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Leaf growth pattern in co-existing evergreen and deciduous species of Kumaon Himalaya

S. DHAILA-ADHIKARI, Y.S. RAWAT and B.S. ADHIKARI

G.B.P.I.H.E.D., Himachal Unit, Kullu Shamshi, 175 126. India

Abstract. Leaf growth patterns were studied in three pairs of evergreen and deciduous species, occurring at an elevation of 2025-2150 m in the Kumaon Himalaya. Leaf initiation occurred earlier in evergreens with an exception of *Litsea umbrosa*. Peak leaf pool size was attained earlier in deciduous species (June to early July), while later (October) in evergreen species.

Rate of leaf expansion was higher in deciduous species. Specific leaf mass in the initial period was higher in evergreen species than in deciduous species. Leaf area was higher in deciduous species as compared to evergreen species, while root length/leaf area unit was greater in evergreen species.

Key words: Leaf growth, co-existing, evergreen, deciduous.

Introduction

The leaf area available for photosynthesis plays a crucial role in biomass production (Shukla and Ramakrishnan 1984). The total leaf area is primarily determined by the patterns of production and fall, and the longevity of leaves (Watson 1956, Newhouse and Madgwick 1968). The evergreen habit in plants has a number of potential advantages, such as conservation of energy, and the capacity to perform photosynthesis over a considerable surface area whenever conditions are suitable. Predominance of evergreens can also be seen at the two opposite ends of water supply spectrum (Moore 1980). The incidence of deciduous species in the tropics is reported to increase with increasing seasonality of rainfall (eg. Beard 1955, Walter 1973, Whitemore 1975, Hall and Swaine 1981).

Inspite of the highly seasonal rainfall pattern in the Central Himalaya, evergreen species occurring below 2,500 m elevation form most of the forests; however, in terms of standing crops, deciduous species are equally abundant (Singh and Singh 1987). The evergreen species of this region are a leaf exchanging type in which old leaf crop is replaced by new leaves and the leaf life span is equal to one year (Ralhan et al. 1985, Dhaila et al. 1995).

The present paper compares leaf dynamics such as leaf initiation, leaf fall, leaf mass accumulation

and specific leaf mass evergreen, and deciduous species sharing same microclimate (except in the rooting depth). Studies on phenology of these two groups have concluded that the leaf growth pattern is different for the two groups in many ways: (1) rapid leaf expansion in deciduous species, (2) leaf population per unit shoot length happens to be greater in evergreen species, (3) leaf expansion rate is higher in deciduous species (Shukla and Ramakrishnan 1984, Ralhan et al. 1985a,b, Sobrado 1991). The present paper compares leaf growth pattern of co-existing evergreen and deciduous species. We sought to test whether deciduous and evergreen species differ substantially in leaf growth patterns when the two types of plants are rooted immediately adjacent to each other. It is important to compare the leaf growth pattern of these two forms in a common environment, because all the previous comparisons have been of evergreen and deciduous species occurring in different sites and microsites. The study of shoot growth pattern shows some significant difference in co-existing evergreen and deciduous species (Dhaila et al. 1995).

Materials and methods

Study site and species selected: The study site was located at 2,025 to 2,150 m elevations at $29\,^{\circ}7^{\circ}$ N lat. and $79\,^{\circ}15^{\circ}$ E long. in the Central Himalaya. The presence of a sufficient number of saplings of evergreen and deciduous species immediately adjacent to each other at the site was the main reason for its selection. Species under study have been given with their leaf longevity in Table 1. Site description and climate in detail has been given elsewhere (Dhaila and Singh 1994; Dhaila et al. 1995).

There are three main seasons: winter with infrequent rainstorms (December to February), early summer which is warm and dry (April to mid June with mean monthly temperature in the range of 18.6 to 23.7°C), and late summer which is warm and wet (mid June to September, when mean monthly temperature is relatively invariant, 17.8 to 18.5°C). Of the 2,279 mm of annual rainfall 1,704 mm occurs during the wet summer.

One hundred newly emerging shoots in each of the 10 individuals per species distributed evenly in the tree crown were marked prior to budbreak (generally during February to early April in 1989). Thus a total of 1,000 shoots were marked for each species. From this marked population of shoots, one hundred leaves (10 leaves from each of the ten individuals of a species from all crown

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positions) were collected at monthly intervals and S. Dhaila, Y.S. Rawat their length and width were measured to the nearest of 0.1 cm. Out of these, 25 leaves were measured for leaf area using a planimeter. The remaining 75 leaves were divided into three sets, each of 25 leaves, and were oven dried at 80°C till constant weight. Leaf units were individual leaves for all species except for those with compound leaves (F. micrantha) in which an individual leaf let was regarded as a leaf unit. Correlation between area by planimeter (n=25) and the area by product of length and width of leaves was developed for all the leaves (Table 2).

On the basis of dry mass of leaves, specific leaf mass was calculated by using the following formula (Evans 1972, Specific leaf mass = SLM):

$$\begin{array}{ccc} & & L_{w} \\ \text{SLM (gm}^{\text{-2}}) & = & ----, & \text{where} \\ & A & & \end{array}$$

A = Leaf area (m^2) and L_w = Leaf dry weight (g). Root length was observed by uprooting the trees. Tap roots were measured with tape, and lateral roots (in case of S.hookeriana) were measured by line intersection technique (Rowse and Phillips 1974).

Results

Leaf recruitment: Among all the pairs (co-stratal) leaf recruitment started early in the season (second

Species	Growth fo	rm	SS Leaf	Longevity (days)
SPECIES PAIR I				
Quercus floribunda				
Lindle ex.A.Cam.	evergreen	tree	late	316.4
Fraxinus micrantha				
Lingelsh	deciduous	tree	mid	129.6
SPECIES PAIR II				
Litsea umbrosa				
Nees	evergreen	tree	late	322.1
Populus ciliata				
Wall.	deciduous	tree	early	159.7
SPECIES PAIR III				
Sarcococca hookeriana				
Baill.	evergreen	shrul	o late	337.2
Rhamnus virgata				
Roxb.	deciduous	shrul	b early	153.8

Table 1. Characteristics of species selected for study (SS - succesional status)

Species	Regression equations		
Evergreen			
O.floribunda	Y=0.029+0.873X;	(r=0.96, P<0.01)	
L.umbrosa	Y=-0.380+0.695X;	(r=0.98,P<0.01)	
S.hookeriana	Y=0.235+0.789X;	(r=0.99, P<0.01)	
Deciduous			
F. micrantha	Y=1.200+0.601X;	(r=0.98, P<0.01)	
P. ciliata	Y=-1.898+0.810X;	(r=0.98, P<0.01)	
R. virgata	Y=0.930+0.536X;	(r=0.92, P<0.01)	

relating leaf area Table 2. Regression equations calculated by product of length and width (X) to be determined by (Y); n = 25.

week of March) in evergreen species. Except, in tree pair II where leaf recruitment in the evergreen tree species L. umbrosa started in the second week of April and in its deciduous counterpart P. ciliata it occurred in the second week of March.

Root length per leaf area unit was greater in evergreens compared to deciduous (3.98 vs 1.99 cm/cm²). Although the leaf area was greater in deciduous species, their root length/leaf area unit was lower than evergreens.

Leaf expansion: The period of leaf expansion ranged from 22 days to 42 days in evergreens, and from 17 to 35 days in deciduous species (Fig. 1). The interspecies variations in leaf area were distinctly wider for deciduous species (20 to 104.5 cm²) than for evergreen species (16.8 to 24.3 cm²). Leaf area was significantly (P<0.01) greater for deciduous species than evergreen species of each pair. The deciduous species of each pair realized significantly greater (P<0.05) leaf expansion rate compared to the evergreen species (1.54 vs 0.54 cm²d⁻¹). The rate of leaf expansion is also affected by position in the forest canopy, for example, the two shrubs studied completed their leaf expansion significantly earlier (P<0.01) and in shorter period than the tree species (19.5 days vs 40.2 days).

The specific leaf mass (SLM) of the evergreen species (average 119 gm⁻²) was significantly greater (P<0.05) than that of the deciduous species (average = 73.3 gm^{-2}). In the initial stage SLM was significantly greater (P<0.01) for each of the evergreen species compared to their deciduous counterparts (Fig. 2). However, at mature stage this significance in difference was maintained only by tree species.

Leaf mass loss: The phase of increasing leaf mass (subsequent to leaf initiation) ranged from 4 months to 6 months in deciduous species, while this range was from 5 to 8 months in evergreen species (Fig.3). The interspecies variation in leaf mass at the mature stage was wider (0.15 to 0.6 g leaf-1) for deciduous species compared to evergreen species (0.12 to 0.31g leaf-1). Leaf mass in the initial stage was significantly (P<0.05) greater for all the evergreen species compared to each of the decidous species of the pair. This significant difference was not maintained at the mature stage by the pair Q. floribunda (evergreen species) and F. micrantha (deciduous species) and a pair of shrub species.

The average percentage of total accumulation of leaf mass (per leaf) during the first two months of leaf initiation was significantly greater (P<0.01) for evergreen species (45.9%) compared to deciduous species. The phase of stable leaf mass was short in deciduous species than those of the evergreen species (1 month vs 3 months on average; Fig. 3).

Leaf Longevity: The average leaf longevity for deciduous species (148 days) was significantly lower (P<0.01) than for the evergreen species (325 days). It ranged from 316 days to 337 days for evergreen species, while the range was from 130 days to 160 days for deciduous species (Table 1).

Discussion

The earlier leaf recruitment in evergreen species

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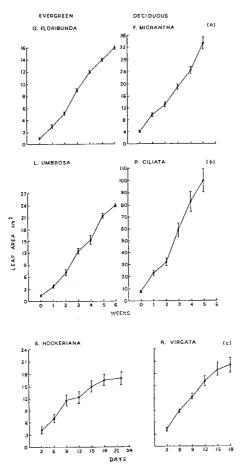


Fig. 1. Monthly changes in leaf area (leaf expansion).

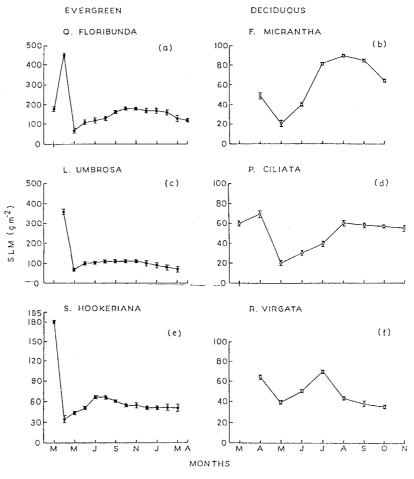


Fig. 2. Monthly changes in specific leaf mass (SLM).

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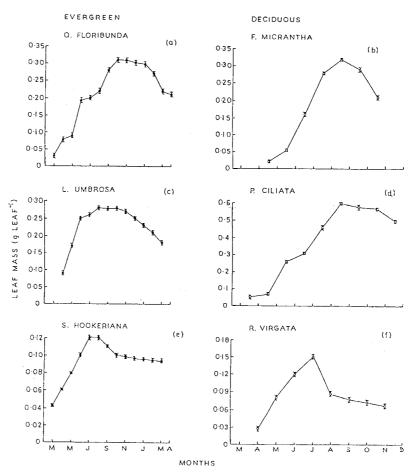


Fig. 3. Monthly changes in leaf dry mass.

(with exception of L. umbrosa) is correlated with earlier recovery from winter stress in them (Dhaila 1991). In winter, water stress (in terms of water potential) remains low in both groups as an alternative of frost hardiness (Morgan 1984), but as the spring proceeds, the evergreen species recover immediately and leaf recruitment starts in them. This is also one of the reasons of deciduous species to complete annual growth earlier (before the onset of dry season) and for lower carbon assimilation rate of evergreens. The leaf expansion rate is also higher in deciduous species. This rapid growth in deciduous species before onset of unfavourable conditions is to compensate for any disadvantage in photosynthetic carbon gain that may occur due to the delay in initiating the growth (Dhaila et al. 1995). This study is also in conformity with the observations of Ralhan et al. (1985) and Singh and Singh (1987). Although the leaf area was greater in deciduous species still their root length/ leaf area unit was lower than evergreens. This feature of evergreens is advantageous over deciduous species and shows drought tolerance of evergreens (Pallardy and Rhods 1993).

The early and rapid foliage development in shrubs may reduce the competitive effect of the canopy species. Further, this time separation in growth activities may stagger the demand for nutrients within an annual cycle at the ecosystem level (Singh and Singh 1987). The production of leaves during favourable period would seem, on energetic grounds, to be the worst possible time for leaf expansion (Givnish 1984). May be, this is

the strategy to avoid leaching of minerals by torrential rains in the following rainy season from the soft leaves, which lack thick cell walls and a heavy cuticle (Sarmiento 1983).

According to Gates (1914), the initial cost of an evergreen leaf may be greater than that of the deciduous leaf of comparable size, because of thicker leaves with a higher specific leaf mass. Sturdier construction may be necessary for leaves that must endure several years of environmental vicissitudes. Greater initial costs means a longer time before a leaf pays back its cost. Leaves of the Japanese deciduous species Zelkowa serrata require only 9-15 days to pay back their initial cost. While leaves of broad-leaf evergreens Shiia sieboldi and Pittosporum tobira take about 30 days because of greater specific leaf weight, and some may take even longer pay back time (Saeki and Nomoto 1958).

There existed a negative relationship between osmotic potential and leaf dry mass per unit leaf area which shows that as the leaf dry mass increases the osmotic potential decreases and in turn, water extraction efficiency from the drying soil increases (Dhaila 1991). Earlier decline in leaf mass in deciduous species shows their inability to extract water from drying soil (at the onset of winter), which they compensate by shedding their leaves. Leaf efficiency of the evergreen in terms of net gain of carbon per unit leaf mass is lower than that of the deciduous species, but stands of evergreen forests produce a larger leaf crop on a unit area basis than the deciduous forest of the region (Singh et al. 1990, Dhaila et al. 1995). Thus the absolute carbon cost

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of leaf production for a forest stand may not differ between evergreen and deciduous species of the region.

The individual leaves of the evergreen species of this region showed a gain in leaf mass for 6-8 months, and in general, leaf longevity of 1 year or just more than one year. The evergreen species of this region showed gradual loss of leaf mass (in contrast to the sharp decline in leaf mass of senescing leaves of deciduous species). Which enables the evergreen species to fix carbon through out the winter, and to retranslocate it to the reservoires of (perennial parts) the plant to be reutilized for the production of long lived efficient leaves of a new crop. During winter the evergreen retranslocate only a small fraction of their nitrogen, which is correlated with the loss of leaf mass (Negi and Singh 1993, Dhaila and Singh 1994). It has been observed by a number of workers (e.g. Chapin 1980, Coley 1985, Reich et al. 1991 a,b,) that there is a strong interdependence among leaf life span, net photosynthesis, leaf N concentration, and SLA. According to Reich et al. (1992), a plant either produces leaves that possess a high photosynthetic assimilation rate but persist briefly, or it provides resistant leaf physical structure with low photosynthetic capacity, so that leaves can assimilate carbon over a longer period of time, but at a lower rate.

In conclusion, the leaf growth pattern of evergreen and deciduous species sharing the same microsites varies in various ways. The deciduous species design their growth in such a way so as to utilize maximum of favourable period to achieve their goal of annual growth and production. While the evergreen leaves with low photosynthetic rate (Reich et al. 1991a), have the whole year to complete their annual growth. Their greater root:shoot ratio (Dhaila et al. 1995) makes them opportunist to take each possible advantage over a long period of time of one year, inspite of occupying the same microsite.

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References

- Beard, J.S. 1955: The classification of tropical American vegetation types. *Ecology*, **36**: 89-100.
- Chapin, F.S. 1980: The mineral nutrition of wild plants.

 Ann. Rev. Ecol. Sys., 11: 233-260.
- Coley, P. D. 1988: Effects of plant growth rate and leaf lifetime on the amount and type of anti herbivore defense. Oecologia (Berlin), 74: 531-536.
- Dhaila, S. 1991: Phenology of deciduous and evergreen species with particular reference to water stress. Ph. D. Thesis Kumaun University, Naini Tal India.
- Dhaila, S. and Singh, S.P. 1994: Foliar nitrogen dynamics in co-existing evergreen and deciduous species in an Oak forest. *Oecologia Montana*, **3**: 19-23.
- Dhaila, S. Singh, S.P., Negi, G.C.S. and Rawat, Y.S. 1995: Shoot growth phenology of co-existing evergreen and deciduous species in an Oak forest. *Ecological Research*, **10**: 151-159.
- Evans, G.C. 1972: The quantitative analysis of plant growth Blackwell Scientific Publication. Oxford, London
- Gates, F.C. 1914: Winter as a factor in the xerophylly

- of certain evergreen ericads. Bot. Gaz., **57**: 445-489. Givnish, T.J. 1984: Leaf and canopy adaptations in tropical forests. In *Physiological Ecology of Plants of Wet Tropics*. (eds. B. Medina, I. Mooney and A. Vasquez-Yanes) pp. 51-84. Dr. W. Junk. The Hague.
- Hall, J.B. and Swaine, M.D. 1980: Distribution and ecology of vascular plants in a tropical rain forest. Dr. W. Junk. The Hague.
- Moore, P. 1980: The advantages of being evergreen. *Nature*, **285**: 535.
- Morgan,J.M. 1984: Osmoregulation and water stress in higher plants. Ann. Rev. Plant Physiol., 35: 299-319.
- Negi, G.C.S. and Singh S.P. 1993: Leaf nitrogen dynam ics with particular reference to retranslocation in evergreen and deciduous tree species of Kumaun Himalaya. Can. J. For. Res., 23: 349-357.
- Newhause, M.E. and Madgwick, H.A.I. 1968: Comparative seedling growth of four hardwood species. Forest Science, 14: 27-30.
- Pallardy, S.G. and Rhoads, J. L. 1993: Morphological adaptations to drought in seedlings of deciduous angiosperm. Can. J. For. Res., 23: 1766-1774.
- Ralhan, P.K., Khanna, R.K., Singh. S.P. and Singh, J.S. 1985a: Phenological characteristics of tree layer of Kumaun Himalayan forests. *Vegetatio*, **60**: 91-101.
- Ralhan, P.K., Khanna, R.K., Singh. S.P. and Singh, J.S. 1985b: Phenological characteristics of shrub layer of Kumaun Himalayan forests. *Vegetatio*, **63**:113-120.
- Reich, P.B. Walters, M.B. and Ellsworth, D.S. 1992: Leaf life span in relation to leaf, plant stand characteristics among diverse ecosystems. *Ecological Monograph*, **62**: 365-392.
- Reich, P.B., Une, C., Walters, M.B. and Ellsworth, D.S. 1991a: Leaf life span as a determinant of leaf structure and function among 23 tree species in Amazonian forest communities. *Oecologia* (Berlin), 86: 16-24.
- Reich, P.B. Une, C., Walters, M.B. and Ellsworth D.S. 1991b: Leaf age and season influence the relationships between leaf nitrogen, leaf mass per area, and photosynthesis in maple and Oak trees. *Plant, Cell and Environment*, **14**: 251-259.
- Rowse, H.R. and Phillips, D.A. 1974: An instrument for estimating the total length of root in a sample. J. Appl. Ecol., 11: 309-314.
- Saeki, T. and Nomoto, N. 1958: On the seasonal changes of photosynthetic activity of some deciduous and evergreen broadleaf trees. *Bot. Mag. (Tokyo)*, **71**:235-241
- Sarmiento, G. 1993: Ecology of neotropical savannas. Harvard University Press, Cambridge, Mass.
- Singh, J.S. and Singh, S.P. 1987: Forest vegetation of the Himalaya. *Bot. Rev.*, **52**: 80-192.
- Singh, S.P., Singh, R.P. and Rawat, Y.S. 1990: Patterns of soil and vegetation and factors determining their forms and hydrologic cycle in Nanda Devi Biosphere Reserve. 2nd Annual Report, submitted to Ministry of Environment and Forests, Govt. of India, New Delhi.
- Shukla, R.P. and Ramakrishnan, P.S. 1984: Leaf dynamics of tropical trees related to successional status. *New Phytol.*, **97**: 697-706.
- Sobrado, M.A. 1991: Cost benefit relationships in deciduous and evergreen leaves of tropical dry forest species. Functional Ecology, **5**: 608-616.
- Walter, H. 1973: Vegetation of the earth in relation to climate and ecophysiological conditions. Springer-Verlag, New York.
- Watson, D.J. 1956: Leaf growth in relation to crop yields. In *The Growth of Leaves* (Ed. F.L. Milthorpe), pp. 178-191. Butterworths, London. Whitemore, T.C. 1975: Tropical rain forests of the Far
- Whitemore, T.C. 1975: Tropical rain forests of the Fal East. Clarendon Press, Oxford.

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