INTRODUCTION

Phenology embraces all studies of the relationship between climatic factors and periodic phenomenon in organisms (Daubenmire 1947). Lieth (1970) has described phenology as the art of observing the life cycle phases of living organisms in their habitat throughout the year. Phenological observations provide a general background for viewing and synthesizing detailed quantitative information and development of plant species. This
science can be dealt as the bio-morphological adaptability in the organisms as resulted by competition among them and interacting environmental factors and can be regarded as a function of evolutionary tendency among the organisms. The phenological knowledge contributes towards our understanding of how the organisms phase their phenological events in time and space which in turn helps in a better appraisal of functioning of the ecosystem.

Lieth (1974) has pointed out that there are many aspects of productivity studies which can be categorised, predicted and evaluated on the basis of phenological attributes. Appropriate date for many important biological events, e.g., beginning and end of the growing season; germination and seed set etc. are needed for analysis of several aspects of ecosystem functioning. According to Wielgolaski (1974) not only the classic phenological plant studies, but also length of shoots and number of shoots at different times of the vegetation period, as well as number of leaves and leaf area of various stages should be considered. In phenological studies of the Miombo ecosystem, Malaisse (1974) concluded that although rainfall remains the principal factor for various phenological changes, temperature must also be taken into account for the same.

Seasonal changes in leaf area are critical for fluxes of carbon, solar energy and water in forested ecosystems (Marshall and Waring 1986). For photosynthesis, transpiration, respiration and light interception can be directly related to leaf area (Gholz
et al. 1976; Jarvis and Leverenz 1983), and these processes underlie correlation between Leaf Area Index and productivity (Gholz 1983; Schröder et al. 1982; Waring 1983). Borghetti et al. (1986) concluded that a reliable estimate of leaf area is of great importance to model ecophysiological processes and growth efficiency.

The amount of growth and its seasonal variation caused by environmental factors have been mostly studied for temperate trees (Kienholz 1934; Mark 1970; Mikola 1962; Reed 1980; Pietarinen et al. 1982; Zobel 1983). Information on shoot growth of tropical and subtropical trees is scanty. Recently, Boojh and Ramakrishnan (1982a and b) have collected some data on tree growth of Eastern Himalaya and Ralhan (1985) and Negi (1989) on the representative trees and shrubs of Kumaon Himalaya forests occurring between 300 - 2150 m elevation.

The present chapter deals with the periodicity of major phenophases, shoot growth (radial and elongation) and leaf dynamics of *L. camara* community. The main objective of the study was to collect information on 'how this exotic shrub, a recent invader of this region interacts and compares with the prevailing natural forest communities of this region'.
METHODS

General Phenophases

Phenological records were made for seven phenophases of *L. camara*, viz., vegetative bud formation, leafing, flower bud formation, flowering, fruiting, fruit ripening and leaf drop for a period of one year, from March 1986 to February 1987. These phenophases were recorded in 100 marked individuals of similar sizes distributed throughout the study site so to represent the average situation.

The observations were made at weekly intervals during high activity period (March to July) and at 3 - 4 weeks intervals in the stages when changes were slow to occur. If a given phenophase was observed in 5 - 10% individuals it was considered to have initiated and the individuals were considered to be in that phenophase as long as that phenophase was represented by at least 5 - 10% individuals. Because of the low height of the shrubs it was possible to make observations without the help of binocular or step-ladder.

Shoot Growth

To determine the annual extension and radial growth of leader and lateral shoots, three representative individuals of
similar sizes were selected and three lateral and three leader shoots in each of these three individuals were marked at the time of their emergence in April 1986.

In the marked shoots, length was recorded to the nearest 0.1 cm and the diameter to the nearest 0.1 mm by the help of a screwgauge in two directions (at right angles to each of the sides) so as to minimise the error. These observations were taken at monthly intervals.

Leaf Longevity, Leaf Population and Leaf Development

To determine the leaf longevity, 50 leaves representing all crown positions in five representative individuals were marked in April 1986. Their number was counted in each visit till they survived.

To determine the changes in leaf number per shoot, 500 vegetative buds were marked at the time of their opening in early April in the representative individuals. From this marked population 50 shoots were harvested randomly at monthly intervals throughout the period the individuals bore the leaves. These harvested shoots were brought to the laboratory and leaves per shoot were counted. One Hundred leaves from the shoots of all
crown position were sorted out to determine leaf area and leaf dry mass. The length and width of the leaves were measured to the nearest 0.1 cm, and 25 leaves were traced to measure the leaf area by planimeter. They were then oven dried at 70°C for 48 hours and weighed in an electric balance. The total dry weight of the sample leaves was divided by the number of leaves in the sample to determine dry weight per leaf.

On the basis of leaf dry mass the relative growth rate (RLGR) and specific leaf area (SLA) were calculated by using following expression (Evans 1972).

Relative leaf growth rate (RLGR)

\[ RLGR \text{ (g g}^{-1}\text{ day}^{-1}) = \frac{\log w_2 - \log w_1}{T_2 - T_1} \]

Where, \( w_1 \) and \( w_2 \) are the leaf dry weight (g) in time \( T_1 \) and \( T_2 \), respectively.

Specific leaf area (SLA)

\[ SLA \text{ (cm}^2 \text{ g}^{-1}) = \frac{A}{L \times W} \]

Where, \( A \) = leaf area (cm\(^2\)) and

\( LW \) = leaf dry weight (g).
Regression equation was also developed relating leaf area calculated by the product of length and width (X) determined by planimeter (y), n = 20.

\[ y = 1.10 + 0.60 \times X \ (r = 0.83, \ P < 0.01) \]

RESULTS

Periodicity of Major Phenophases

The periodicity of different phenophases of *L. camara* in one year cycle is given in Fig. 3.1. It is difficult to indicate the exact time when the vegetative bud primordia initiated. The vegetative buds became visible to the naked eye in the last week of March, the bud formation peaked at mid-April, but buds were seen up to mid-June. Leafing began after two weeks of the peak bud formation (i.e., last week of April) and continued till late August, and the leafing period was of 20 weeks. The leafing peaked during June and July and this was followed by peak flower bud formation during July and August. Flowering began after one week of flower bud formation and showed two peaks one in August and the other in mid-October. Flowering continued until mid-November. Fruit formation began after two weeks of flowering and peaked once in August and then in October. Fruits
Fig. 3.1 Representation of various phenophases of *L. camara* in an annual cycle. ■ represents seed dispersal, ● formation of seeds, □ flower bud bursting, ●●● flower bud formation, ●●●● leaf drop, ●● leaf senescence, ●●● leaf flush and ●●● leaf bud formation.
ripened after two weeks of fruit formation and simultaneously the fruit dispersal took place, which continued till mid-December. Leaf senescence started in the beginning of December and continued until February. This was followed by leaf drop, which was concentrated during January and by the end of February all the individuals became leafless. Thus, the individuals experienced a leaf less period of about seven weeks.

Shoot Elongation

Shoot elongation occurred slowly after vegetative bud bursting. However, it could attain a measurable size only when the shoot attained four-leaf stage. The leader shoot attained four-leaf stage in early May, compared to the May-end in lateral shoots. The pattern of shoot elongation is indicated in Fig. 3.2. We did not find any marked difference in the shoot elongation pattern between leader and lateral shoots. Shoot elongation in both the leader and lateral positions was slow until June, resulting in only about 20% of the total shoot elongation. Thereafter, a phase of rapid shoot elongation was initiated. In the period about 80% of the total shoot elongation was accomplished in both leader and lateral shoots. The amount of shoot elongation attained at the end of growth (October) was 181.0 + 9.08 and 201.90 + 15.30 mm in the leader and lateral shoots, respectively. The approximate shoot elongation period was seven months both for leader and lateral shoots.
Fig. 3.2  Cumulative per cent shoot elongation in leader and lateral shoots of *L. camara*. Open circles indicate lateral shoot and closed circles leader shoot.
FIG. 3.2
Estelar
Diameter Growth

At the first measurement (i.e., four leaf stage of the shoots), the average diameter of leader (1.03 ± 0.06 cm) shoots was markedly greater than the lateral shoots (0.20 ± 0.013 cm). Shoots of both the crown positions showed a rapid increase in diameter from June to August. During these three months about three-fourth of the total diameter increment occurred (Fig. 3.3). At the end of growing season the average diameter increment realized by the leader shoot (0.45 ± 0.025 cm) was about 1.2 times greater than realized by lateral shoots (0.37 ± 0.016 cm).

Both leader and lateral shoots showed shrinkage during November and December, accounting for about 5% in leader shoot and 8% in lateral shoot of the total diameter gained by them. This amount of shrinkage was 0.22 ± 0.013 mm in leader and 0.30 ± 0.010 mm in lateral shoots. As leaf fall progressed the diameter became stabilized.

Leaf Population Dynamics

The leaf number increased gradually through the season and attained a maximum of 25 ± 4.25 leaves per shoot in mid-September and remained stable until mid-October. The leaf production was relatively greater in July and August, and
Fig. 3.3 Cummulative diameter changes in leader (□)
and lateral (■) shoots of L. camara.
FIG. 3.3

CUMULATIVE DIAMETER CHANGES %

MONTHS

A M J J A S O N D J
during July and August, about half of the total leaf population was produced (Fig. 3.4). After mid-October, leaf shedding occurred, rather slowly until December and rapidly (about one-third of total leaf shed) in January.

**Leaf Area**

The total period of leaf expansion for individual leaves was about four weeks. In the first two weeks, the leaves made up about three-fourth of the total leaf expansion (Fig. 3.5). The average leaf area at fullest expansion was 18.30 cm\(^2\) and the average rate of leaf expansion was 0.61 cm\(^2\) day\(^{-1}\).

**Leaf Mass**

Monthly variation in leaf mass is shown in Fig. 3.6. Three phases of leaf mass changes in leaves were obvious (i) the phase of increasing leaf mass (ii) the phase of comparatively stable leaf mass; and (iii) the phase of declining leaf mass. Leaf gained in mass continuously until August. At the phase of stable leaf dry weight during August to September, the average leaf weight was 226.00 mg.

The leaf mass started declining in October and the average value just prior to leaf shedding in December was 150.00 mg. Thus, the loss of leaf mass was 33.6 per cent
Fig. 3.4 Periodicity of leaf recruitment in *L. camara* shoots. Bars indicate the cumulative percent of total leaves produced/shoot and closed circles indicate the number of leaves per shoot.
Fig. 3.4

Cumulative % of total leaf production/shoot

No. of leaves per shoot

MONTHS

A  M  J  J  A  S  O  N  D  J

30
20
10
0
-10
-20
-30
Fig. 3.5 Changes in leaf area (cm²/leaf) from bud bursting to the culmination of leaf expansion of L. camara.
FIG. 3.5

LEAF AREA cm² LEAF⁻¹

WEEKS

Estelar
Fig. 3.6 Changes in leaf mass (g/leaf) from bud bursting to the senescence of leaf of *L. camara*.
Specific Leaf Area

The specific leaf area (SLA) increased sharply in the first month of leaf initiation (Fig. 3.7). Thereafter, it declined gradually until August. Then, came a phase of stable SLA which lasted until September. This was also the phase of stable leaf mass. At this phase, the SLA was about 80 cm$^2$ g$^{-1}$. A substantial increase in the SLA occurred after this phase, which continued till the leaf abscission. Obviously, this was a result of loss in leaf weight.

Relative Leaf Growth Rate

The relative leaf growth rate is indicated in Fig. 3.8. One clear peak of R_LGR was discernible following the bud bursting, whereafter it tended to decline, but with marked fluctuations. The highest value of R_LGR, recorded in May was 0.018 g g$^{-1}$ day$^{-1}$.

Leaf Longevity

The average leaf longevity was 267 ± 4.03 days (that is about 9 months), with a range of 210 to 308 days. Of the tagged leaf population, first leaf was shed in October and the last in January.
Fig. 3.7 Changes in specific leaf area (cm$^2$/g) from bud bursting to the senescence of leaf of *L. camara.*
FIG. 3.7

MONTHS

SLA (cm²/gg)

A    M    J    J    A    S    O    N
Fig. 3.8 Relative growth rate (g g$^{-1}$d$^{-1}$) of leaf of L. camara from bud bursting to the senescence of leaf.
RELATIVE GROWTH RATE OF LEAF (g g\(^{-1}\) day\(^{-1}\))

MONTHS

FIG. 3.8
Discussion

The initiation of growth in *L. camara* during the dry and warm season (April) of the year is a feature, also shared by most of the woody species of the Central Himalayan region. However, most of the leafing in the native woody species is completed well before the commencement of the rainy season, while in *L. camara*, the leafing peaks only during the rainy season.

A lengthy leafing period and display of flowers and fruits during most of the growing period are some other phenological features, which indicate the tropical affinity of this shrub (Shimizu 1983). Though a native of South America, the shrub is now truly native in this region. Negi (1989) has reported that three species, *Shorea robusta*, *Tectona grandis* and *Bauhinia variegata* (which are among the major forest forming species of southern and central India, respectively) also exhibit leaf initiation in late summer (or just prior to the monsoon sets in) and a lengthy leafing period. In contrast, brief leafing period is a characteristic feature of the native species of the Central Himalaya (Ralhan et al. 1985a, 1985b).

In the tropical climates suppression of leafing until the onset of rainy season due to low soil moisture has been reported by several workers (Boaler 1966, Daubenmire 1972, Frankie et al. 1974, Longman and Jenik 1974). Though in many
tropical areas of seasonally dry climates, woody plants start leafing during dry summer season (Reich and Borchert 1982).

Unlike the native tree species of this region which complete most of their leaf production well before the onset of rainy season (Singh and Singh 1987, Negi 1989) in *L. camara* the rapid leaf production is suppressed until the onset of rainy season. This phenomenon helps *L. camara* to put newly formed leaves in favourable condition of wet and warm rainy season with active metabolic activity to exploit temporary conditions of resource availability effectively. The extended period of leaf production in early successional species enables them to have a large photosynthetic area to exploit effectively temporary conditions of resource availability which follows disturbance (Boojh and Ramakrishnan 1982). This is a feature which is different from most of the other native species of late successional habitats studied in this region earlier. This character has been referred to as opportunistic growth pattern by Pook (1984) in *Eucalyptus maculata* and by Negi (1989) in *Alnus nepalensis*.

Growth analysis of some tropical trees (Coombe 1960, Coombe and Hadfield 1962) has revealed that the rapid growth of early successional species does not lie in particularly efficient energy conversion but rather their capacity to unrestricted leaf production. This results in producing a considerable proportion of foliage and reproductive parts, which may be one of the
potentials which enables them to behave exploitatively in the ecological niche they occupy.

Tropical plants are known to exhibit flowering and fruiting many times a year (Shimizu 1983). *L. camara* produces flower and fruits almost continuously during most of the period the individuals grow.

Shoots of *L. camara* elongate slowly in the initial two months of growth, and rapidly only when the rainy season commences. This seasonal pattern of growth has been recorded for successional species of the humid eastern Himalaya. They make only about 50% of the annual extension growth in the beginning of the growing season and continued to grow almost all through the favourable growth season (Boojh and Ramakrishnan 1982). In total *L. camara* showed a shoot elongation period of 28 weeks compared to the average of 20 weeks for tree species of Central Himalaya (Negi 1989).

The diameter increase in the shoots of *L. camara* followed the same pattern as did the native deciduous species of this region (Ralhan 1983). The rate of diameter increment was a bit slower in Summer and became faster at the onset of rainy season. Undoubtedly, much of the observed variations in diameter growth is related to hydration changes in the stem which are superimposed on actual cambial growth (Kozlowski 1972, Kramer
and Kozlowski 1971). The diameter growth ceased somewhat earlier (mid-September) in leader shoots than the lateral shoots (October).

Winter stem shrinkage of plants has been observed by many workers (e.g., Fraser 1956, Winget and Kozlowski 1965). In L. camara, most of the stem shrinkage occurred during November and January, whereafter, the stem diameter stabilized as leaf shedding progressed. Similar observations were made by Ralhan (1985) for the native deciduous trees and shrubs of this region. Fielding and Millet (1941) found that the stems of monitery pine were constantly shrinking and swelling in response to atmospheric conditions and growth. Stem diameter never remained the same for more than a few hours, they concluded that study of actual growth with dendrometers was complicated sometimes and then it was difficult to determine with dendrometer measurements exactly when cambial activity begins or ends.

The leaf expansion phase was longer for L. camara (4 weeks) compared to the average of 2.5 weeks reported for the native shrub species of this region (Ralhan 1983). This resulted because L. camara is a light demander species (Troup 1921) and enjoys full light intensity with almost no competition for light with other associated shrub species. The native species expand their leaves in a relatively shorter period because the canopy shade becomes limiting to them in the later stages.
The maximum leaf expansion rate for *L. camara* was 1.13 cm\(^2\) day\(^{-1}\) during the second week and the minimum 0.2 cm\(^2\) day\(^{-1}\) on the last week of expansion period. Chapin and Tryon (1983) found more rapid leaf growth rate which occurred early in growing period for deciduous than for evergreen species as is typical of northern and temperate trees and shrubs (Kozlowski 1971, Chapin et al. 1980). At the fullest expansion, the leaf area of *L. camara* (19.50 cm\(^2\)) was comparable with the range, 6.10 - 58.40 cm\(^2\) reported for the native shrubs of this region (Ralhan 1985).

The leaf mass loss (33.10%) in the senescing of *L. camara* leaves was similar to the values (29.70 - 34.10%) reported for the deciduous woody species of this region (Ralhan 1987, Negi 1989). Considerably higher magnitudes of leaf mass loss (48 - 60%) has been reported for deciduous species, *Acer rubrum* (Gizzard et al. 1976) and *Populus deltoides* (Bakey and Blackmon 1977). Most of this loss in leaf mass occurs during the month prior to abscission.

The specific leaf area of *L. camara* (average being 95.12 cm\(^2\) g\(^{-1}\)) was about 1.5 times greater than that reported for the evergreen species of the region (Negi 1989), indicating that its leaves were distinctly thinner than those of evergreen species. Our value of mean SLA (95.12 cm\(^2\) g\(^{-1}\)) lies in the mid point of the range 70.80 - 102 cm\(^2\) g\(^{-1}\) reported for deciduous species by Gholz et al. (1976), Del Rio and Berg (1979) and Negi (1989).
Similar to other prevailing deciduous species of this region (Ralhan 1985, Negi 1989), the \( R_{LGR} \) of leaves attained peak value at the bud burst for all the species. This sudden drop in the \( R_{LGR} \) in June can be related to the water deficit (Singh et al. in press) which becomes constant during wet conditions in rainy season suggesting the water-limited growth. The leaf longevity of \( L. \) camara \((267.00 \pm 4.03 \) days) lies in the midpoint of range reported for the prevailing shrub species of this region (Ralhan 1985).