Shoot demography of some evergreen and deciduous tree species of Kumaun Himalaya, India, along an altitudinal gradient

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The shoot diameter and shoot length extension growth studied in 10 tree species occurring between 350 to 2500 m elevation in the Kumaun Himalaya. Effects of temperature on shoot growth were studied under natural conditions. Shoot length growth was significantly affected by the temperature during shoot elongation (p<0.01). The optimum temperature for elongation was ranged from 21 to 36°C across the altitudinal gradient. The shoot elongation growth was positively correlated with the shoot diameter growth in all species. The peak activity of leafing takes place during March–April when photoperiod and temperatures are incrementing. All species showed a clear peak value of radial growth in the first few months of growing season. Over 90% of the radial growth was accomplished by the late summer season in the most species; only in a few species it was extended upto the later part of the rainy season. On the basis of successional status, early successional species show a faster shoot extension growth than late successional species.

Key words: Deciduous trees, semideciduous trees, evergreen trees, shoot length growth, shoot diameter growth.

INTRODUCTION

Two contrasting patterns of bud and shoot development are generally recognized in temperate trees (Tomlinson, 1978). In one pattern, found in most conifers, the vegetative shoot is fully “preformed” in the resting bud (Lanner, 1976). In the other hand, at least some shoots are not entirely preformed in the resting buds and a portion of the leaves are formed in the season that the shoot extends (“neoformed”) (Halle et al., 1978). Lechowicz (1984) reported that, with the onset of spring in the temperate deciduous forests of eastern North America, tree leaves do not all emerge in perfect synchrony. It is less clear what causes phenological differences among tree species in a particular region (Ahlgren, 1957). Even within single forests, leaf emergence in spring varies over several weeks among co-existing native trees, and species produce leaves at quite different rates during the rest of the growing season. This has been reported for Populus (Critchfield,
1960), *Fraxinus* (Gill, 1971) and *Quercus* spp. (Reich et al., 1978). Temperate trees exhibit periodicity of both extension and radial growth, which is clearly correlated with seasonal fluctuations in climate (Zimmermann and Brown, 1971). Continuous stem shrinkage, even for several years during rainless periods, has been reported for many trees (Kozlowski et al., 1962). A greater stem shrinkage in deciduous species (DS) compared to evergreen species (ES) have been observed by many workers in the central Himalayan region (Singh et al., 1990; Dhaila et al., 1995) and elsewhere (Fraser, 1956; Winget and Kozlowski, 1965), following a severe drought (Baker et al., 2002).

This shrinkage is highly correlated with atmospheric water deficits (Hinckley et al., 1978; Reich and Borchert, 1982). A few studies in this region (Ralhan et al., 1985; Rawal et al., 1991) and the north-eastern Himalayan region (Booji and Ramakrishnan, 1982; Shukla and Ramakrishnan, 1982) have described some phenological traits of the forest vegetation and have stressed the need to carry out more studies. In a subtropical savanna, Nelson et al. (2002) found that DS were more deterministic and constrained in their growth responses to increased moisture availability than ES. Baker et al. (2002) reported that, despite similar rainfall, the soil water availability during dry season in an evergreen forest site was more than in the semi-deciduous forest in a tropical rain forest of Ghana. Phenology has recently emerged as an important focus of ecological research and could have a contribution to climatic change studies.

In this study, shoot elongation and shoot diameter growth in 10 tree species (7 ES, 1 SD and 2 DS) of the Kumaon Himalaya were recorded. The main objective of this study was to recognize shoot growth phenotype of evergreen and deciduous species and to understand how shoot growth phenotype is linked with the climatic condition of the region.

**MATERIALS AND METHODS**

**Site description**

The six study sites were located close to 29° 22’ N latitudes and 79° 29’ E longitudes along an elevation transect of 350 to 2500 m in Kumaon Himalaya (Table 1; Figure 1). In general, from lower to higher elevations domination of following forest prevailed: Sal (*Shorea robusta*) forests below 1000 m; Chir pine (*Pinus roxburghii*) forest between 1000 – 1600 m; Banj oak (*Quercus leucotrichophora*) forests between 1600 to 2200 m. Among the dominant trees, chir pine is an early successional species, whereas all the oak and sal are regarded as late successional species, forming the climax vegetation of this region (Champion and Seth, 1968).

The soil was sandy loam, with sand percentage being highest at 400 to 900 m elevation and lowest at 1600 to 1700 m elevation. An increasing trend with elevation was found for soil organic matter content (r=0.67, P<0.05), clay (r=0.89, P<0.01) and water holding capacity (r=0.84, P<0.01). Soil pH ranges from 5.1 and 7.9. Among the soil nutrient the available Nitrogen concentration increases with increasing elevation (r=0.81, P<0.05). Available P was maximum in the soil of high elevation sites, occupied by forest of oaks (*Quercus spp.*) and least in low elevation site occupied by *S. robusta* forest. The soil of oak forests was markedly richer in K than those of other forest types such as *S. robusta* forest and *P. roxburghii* forest.

**Climate of the study area**

Data obtained from the State Observatory at Nainital for the study years (2008 to 2009) indicate that within the elevation transect of 1000 to 2500 m, the mean monthly maximum temperatures range from 14°C in November to 30°C in May; mean monthly minimum temperatures from -2°C in January to 16°C in October and mean monthly rainfall ranges from 4 mm in December to 611 mm in August. Data obtained from the O/I Agromet Observatory, Pantnagar indicated that within the elevation transect of 400 to 1200 m, the mean monthly maximum temperatures range from 20°C in January to 36°C in May; mean monthly minimum temperatures from 7°C in January to 26°C in July and mean monthly rainfall ranges from 1 mm in January to 148 mm in August. A rise of 270 m in altitude corresponds to a fall of 1°C in the mean temperature up to about 1500 m, and above 1500 m the fall in temperature is more rapid (Singh and Singh, 1987). The year is divisible into three seasons: the winter, a cold and relatively dry season extending from mid-December through February; the summer, a warm and dry season extending from mid-April to mid-June; and the rainy, a warm and wet season extending from mid-June to mid-September. Transitional periods between summer and winter and between winter and summer are referred to as autumn and spring, respectively.

**Twig sampling**

Six forest types, that is, tilonj oak forest, banj oak forest, oak-mixed broadleaf, mixed broadleaf forest pine mixed with Sal forest and Sal forest were investigated (Table 1). A total of ten species belonging to four genera of ten families were sampled for the six forest types. In the forest, Site 1 ha permanent plot was established by fencing the area. Within 1 ha, permanent plot ten individuals of each of the canopy, subcanopy were randomly selected for collecting seasonal data on shoot elongation and diameter changes. One healthy lateral branch from each stratum viz., upper, middle and lower was marked. To assess the shoot elongation, the distance from the mark to the end of the shoot was measured to the nearest millimeter approximately fortnightly starting from late winter of 2007 for a period of two years (Figure 2a). The diameter changes for marked branches were measured by vernier calliper in two directions at right angle to one another to compensate, to extent, for any eccentricity in the shoots. The observations for diameter changes were made each month at approximately the same time of the day on each reading date to reduce effect of thermal expansion and hydration for period of 12 to 13 month.

**Data analyses**

A one-way ANOVA was performed to compare means and Tukey’s HSD test was used for subsequent multiple comparisons using SAS (Version 9.3). The coefficients of linear regression equation were determined with the analytical statistical software SPSS (Version 21.0).

**RESULTS**

**Vegetation**

Total tree density ranged from 1950 ind./ha in banj oak.
Table 1. List of species selected for study in the Kumaun Himalaya.

| Forest type          | Locality | Elevation (m) | Selected species       | Growth form and leaf persistence | Successional status | Species group |
|----------------------|----------|---------------|------------------------|----------------------------------|---------------------|---------------|
| Tilonj-oak forest    | Nainital | 1900-2200     | Ilex dipryema Wall     | S,E                              | L                   | 2             |
|                      |          |               | Acer oblongum Wall. ex. D.C. | S,E                              | L                   | 2             |
| Banj-oak forest      | Kailakhan| 1700-2000     | Quercus leucotrichophora A. Camus | C,E                              | L                   | 1             |
|                      |          |               | Myrca esculenta Ham. ex D. Don | S,E                              | L                   | 2             |
|                      |          |               | Rhododendron arboreum Smith | S,E                              | L                   | 2             |
| Oak-mixed broadleaf  | Bhowali  | 1600-1700     | Prunus cerasoides D.Don  | S,D                              | E                   | 3             |
| Mixed broadleaf      | Ratghat  | 1000-1100     | Bauhinia variegata Linn. | S,D                              | E                   | 3             |
| Pine mixed with Sal  | Mangoli  | 900-1200      | Pinus roxburghii Roxb.  | C,E                              | L                   | 1             |
| Sal forest           | Kaladungi| 400-900       | Shorea robusta Gaertn.f. | C,SD                             | L                   | 1             |
|                      |          |               | Mallotus philippinensis (Lam.) Muell.-Arg. | S,E                              | L                   | 2             |

C: Canopy, S: subcanopy, E: Evergreen, D: Deciduous, SD: Semideciduous, E: Early successional, L: Late successional, 1: Canopy; 2: Subcanopy and 3: Around cropfields.

Forest to 360 ind./ha in mixed broadleaf forest followed by oak-mixed broadleaf (900 ind./ha), sal forest (1280 ind./ha), pine mixed with sal forest (1350 ind./ha), tilonj oak forest (1610 ind./ha). Across the sites, the maximum species richness of trees (12) was recorded at sal forest. Diversity of trees ranged between 0.62 and 1.97, concentration of dominance ranged between 0.21 and 0.75, β diversity ranged from 1.09 to 2.12 for tree layer across the species.

Stand structure and leaf recruitment

Majority of species leafing started in March and May except Morchella esculenta (ES) in which it was earliest in February. Three species, that is, Mallotus philippinensis (SD), Bauhinia variegata (DS) and Ilex dipryrena (ES) were last to initiate leaves in May. However, in Prunus cerasoides (DS) leafing occurred during autumn season. The concentrated spring/summer leaf drop in the evergreen species accounted for 80% of the total leaves produced in a year; the remaining 20% leaves were retained till rainy season in M. esculenta; till winters in Q. leucotrichophora and I. dipryrena (all ES). Acer oblongum (ES) differed from rest of the evergreen species shedding all the old leaves in a single summer leaf drop episode. A minor leaf drop occurred in most of the deciduous species during rainy season (Figure 2b). The DS, that is, B. variegata retained some leaves until the late winter (January and February).

Shoot diameter growth

Of the total diameter increment, the percentage realized in one month of bud-break ranged between 62.54% in A. oblongum to 82.94% in P. roxburghii. The average value of shoot diameter was maximum (73%) for the subcanopy forest species and minimum for open grown species (63%). A value comparable to that of the subcanopy forest species was also realized by canopy species of forests (72%). The duration of shoot diameter increment ranged from nearly three-four months in P. roxburghii, Rhododendron arboreum and A. oblongum to five-eight months in remaining species, respectively. The average periods of diameter increment was higher for the subcanopy forest species (6 months) than for the canopy forest species (5 months) and for the species of open natural environments (4 months). This period was longer for agro-forestry tree species (7 months).

Distribution of species in different diameter increment classes are listed as follow: R. arboreum (3 to 4 mm); S. robusta, Q. leucotrichophora, P. cerasoides, M. esculenta (4 to 5 mm); I. dipryrena, A. oblongum, B. variegata and M. philippinensis (5 to 6 mm). P. roxburghii showed markedly high value of shoot diameter (18.52 mm) among the evergreen tree species. The average values of diameter increment were similar for canopy (4.96 mm; excluding P. roxburghii) and subcanopy (5.25 mm) species of natural forest community. It was markedly higher for open grown DS species (6.22 mm) (Figure 3 a, b).

Shoot elongation

In P. cerasoides, 90% shoot elongation was completed by February, in P. roxburghii it completed by June, prior to the commencement of rainy season and in Q. leucotrichophora and R. arboreum it completed during rainy season (July and August). In S. robusta, M. philippinensis and I. dipryrena it was completed by the end of rainy season (that is, in September) and in B variegata and M. esculenta it in completed by October.
Figure 1. Location map of the study area.
Figure 2. (a) Schematic representation of shoot measurement, (b) The periodicities of leafing and leaf drop in 2009 in the tree species selected for study, where 1 = first day of the year (2009).

The shoot length growth of evergreen, semideciduous and deciduous species was found significant at the $p < .001$ [F (2,124) = 19.997] (Figure 5). Post hoc comparison using Tukey HSD test showed the mean score for the ES ($M = 12.11$, $SD = 5.03$) was significantly different from the DS ($M = 22.69$, $SD = 13.82$). However, the SD ($M = 17.04$, $SD = 4.04$) did not significantly differ from the ES and DS. Shoot length growth was also found significant at the $p < .01$ across all species group, that is, canopy, subcanopy, open-grown and agro-forest [F (3, 123) = 4.726, $p < .05$]. Post hoc showed the mean score for the open-grown species ($M = 5.43$, $SD = 1.30$) was significantly different from the canopy species ($M = 4.28$, $SD = 0.80$) and subcanopy species ($M = 4.59$, $SD = 1.10$). However, the agro-forest species ($M = 4.86$, $SD = 1.30$) was not significantly different from the other groups.
Figure 3. Rate and duration of shoot diameter growth in (a) *A. oblongum*, *B. variegata*, *I. dipyrena*, *M. esculenta*, *M. philippinensis*, *P. cerasoides*, *Q. leucotrichophora*, *R. arboreum*, *S. robusta* and (b) *P. roxburghii*.
DISCUSSION

Day length and air temperature induce leaf flushing (Frankie et al., 1974; Hanninen, 1995), which holds true for the present study where peak leafing takes place during March–April when photoperiod and temperatures are increasing. Further, the role of isolated rain showers to begin leafing by replenishing water content has been frequently accentuated (Borchert et al., 2002). Isolated rain showers broken the long dry spells from October to June and helping leaf emergence during March–April. Singh et al. (1994) have reported density value ranging from 250 to 2070 tree/ha for different Central Himalayan forests.

The canopy species achieved more shoot extension compared to the subcanopy species (18.64 cm vs. 10.86 cm), which helps to gain more height and exploit more light regime in the forests. Subcanopy species grows under low light regimes where resources are often limiting; they likewise deliver the power to adapt their growth pattern favorably in the forest canopy. Time-separation in growth activity of species in a given community would protect the species from one another with respect to competition for resources, such as nutrients and solar radiation. Height growth of many temperate zone species is completed early in the season and often long before the drought of midsummer and late-summer (Kozlowski, 1971a). Interestingly in this montane region of subtropical latitudes where climate is governed by the monsoon pattern of rainfall, the late summer (July to mid-September) is wet, yet most of the shoot extension is either before the onset of wet summer season or in the middle of the wet summer season. This phenological strategy which involves maximum production of shoots and hence the foliage prior to the onset of rainy season enables the species to utilize maximally the most favourable growth condition of rainy season (with regard to moisture and temperature). Thus, the late summer season which is wet, is responsible for a longer favourable period for plant productivity in this region, compared to that in temperate region. The peak leaf area was found smallest in I.
Figure 5. Relationship between shoot diameter growth and shoot length extension in evergreen, deciduous and semi deciduous tree species.

dipyrena (18.65 cm²) and largest in S. robusta (179.14 cm²). On an average the peak leaf area for DS (87.71) was greater than for the ES (33.67 cm²) (Kumar et al., 2013).

The ecological strategy of trees had been linked to shoot morphogenesis (Bormann and Likens, 1975, Marks, 1975). Though plastic modifications can occur in response to changes in conditions (e.g. nutrients, water stress, temperature) during shoot elongation) the internode lengths and total shoot lengths are ultimately heritable traits (Cannell and Smith, 1983) which cannot easily be extended beyond a norm for a particular species (Lanner, 1976). A majority of the species studied followed a unimodal pattern of growth, that is, peak extension growth being in the summer season (April – June). The average shoot elongation period for the canopy species of natural forest communities (5 months) was shorter than that for the subcanopy species (6 months). This is due to the higher number of subcanopy species (4 species) compared to canopy species (3 species). These values are markedly longer than 2 to 8 weeks reported for tree species of temperate region (Kienholz, 1941; Kozlowski and Ward, 1961; Kozlowski, 1964a and b). For a number of species studied, the shoot elongation period exceeded 8 weeks, the maximal being 16 weeks, which approaches the value reported for Cottonwood (20 weeks) by Minckler and Woerheide (1968). The shoot diameter and shoot length growth was significant (p < .01) in all ES, SD and DS (Figure 5). Analysis of variance of shoot length \([F(9, 116) = 31.31, p < .0001]\) and shoot diameter growth \([F(9, 116) = 228.30, p < .0001]\) across the species showed a significant variation. Mean monthly temperature and shoot elongation shows a significant relationship \((r = 0.276, df = 124, p < 0.01)\).

Studies based on comparisons of individuals of ES and DS species indicated that DS species initiate and complete growth earlier in the season than ES species (Miller, 1947; Harvey and Mooney, 1964; Mooney and Dunn, 1970; Aljar et al., 1972; Gray, 1982). The present study shows that the average amount of shoot elongation was markedly greater for DS (29.79 cm) and SD (20.11 cm) than for the ES (14.35 cm). The rapid shoot growth enabled the two DS species to accomplish greater shoot
extension growth earlier in the season compared to ES species. With respect to this, our findings are in accordance with the findings of earlier workers (Mooney and Dunn, 1970; Gray, 1982).

This rapid growth in DS species during the favourable period of the year should compensate for any disadvantage in photosynthetic carbon gain that may occur due to the delay in initiating the growth, during the early part of the growth period. In the present study all the ES species are generally late successional while the DS species are early successional (Troup, 1921; Champion and Seth, 1968; Dhaila et al., 1995). On the basis of successional status, the present study agrees with the investigations of previous workers (Boojh and Ramakrishnan, 1982; Shukla and Ramakrishnan, 1984). They stated that early successional species show a faster shoot extension growth than late successional species.

All species showed a clear peak value of radial growth in the first few months of growing season. Over 90% of the radial growth was achieved by the late summer season in the most species; but in a few species, it was extended up to the later part of the rainy season (September). P. cerasoides and R. arbores were unusual species for in them radial growth occurred until the winter season. Undoubtedly, much of the remarked variation in diameter growth during the rainy season was related to hydration changes in the shoot which are superimposed on cambial growth (Kozlowski, 1972, Kramer and Kozlowski, 1979). However, no previous study related to temperature effect on shoot phenology of this region on selected tree species was found. This is an initiative step to know the effect of rising temperature on shoot growth.

Conflict of Interest

The authors have not declared any conflict of interest.

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