of the six interior flat needle surfaces within each fascicle were estimated based on the radius of the fascicle. Water potential was measured on one sample from each tree using a pressure chamber (Model 1000, PMS Instrument Co., Corvallis, Oregon, USA).

Results

1 Mature leaves on trees

Average leaf conductance of mature, current-year leaves on

trees ranged from 41.5–81.5 mmol m⁻² s⁻¹ across four sample sites and two times of day (Table 3). Over all sites, leaf conductance did not vary between morning and afternoon (analysis of variance, $p = 0.234$). Sites differed ($p < 0.0001$), with Bhowali and Kailakhan 2 being significantly lower than Mangoli and Kailakhan 1 (Tukey's multiple range test, $p = 0.05$). Leaf conductance values were not related to water potential ($r^2 = 0.044$, $p = 0.619$).

2 Comparison of mature leaves among tree sizes

Five comparisons were possible between mature leaves on trees and mature leaves on saplings and seedlings measured on the same site at the same time (Table 3). At Mangoli and Kailakhan 2, mature leaves had higher leaf conductance on saplings and seedlings than on trees; at Kailakhan 1, there was no difference between tree sizes. At Mangoli, there was no difference between saplings and seedlings, and data are combined in Table 3.

3 Comparison of primary leaves on seedlings and saplings to mature leaves on trees

In two situations (Mangoli and Kailakhan 1 in the afternoon), primary leaves on seedlings and saplings had lower conductance than mature leaves on trees; in three situations (Bhowali, Kailakhan 1 in the morning, and Kailakhan 2 in the afternoon), there was no significant difference; and at Kailakhan 2 in the morning seedling primary leaves had higher conductance (Table 3).

4 Comparison of leaf types on the same individuals

Comparisons of leaf types within the same saplings and seedlings (Table 3) showed higher values of leaf conductance for mature leaves than for primary leaves at both Mangoli (analysis of variance, $p = 0.034$) and the combined Kailakhan sites ($p = 0.034$). The single comparison of leaf types on a mature tree, with one sample of primary leaves and two of mature leaves at Mangoli (not shown in Table 3), showed the opposite pattern, with higher values for primary leaves (158.1 mmol m⁻² s⁻¹ compared to 85.4 ± 7.5 for mature leaves).

Table 3 Morning and midday leaf conductance (mmol m⁻² s⁻¹) at each study site.

Site	Tree size (number of trees)	Leaf type	Leaf conductance ¹	
			Morning	Afternoon
Bhowali	Tree (9)	Mature	41.5 (4.1)	47.0 (3.8)
	Seedling (4)	Primary	—	46.6 (9.5)
Mangoli	Tree (5)	Mature	70.7 (6.7)	81.5 (6.7)
	Sapling/seedling (5)	Mature	—	112.4 (17.9)
	Sapling/seedling (5)	Primary	—	60.2 (12.1)
Kailakhan 1	Tree (5)	Mature	67.3 (4.4)	67.8 (4.4)
	Seedling (4,3)	Mature	75.8 (19.2)	61.7 (12.2)
	Seedling (4,3)	Primary	59.3 (21.5)	28.0 (13.1)
Kailakhan 2	Tree (5)	Mature	52.0 (2.5)	48.9 (2.5)
	Seedling (4,3)	Mature	120.8 (7.0)	69.0 (6.5)
	Seedling (4,3)	Primary	66.5 (12.0)	38.3 (11.2)

¹ Each mean (+ SE) for trees is for two samples/tree for conductance, with one for most seedlings and saplings.

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