

Seasonal changes in stem diameter and leaf development in a tropical montane forest

Singh, S. P.¹, Ralhan, P. K.², Upadhyay, V. P.¹ & Negi, G. C. S.¹

¹Department of Botany, Kumaun University, Naini Tal, 263 002 India ²Department of Forestry and Natural Resources, Punjab Agricultural University, Ludhiana, 141 004 India

Abstract. Seasonal patterns of stem diameter changes in evergreen and deciduous species of a tropical montane forest in the Central Himalayas (300-2250 m a.s.l.) were investigated in relation to leaf development. Ca. 75 % of the annual rainfall in this region occurs in a short period, from mid-June to mid-September and the remaining months are dry. It was assumed that changes in stem diameter are correlated with changes in water stress. Each evergreen species could be characterized by leaf longevity of about one year; each species showed pronounced summer leaf drop and simultaneous new leaf formation. Winter stem shrinkage was more pronounced in deciduous species than in evergreen ones. The deciduous species also showed a greater proportional loss of leaf mass (before abscission) than the evergreen species. Winter leaf fall in deciduous species was related to the pronounced stem shrinkage. The leaf fall enabled these species to control further water loss. Being more resistant to desiccation, the evergreen species retained their leaves throughout the winter but showed gradual loss of leaf mass, presumably in order to control water loss. In all species, leaf expansion was completed before the onset of the rainy season, when water stress was high. This strategy has definite advantages in a climate with a monsoon pattern of rainfall. Evergreen species, showing pronounced leaf drop in summer, have advantages over deciduous species; hence their preponderance in the region.

Keywords: Central Himalayas; Deciduous; Evergreen; *Quercus*; Seasonally dry climate; Water stress.

Nomenclature: Osmaston (1926).

Introduction

Seasonally dry tropical climates differ ecologically from wet tropical climates in that they are less suitable for plant growth during the dry period (Lieberman 1982).

In the Central Himalayan mountains, the warm months of the year (March-September) can be broadly divided into a warm and dry season from March to mid-June, and a warm and wet season from mid-June to the end of September. The first, dry part is usually referred to as summer season (including the spring) and the second, wet part, which receives 75 % of the annual rainfall, is known as the monsoon or rainy season. The warm and wet season is followed by an other dry period from October to February, the winter season.

All dominant forest trees of the Central Himalayas, between 300 and 2250 m a.s.l., are evergreen and characterized by pronounced summer leaf drop and simultaneous new leaf formation (Ralhan et al. 1985a, b), with leaf longevity of about one year. In these evergreen species, as well as in deciduous species present in this region, the new foliage is completely developed before the onset of the rainy season. This feature has also been noted for some other tropical dry forests (e.g. Webb 1959; Boaler 1966; Daubenmire 1972; Longman & Jenik 1974). While changes in temperature (Longman & Jenik 1974) or photoperiod (Daubenmire 1972; Frankie, Baker & Opler 1974) have been suggested as the possible triggering factors of leaf initiation, the key question concerning the trees' leaf forming capability during a continued dry season has not been considered properly.

Worrall (1966), Hinckley, Lassoic & Running (1978) and Reich & Borchert (1982) have shown that diurnal and seasonal variations in stem circumference are closely correlated with temporal fluctuations in the water stress of trees. Assuming that this correlation would also hold for trees of our region, we followed stem diameter changes in both evergreen and deciduous species in these representative forest types of the Central Himalayas. In addition, we collected data on leaf development, particularly on the periodicity of leaf expansion, decline in leaf weight as an index of senescence, and leaf fall in relation

The objectives of this study were thus to address the following questions:

1) how is seasonal periodicity of leaf development

Table 1. Some climate data of the forest sites. Forest names are explained in the text.

Forest site	Altitude (m)	Soil texture*	Temp.**	Rain (mm)	P-E index***		
					summer	winter	rainy
Sal forest	300	loamy sand (80)	23.0	2 076	2.33	6.23	62.70
Chir pine forest	1750	sandy loam (66)	15.8	2 185	4.92	3.55	88.77
Banj oak-pine forest	1850	sandy loam (61)	15.8	1 373	5.10	8.71	43.40
Mixed tilonj oak-rianj oak forest	2250	sandy loam (62)	14.9	2 488	6.40	13.20	101.73

* Values in parentheses are % sand figures;
 ** Mean annual temperature in °C;
 *** P-E (Precipitation Effectiveness) index calculated after Thornthwaite (1931).

related to changes in the water status of trees?

2) How do deciduous species differ from evergreen species in this respect?

3) Why are evergreen species predominant in the region?

Study sites

Four study sites were located along an elevational gradient from 300 - 2250 m elevation in the Naini Tal district, Central Himalaya (29° 7' - 29° 38' N and 79° 27' - 79° 48' E). They are characterized by sal (*Shorea robusta*), chir pine (*Pinus roxburghii*), banj oak (*Quercus leucotrichophora*) - pine, and a mixed oak forest respectively. Along this transect the mean monthly temperature ranges from 13 - 32 °C at 300 m, 8 - 21 °C at 1500 m, to 6 - 20 °C at 2250 m a.s.l. There is some snow in winter (December-February) from ca. 2000 m. The annual rainfall along this transect ranges from ca. 1300 to ca. 2500 mm (Table 1). 75 % of the annual rainfall generally occurs in the monsoon or rainy season (mid-June to mid-September).

Values of the P-E (Precipitation Effectiveness) index, calculated according to Thornthwaite (1931), tend to increase with increasing elevation, indicating that the sites at higher altitudes were more mesic than those at lower altitudes (Singh & Singh 1987). The seasonal pattern of Köppen's (1931) aridity index at the lowest altitude of the gradient is about the same as at the highest altitude. However, the lower part is drier than the higher part. March, April, May, October and December are extremely dry months at the lowest sites, with the aridity index < 1.25. At the highest site, April and November are extremely dry (Table 2).

The soil is loamy sand at the sal forest site and sandy loam at the other forest sites. The soil moisture content increases from lower to higher elevations (Table 1). For 1982-83, Bisht & Bisht (1984) collected soil moisture data (0 - 30 cm) for different months at the sal forest site (Table 2). From the relationship between soil moisture

content and water potential, as given for loamy sand (Slatyer 1967), we derived a water potential of ca. 1.5 MPa in May; hence, there would be considerable water stress in June and from November to April. Only from July to October would soil water be favourable for plant growth.

At each of the four forest sites the following species were selected:

Sal forest: *Shorea robusta* (canopy), *Mallotus philippensis* (subcanopy), *Murraya peniculata* (shrub);

Chir pine forest: *Pinus roxburghii* (canopy), *Symplocos ramosissima* (subcanopy), *Glochidion velutinum* (shrub); Banj oak-pine forest: *Quercus leucotrichophora* (canopy), *Myrica esculenta* (subcanopy), *Myrsine semiserrata* (shrub);

Mixed tilonj oak-rianj oak forest: *Quercus floribunda*

Table 2. Aridity index and soil moisture content (only for the sal forest site) for two sites representing elevational extremes.

	1	2	3
Jan	1.91	9.3	4.40
Feb	2.24	9.3	4.63
Mar	0.96	11.5	3.06
Apr	0.37	10.4	1.16
May	0.86	4.5	2.71
June	8.38	8.2	12.79
July	15.18	24.4	26.34
Aug	16.70	21.8	25.54
Sep	8.03	15.0	12.68
Oct	1.11	17.0	2.45
Nov	0.10	9.8	0.54
Dec	0.79	9.5	1.41

1 = Sal forest site: Aridity index $a = \frac{P}{t-10}$

where P = precipitation and t = temperature (Köppen 1931).

2 = Sal forest site: Soil moisture content (%): averages of 0-10 and 10-30 cm soil depths.

3 = Mixed tilonj oak-rianj oak forest: Aridity index.

(canopy), *Q. lanuginosa* (canopy), *Lyonia ovalifolia* (subcanopy), *Viburnum cotinifolium* (shrub).

Chir pine is an early successional, stress-tolerant species able to colonize thin soils, whereas all the oaks and sal are regarded as climax species. Frequency of both managed and accidental fire is high in chir pine forests, comparatively lower but still substantial in sal forest, and negligible in oak forests (Singh & Singh 1987). With the exception of chir pine, all forest types form closed canopies. The sal forest is a typical Indian forest type. Sal (*Shorea robusta*, *Dipterocarpaceae*) is a tall tree up to 40 m, with leaves of mesophyll size. It forms extensive forests on loamy, well-drained soils in the foothill belt of the Himalayas.

Methods

Within a 1-ha permanent plot at each of the selected sites, five similar individuals of each of the canopy-, subcanopy- and shrub layer species were randomly selected for the purpose of collecting data on shoot diameter changes. The sample individuals were 2-5 m tall with 1-5 cm DBH (diameter at breast height, i.e. at 1.37 m). DBH and DGL (i.e. diameter at ground level) were measured by a screw gauge facing in two directions at right angles. Measurements were taken at monthly intervals, at the same marked places at approximately the

same time of the day on each reading date, over the period of July to August of the following year.

From each individual tree or shrub six marked leaves (of the current year leaf crop) were measured for leaf expansion. For this purpose the length and width of the leaves were measured to the nearest 0.1 cm and they were traced to determine the leaf area with a planimeter. Correlations between area by planimeter and area by the product of length and width were determined for all species (Ralhan & Singh 1987).

On five additional individuals, several leaves were tagged at the time of peak bud-bursting. From these individuals, composite sampling of nine tagged leaves from different crown positions was done at monthly intervals to determine temporal variations in leaf dry mass. The samples were brought to the laboratory in airtight polyethylene bags within three hours and oven dried at 70 °C for 48 h and weighed. The surface area of these weighed leaves was measured prior to oven-drying. Leaf expansion was measured weekly with a starting point zero at the time of bud-bursting. The time between bud-bursting and the day that no further leaf expansion was measured, was considered the leaf expansion period.

For seasonal periodicity of leaf drop, leaf formation and flowering, data from Ralhan et al. (1985a, b) were used.

Results

Seasonal periodicity of leaf drop and leafing

All the dominant species of the Central Himalayas including the conifer, *Pinus roxburghii* are evergreen with concentrated summer leaf drop and simultaneous leafing (Table 3). The dominant species of the foothill site, *Shorea robusta* is never entirely without leaves but the foliage is clearly thinned out during the leaf-exchange phase (March-April). Trees of this species become fully naked in the Ganges plains (Singh 1974). At the time of leaf exchange, the foliage is relatively less thinned out in the dominant species of intermediate altitudes (800-1800 m), viz. *P. roxburghii*. Thinning out is scarcely perceptible in the dominant species of higher altitudes (1800-2250 m), *Quercus floribunda* and *Q. leucotrichophora*. In deciduous species, initiation of leaf drop followed the rainy season, with the start of the cool dry season (Table 3). In *Lyonia ovalifolia* (a deciduous undercanopy tree species), leafing (April to June) immediately followed leaf drop (October to March), but in other species, gaps of two to three months (January to February or January to March) occurred between leaf drop and leafing.

Table 3. Periodicity of leaf drop, leafing and flowering of the forest species. The numerals indicate months of the year.

Species	Phenophases		
	Leaf drop	Leafing	Flowering
Trees			
Canopy trees			
<i>Shorea robusta</i>	3-6	3-5	4-5
<i>Pinus roxburghii</i>	5-6	2-4	2-3
<i>Quercus leucotrichophora</i>	4-5	3-4	3-4
<i>Quercus lanuginosa</i>	1-4	5-6	4-5
<i>Quercus floribunda</i>	4-5	5-6	4-5
Undercanopy trees			
<i>Mallotus philippensis</i>	3-6	4-6	9-10
<i>Lyonia ovalifolia</i>	10-3	4-5	4-6
<i>Symplocos ramossissima</i> D	9-12	4-5	4-5
<i>Myrica esculenta</i>	5-6	5-6	8
Shrubs			
<i>Murraya peniculata</i>	4-6	4-6	9-10
<i>Myrsine semiserrata</i>	3	1-11	10
<i>Glochidion velutinum</i> D	10-12	3-4	4
<i>Viburnum cotinifolium</i> D	10-12	3-4	4-6

D = deciduous; other species are evergreen.

Table 4. Mean values of annual added increment, total cumulative increment after one year and winter shrinkage in stems (Nov.-Feb.). DBH = diameter at breast height; DGL = diameter at ground level; LSD = least square difference. For full species names see Table 3.

	Mean of annual added increment (mm)		Total cumulative annual increment (mm) (\pm ISE)		Winter shrinkage			
	DBH	DGL	DBH	DGL	DBH		DGL	
					mm	%	mm	%
Tree canopy								
<i>S. robusta</i>	2.290	2.277	4.20 \pm 0.213	4.40 \pm 0.135	0.93	22.14	0.97	22.05
<i>P. roxburghii</i>	3.142	3.551	4.55 \pm 0.199	5.30 \pm 0.145	0.32	7.03	0.69	13.03
<i>Q. leucotrichophora</i>	3.411	3.137	4.80 \pm 0.237	5.40 \pm 0.237	0.43	8.96	0.65	12.04
<i>Q. floribunda</i>	2.227	2.668	4.80 \pm 0.245	5.60 \pm 0.214	0.72	15.00	1.06	18.93
<i>Q. lanuginosa</i>	2.756	3.420	4.60 \pm 0.172	5.30 \pm 0.095	0.09	1.96	0.48	9.06
LSD	(0.246)	(0.371)				(8.94)		(8.95)
Subcanopy								
<i>M. philippensis</i>	1.815	2.419	3.30 \pm 0.092	4.10 \pm 0.148	0.54	16.36	0.57	13.90
<i>L. ovalifolia</i>	1.158	1.307	2.80 \pm 0.061	3.20 \pm 0.135	1.38	49.29	1.51	47.19
<i>S. ramosissima</i>	0.758	0.819	4.09 \pm 0.100	4.49 \pm 0.050	1.10	26.89	1.67	37.19
<i>M. ascudenta</i>	1.695	2.057	3.80 \pm 0.149	4.20 \pm 0.130	0.15	3.95	0.21	5.00
LSD	(0.269)	(0.348)				(9.68)		(7.89)
Shrub layer								
<i>M. peniculata</i>	0.496	0.607	1.70 \pm 0.146	2.00 \pm 0.073	0.29	17.06	0.24	12.00
<i>M. semiserrata</i>	0.920	1.274	1.90 \pm 0.055	2.40 \pm 0.09	0.27	14.21	0.50	20.83
<i>G. velutinum</i>	0.517	0.715	2.10 \pm 0.056	3.40 \pm 0.076	0.84	40.00	1.80	52.94
<i>V. cotinifolium</i>	0.661	0.999	2.40 \pm 0.122	3.60 \pm 0.229	0.91	32.92	1.51	41.94
LSD	(0.126)	(0.292)				(9.69)		(10.23)

Changes in stem diameter

Analysis of variance of mean annual diameter increment indicated significant differences between most of the species ($p < 0.01$) when DBH was concerned, and between most of the species when DGL was concerned (Table 4). Shrinkage in stems occurred in different periods for different species, usually from October to March, and most conspicuously from December to February (Figs. 1-3). In most species, the extent of shrinkage at ground level was greater than at breast height. We did not find a relationship between the extent of stem shrinkage of species and altitude of their occurrence, but deciduous species (with 13.9 - 52.9 %) had a greater extent of shrinkage than evergreen species (0 - 37.9 %) (Table 4). Among the dominant evergreen canopy species, *Shorea robusta* with a leaf-exchange pattern similar to that of deciduous species, showed more shrinkage than other evergreen species (22.05 - 22.15 % vs. 1.96 - 18.93 %). Furthermore, the oak with the shortest leaf longevity, *Quercus lanuginosa* (Raihan & Singh 1987) showed more shrinkage (15.00 - 18.93 %) than the oak with longest leaf longevity, viz. *Q. floribunda* (1.96 - 9.06 %). Analysis of variance indicated that the

differences in winter shrinkage of shoots among canopy, subcanopy and shrub layer species were significant ($p < 0.01$). Among the tree canopy species, *Shorea robusta* among the sub-canopy species *L. ovalifolia* and *S. ramosissima*, and among the shrub-layer species *G. velutinum* and *V. cotinifolium* experienced a significantly greater degree of stem shrinkage than other species in their respective layers, both at DBH and DGL. These species are all deciduous, or in the case of *S. robusta* semideciduous.

In all evergreen species the start of loss of leaf mass approximately coincided with stem shrinkage (Figs. 1-3). Aridity index values at the start of diameter increase were somewhat lower than those during the stem shrinkage period. (Table 2). However, soil moisture had marginally increased by the time stems showed a marked diameter increase. This may have occurred partly as a result of reduction in transpiration rates of highly senescent leaves of evergreen species. In deciduous species the decline of leaf mass also coincided with stem shrinkage as well. Subsequent to leaf drop, the stem diameter became more or less constant, indicating that water stress did not increase further, despite the continued drought.

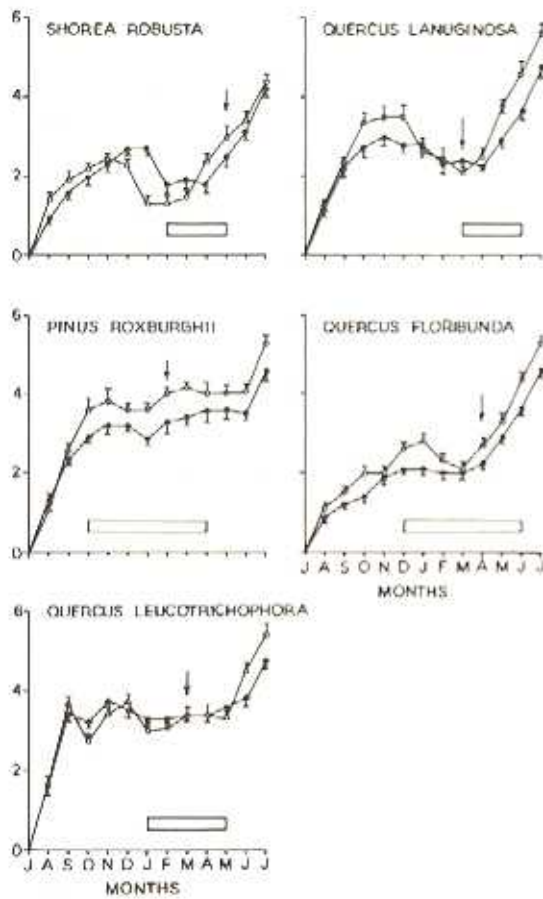


Fig. 1.

Figs. 1-3.

Cumulative diameter changes (mm) in the stems of Central Himalayan forest species in different months in relation to certain phases of leaf development. (Solid circles, diameter at breast height and open circles, diameter at ground level.) The open bars adjacent to curves of diameter indicate the time period when leaf mass declined; the left side of the bar indicates the start of loss of leaf mass and the right side marks the leaf abscission. The arrow indicates the start of leafing. Fig. 1, canopy trees; Fig. 2, undercanopy trees and Fig. 3, shrubs.

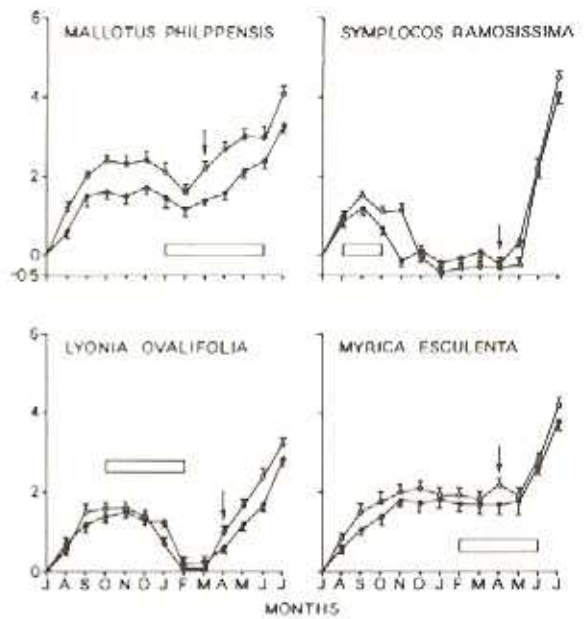


Fig. 2.

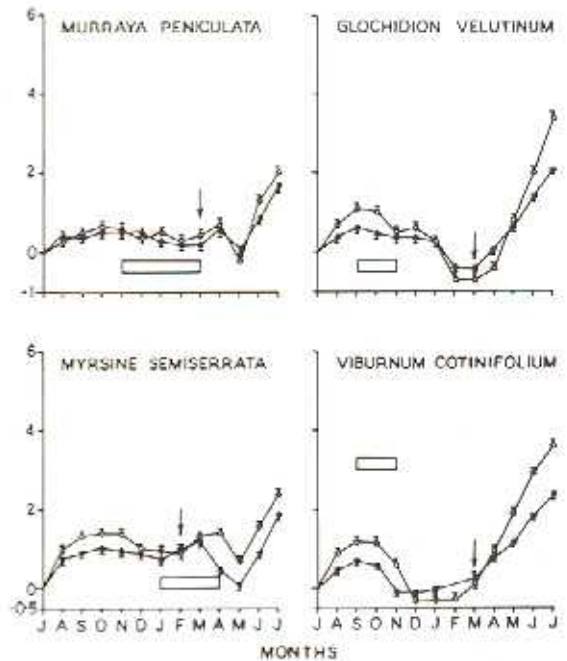


Fig. 3.

Table 5. Percent dry mass loss (as % of the dry mass of mature leaf) from the leaves during senescence (values of leaf mass based on periodical sampling are given in Ralhan & Singh 1987).

Species	Upper crown	Lower crown	Average
Trees			
Canopy trees			
<i>Shorea robusta</i>	24.0	16.7	20.4
<i>Pinus roxburghii</i>	25.0	20.3	22.7
<i>Quercus leucotrichophora</i>	15.0	18.0	16.5
<i>Quercus lanuginosa</i>	13.2	12.3	12.8
<i>Quercus floribunda</i>	10.2	14.4	12.3
Subcanopy trees			
<i>Mallotus philippensis</i>	13.3	10.3	11.8
<i>Lyonia ovalifolia</i>	37.8	30.3	34.1
<i>Symplocos ramosissima</i>	17.9	25.0	21.5
<i>Myrica esculenta</i>	18.3	18.8	18.6
Shrubs			
<i>Murraya peniculata</i>	22.7	17.1	19.9
<i>Myrsine semiserrata</i>	16.4	13.8	15.1
<i>Glochidion velutinum</i>	32.5	24.3	28.4
<i>Viburnum cotinifolium</i>	24.3	35.1	29.7

Table 6. The beginning (bud-bursting) and the end of leaf expansion (when maximum leaf area is reached) and the percentage of total leaf expansion attained in the first four weeks following the bud break.

Species	Period of leaf expansion	% Total leaf expansion*
Trees		
Canopy trees		
<i>Shorea robusta</i>	7.4 - 20.5	87
<i>Pinus roxburghii</i>	26.2 - 15.4	76
<i>Quercus leucotrichophora</i>	24.3 - 25.5	100
<i>Quercus lanuginosa</i>	24.5 - 5.7	89
<i>Quercus floribunda</i>	29.4 - 3.6	98
Subcanopy trees		
<i>Mallotus philippensis</i>	29.5 - 3.7	85
<i>Lyonia ovalifolia</i>	27.4 - 25.5	100
<i>Symplocos ramosissima</i>	27.4 - 18.5	100
<i>Myrica esculenta</i>	25.4 - 30.5	98
Shrubs		
<i>Murraya peniculata</i>	26.4 - 15.4	100
<i>Myrsine semiserrata</i>	1.3 - 22.3	100
<i>Glochidion velutinum</i>	1.4 - 15.4	100
<i>Viburnum cotinifolium</i>	28.2 - 14.3	100

* in the first four weeks

Leaf mass loss and leaf expansion

The percentage of leaf mass loss (see Ralhan & Singh 1987) corresponded with that of stem shrinkage. Regardless of the site, it was conspicuously higher in deciduous species (21.5 - 34.1% of the peak dry leaf mass) than in evergreen species (11.8 - 22.7%) (Table 5). The difference between the deciduous and evergreen species of the same forest was significant as well. To give an example, the loss of mass for the leaves of the lower crown position at the site of the highest elevation was 35.1% for the deciduous species *Viburnum cotinifolium* and 14.4% for the evergreen species *Quercus floribunda*. Most species realized their full leaf expansion well before the beginning of the rainy season (Table 6). All shrubs completed their leaf expansion by mid-April, three of the four under-canopy tree species by May and four of the five canopy species between 15 April and 3 June. In only two of the 13 species did the leaf expansion continue up to the start of the rainy season. However, almost all species completed at least 75 % of the total leaf expansion before the start of the rainy season when the photoperiod increases; this may have been the triggering factor for leaf initiation.

Discussion

Differences in girth fluctuations between species of different communities may have been the result of different strategies of water conservation and metabolism (Bruce, Miller & Chabot 1977). The evergreen species of the Himalayas, which retained their leaves during the long dry season, until new leaves were formed, showed lower stem shrinkage than the deciduous species. Assuming that the degree of stem shrinkage was directly related to water stress, we suggest that the deciduous species included in this study failed to retain their leaves long after the rainy season because of their declining water potential. Because they shed their leaves, the water potential did not decline below a critical level. Stem diameter in these species stabilized subsequent to leaf fall. This has also been observed for certain deciduous species in dry tropical parts of Costa Rica (Borchert 1980).

Senescing leaves of evergreen species showed lower proportional loss of leaf mass and nutrient retranslocation than deciduous species (Ralhan & Singh 1987). The gradual progression of senescence (as indicated by the gradual loss of leaf mass) enabled the evergreen species to rehydrate their stems to some extent, as evapotranspiration losses diminished. Deep rooted evergreen species were restricted to areas with deeper soil profiles, in contrast to widely distributed shallow-rooted deciduous

species. Lack of rehydration in the deciduous species of the study area may have been related to their relatively more shallow root depths. Subrado (1986) suggested that the leaf tissues of evergreen species develop higher turgor pressure than the leaf tissues of deciduous species, and sustain a higher turgor as water potential decreases.

The capacity of evergreen species to retain leaves during the dry winter season and to maintain their water status give them an advantage over the deciduous species, because they can maintain some photosynthetic activity during most of the winter season. The longer duration of photosynthetic activity often enables evergreen species to realize a higher productivity in spite of the lower photosynthetic capacity as compared with deciduous species (Murphy & Lugo 1986). Thus, the maintenance of leaves during the winter season in combination with the development of new foliage at the beginning of the summer season provides the evergreen species with a competitive advantage over the deciduous species of the region. This situation contrasts with that of many temperate regions, such as the Pacific North-west of the USA, where the precipitation pattern is reversed, i.e., the early summer is wet and the late summer is dry (Wolfe 1979). It is possible that the dry summer season does not produce low water potentials in the evergreen species of Central Himalaya (Meinzer, Seymour & Goldstein 1983). We also assume that the pre-monsoon rain storms will somewhat counteract plant water stress. Reich & Borchert (1982) observed that tropical deciduous trees may require the return of higher water potentials for leafing and flowering; these may be provided by spring thunderstorms. In March and April when leaf formation occurs in the Central Himalayan species, 63 and 29 mm rain can occur in the course of four to seven rain storms. This means an average rain storm addition of about 9-15 mm of rain per storm occurring in March and about 4-7 mm per storm in April.

Furthermore, increased biological activity, triggered by increasing photoperiod and temperature, might have enabled species to utilize residual soil moisture more efficiently. After being subjected to drought-induced loss of leaf mass (in evergreen species), or leaf shedding (in deciduous species), trees and shrubs would produce leaves and flowers, as they have attained the water potential required for the occurrence of developmental processes involving cell elongation.

Finally, we discuss the typical phenological characteristic of foliage mass development during the driest part of the year. We suggest that the initiation of leafing, which is also accompanied by flowering in most species, enables them to develop mature seeds during the rainy season. In most of these species seed germination coincides with the rainy season (Singh & Singh 1987),

provided adequate soil moisture is ensured. Availability of water is a critical factor in the seed germination of most woody species of the region, and many of the species with restricted distribution are those whose seed germination is most vulnerable to water stress (Singh & Singh 1987). Secondly, this may enable the trees to have mature leaves with fully developed secondary metabolites at the beginning of the rainy season.

Acknowledgements. Financial support from the Department of Environment, New Delhi is gratefully acknowledged.

References

- Bisht, J. S. & Bisht, J. S. 1984. Ecology of termites in a tropical forest. In: Singh, J. S. & Singh, S. P. (eds.), An integrated ecological study of eastern Kumaun Himalaya with emphasis on natural resources, pp. 305-351. Final Report (HCS/DST/187/76), Kumaun University, Naini Tal.
- Boaler, S. B. 1966. Ecology of a miombo site, Lupa North Forest, Tanzania II. Plant communities and seasonal variation in the vegetation. *J. Ecol.* 54: 465-479.
- Borchert, R. 1980. Phenology and ecophysiology of tropical trees: *Erythrina poeppigiana* O. F. Cook. *Ecology* 61: 1065-1074.
- Brice, I. A., Miller, L. N. & Chabot, B. F. 1977. Competitive exploitation of soil water by five eastern north American tree species. *Bot. Gaz.* 138: 168-173.
- Daubenmire, R. 1972. Phenology and other characteristics of tropical semi-deciduous forests in north-western Costa Rica. *J. Ecol.* 60: 147-170.
- Frankie, G. W., Baker, H. G. & Opler, P. A. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *J. Ecol.* 62: 881-919.
- Hinckley, T. M., Lassoie, J. P. & Running, S. W. 1978. Temporal and spatial variations in the water status of forest trees. *For. Sci. Monogr.* 20. Society of American Foresters, Washington, D.C., USA.
- Köppen, W. 1931. *Grundriss der Klimakunde* (2nd ed.). Bornträger, Berlin.
- Lieberman, D. 1982. Seasonality and phenology in a dry tropical forest in Ghana. *J. Ecol.* 70: 791-806.
- Longman, K. A. & Jenik, J. 1974. *Tropical Forest and its Environment*. Longman, London and New York.
- Meinzer, F., Seymour, V., Goldstein, G. 1983. Water balance in developing leaves of four tropical savanna woody species. *Oecologia* 60: 237-243.
- Murphy, P. G. & Lugo, A. E. 1986. Ecology of tropical dry forest. *Annu. Rev. Ecol. Syst.* 17: 67-88.
- Osmaston, A. E. 1926. A forest flora of Kumaun. Intern. Book Distributors, Dehradun.
- Parker, J. 1956. Drought resistance in woody plants. *Bot. Rev.* 22: 241.
- Raihan, P. K., Khanna, R. K. & Singh, S. P., Singh, J. S. 1985a. Phenological characteristics of the tree layer of Kumaun Himalayan forests. *Vegetatio* 60: 91-101.

- Ralhan, P. K., Khanna, R. K., Singh, S. P., Singh, J. S. 1985b. Certain phenological characters of the shrub layer of Kumaun Himalayan forests. *Vegetatio* 63: 113-120.
- Ralhan, P. K. & Singh, S. P. 1987. Dynamics of nutrients and leaf mass in Central Himalayan forest trees and shrubs. *Ecology* 68: 1974-1983.
- Reich, P. B. & Borchert, R. 1982. Phenology and ecophysiology of the tropical tree *Tabebuia neochrysantha* (Bignoniaceae). *Ecology* 63: 294-299.
- Singh, J. S. & Singh, S. P. 1987. Forest vegetation of the Himalaya. *Bot. Rev.* 53: 80-192.
- Singh, S. P., Khanna, R. K. & Singh, J. S. 1985. Accumulation in wood: A nutrient conserving strategy of tropical forests. *Environ. Conserv.* 12: 170-173.
- Slatyer, R. O. 1967. *Plant Water Relationships*. Academic Press, New York.
- Subrado, M. A. 1986. Aspects of tissue water relations and seasonal changes of leaf water potential components of evergreen and deciduous species co-existing in tropical dry forest. *Oecologia* 68: 413-416.
- Thornthwaite, C. W. 1931. The climates of North America according to a new classification. *Geogr. Rev.* (New York) 21: 633-655.
- Webb, L. J. 1959. A physiognomic classification of Australian rain forests. *J. Ecol.* 47: 551-570.
- Wolfe, J. A. 1979. Temperate parameters of humid to mesic forests of eastern Asia and relation to forests of other regions of the Northern hemisphere and Australasia. U.S. Geological Survey Professional Paper 1106.
- Worrall, J. 1966. A method of correcting dendrometer measures of tree diameter for variations induced by moisture stress changes. *For. Sci.* 12: 427-429.

Received 18 August 1989;

Revision received 18 December 1989;

Accepted 18 December 1989.