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Research Article

PLANT WATER RELATIONS AND PHENOLOGICAL SHIFTS IN RESPONSE TO DROUGHT IN *CASTANOPSIS INDICA* AT PHULCHOWKI HILL, KATHMANDU, NEPAL

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ABSTRACT

In the central Himalaya, plants are subjected to a prolonged dry period, thus developing moisture stress. Phenomorphological variations such as leaf expansion and flowering are affected by the interaction between water availability, stem water storage, wood moisture percentage, wood density and wood water. Sensitivity to water stress and phenological processes such as leaf emergence, senescence, flowering, fruiting and their relationship with wood water properties, starch percentage content, specific leaf mass (SLM), nitrogen content in leaves was studied in one Himalayan evergreen tree species, *Castanopsis indica*. Wood moisture, reserved starch percentage and SLM had a strong effect on phenological activities. They increased during the vegetative bud break and leaf emergence and decreased during senescence. Similarly leaf nitrogen in the studied species was at the crest of concentration during leaf initiation then declined, one in expanded leaves as the concentration became diluted by increasing cell wall material, and the other at the time of senescence by resorption.

Keywords: *Castanopsis indica*, phenology, resorption, senescence, specific leaf mass.

INTRODUCTION

Phenological events of the plants are good indicators of climatic differences as leaf life cycle puts strong demands on plant water balance. The timing of leaf production can be predicted using seasonal patterns of rainfall and mechanisms of drought resistance in tropical forest plants[1]. Phenological behaviors are affected by the interaction between water availability, stem water storage, hydraulic architecture and sensitivity to water stress and phenomorphological variations such as leaf expansion, bud set, bud burst, shoot growth and flowering are mostly affected by the tree water status[2,3]. Phenological behaviours are very sensitive to small variations in climate and their responses to climate change can be useful to predict vegetation adjustments and future tendencies in ecosystems[4]; especially in the study of ongoing changes related to global warming[5,6]. Most phenological studies have been conducted in wet and cold regions, where temperature is the main factor determining phenology. In Mediterranean climate regions, water availability is, besides temperature, a key factor determining plant performance[7]. For instance, water may affect flowering phenology[8] and / or restrict growing season length[9] in plants. In the Himalayas, the climate is characterized by concentrated rainfall from mid-June to mid-September. Since winter is basically dry, a small amount of reduction in rainfall in the dry winter and pre monsoon seasons have a profound effect on the adaptational process of plants[10]. There is little information regarding the role of water in controlling leaf phenology of temperate trees especially central Himalayan trees. Most evergreen tree leaves in the central Himalaya have a life span of more than one year, a period longer than for deciduous leaves[11-13]. Phenological processes such as leaf emergence, expansion, flowering and fruiting occur before the onset of monsoon when trees still bear old leaves unlike in deciduous trees where rehydration of leafless twigs becomes a prerequisite for initiation of new leaves[3,14,15] and the loss of leaf dynamics (nitrogen, specific leaf mass, etc.) begins when there is a subsequent decrease in soil water potential and hydraulic conductance. In the prevailing situations to explicate the role of water availability and how expanding leaves of these Himalayan trees withstand the conditions of high evaporative demand during the dry summer, a detail study of phenological events (leaf fall, bud set, bud burst, leaf initiation, expansion, flowering, fruiting and shedding) in relation to their water status would be helpful. This study is focused on the timing of leaf development, leaf dynamics (nitrogen content and specific leaf mass) and senescence associated with the moisture stress and the seasonal changes in wood water reserve, nitrogen and starch content in leaves of broad-leaved evergreen tree species- *Castanopsis indicia* (Roxb.) Miq.

MATERIALS AND METHODS

Study site

The study was carried out at Phulchowki Hill (27^{0}33'N, 85^{0}22'E), 10 km SE of Kathmandu, Nepal. It is a part of the sub-Himalayan Mahabharata range with an altitudinal range of 1400-2715 m with extensive diverse forests mostly dominated by broad-leaved evergreen trees. *Castanopsis indica* is a dominant species co-occurring with *Schima wallichii* at the lower elevation from 1400 m –1800 m. At higher elevations the vegetation is dominated by evergreen oaks. Phulchowki Hill has a typical warm temperate monsoon climate with three seasons round the year: cold and dry winter (October to February), pre monsoon dry summer (March to May) and monsoon (June to September). Mean long-term air temperature ranges between 2.6-18.7^{0}C in winter and 15.8-28.2^{0}C in summer and mean long-term annual rainfall is 1882 mm with about more than 80 % of this occurring between mid-June and mid-September. The annual precipitation at Kathmandu for 1999 was 1729 mm. Precipitation was zero from December 1998 to March 1999 and a sparse rainfall of 4 mm occurred on January 27 and 6 mm on April 9, 1999, respectively. In the year 2000, precipitation was 1407 mm. Early winter had negligible rainfall, a total of 0.2 mm during November and December 2000[16].

Measurements

Phenological observations were done by selecting three representative trees and on each sampled tree many twigs were marked. Phenological events (leaf senescence, leaf emergence, flowering and fruiting, bud initiation and bud burst) were tabulated on each sampled tree every month. Non-sampled trees were kept under observation for general acuity and phenological spectrum was created on events such as leaf senescence, leaf emergence, twig emergence, shoot elongation, bud formation, flowering, and fruiting. Wood water properties (wood moisture percentage, wood density and water in wood per volume), starch percentage, specific leaf mass, nitrogen content in leaves were measured on a monthly basis on the sampled tree. Measurements were taken for 28 months including three consecutive winter and summer dry months from December 1998 to April 2001. One monsoon month's observation was made in September 1999. Wood water properties, i.e. volume of wood, fresh weight and dry weight were determined from the sapwood of the marked trees and Specific Leaf Mass (SLM) was measured in five leaves from three branches of the marked trees. Measurements were done according to Poudyal[17]. Percentage Nitrogen content in leaves was estimated by the micro – Kjeldahl method in modified form PCARR[18]. Estimation of twig starch content was done according to Zobel[19]. As the starch level may vary with the age of the twig, two groups of twigs were measured: 0–year old (starch$_0$- refers to current year growth) and 1–year old (starch$_1$- refers to last year growth). Analysis of variance (ANOVA) and Least Significance Difference (LSD) tests were done separately for each variable. Factors in the ANOVA were sampling months and year numbers. Spearman rank correlation analysis was used to express the relationship between the sampled variables. The statistical package used was StatGraphics Plus ver. 4.0 (Statistical Graphics Corp., Rockville, MD, USA).

Table 1

W_C	W_D	W_W	starch$_0$	starch$_1$	SLM	N
73.1 ± 1.8	0.53 ± 0.01	0.39 ± 0.01	64.1 ± 4.1	61.7 ± 3.4	0.94 × 10^{-2} ± 0.06	2.0 ± 0.04

Mean values (± SE) of measurements in *C. indica* during all sampling dates. Mean wood moisture percentage (W_C), wood density (W_D), water in wood per volume (W_W), starch percentage in zero year twig (starch$_0$), one-year old twig (starch$_1$), specific leaf mass (SLM) and nitrogen content (N).
Units for W_D and W_W are g cm^{-3}, SLM is g cm^{-2}, nitrogen and starch content in percent

Table 2

Variables		W_C	W_D	W_W	starch$_0$	starch$_1$	SLM	N
Years	1	66.2 a	0.49 a	0.33 a	91.9 b	86.9 b	0.93 X 10^{-2} a	2.12 b
	2	72.5 b	0.57 c	0.41 b	66.0 ab	70.3 b	0.92 X 10^{-2} a	1.94 a
	3	79.7 c	0.53 b	0.42 b	43.8 a	35.4 a	1.05 X 10^{-2} a	1.93 a

Mean values (± SE) of measurements of wood moisture percentage (W_C), wood density (W_D), water in wood per volume (W_W), starch percentage in zero year twig (starch$_0$), one-year old twig (starch$_1$), specific leaf mass (SLM) and nitrogen content (N) in *C. indica* during three sampling years.
Year 1 = December 1998 to June 1999, Year 2 = November 1999 to June 2000 and Year 3 = October 2000 to April 2001 (value of September excluded).
Within columns, different letters indicate significant differences (P = 0.05, Fisher's multiple range test)

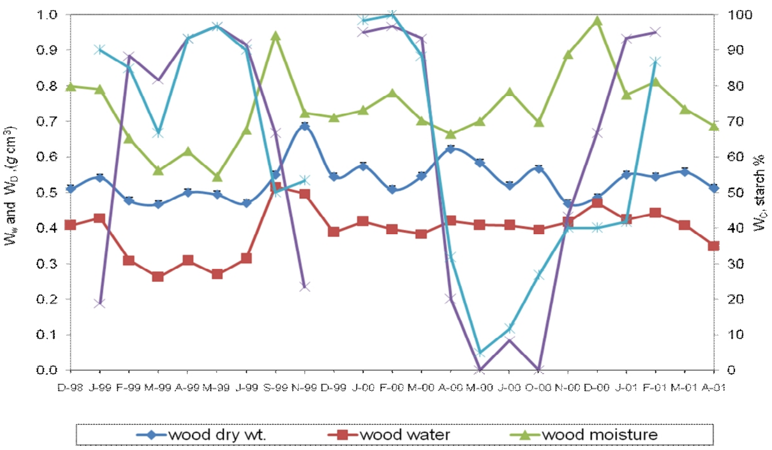

Figure 1:
Volume of wood water(W_W), dry wood (W_D), wood moisture ,content (W_C) starch$_0$ and starch$_1$ year percentage content in *Castanopsis indica*

Figure 1: Volume of wood water (W_W), dry wood (W_D), wood moisture content (W_C) starch$_0$ and starch$_1$ year percentage content in *C. indica*

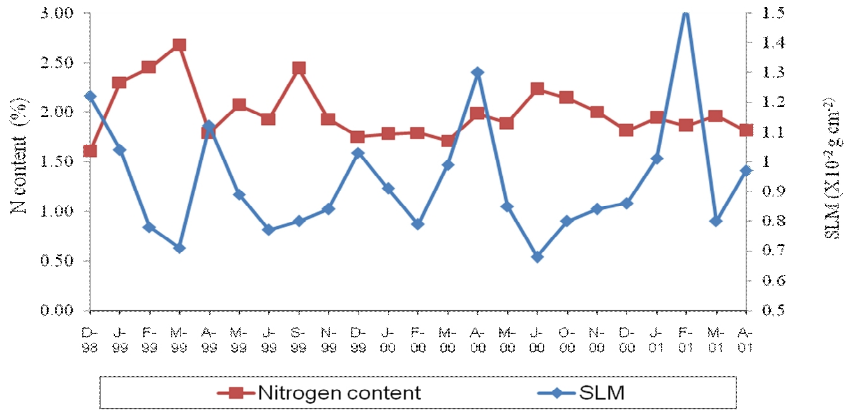

Figure 2:
Nitrogen content (%) and Specific leaf mass (SLM) in *Castonopsis indica*

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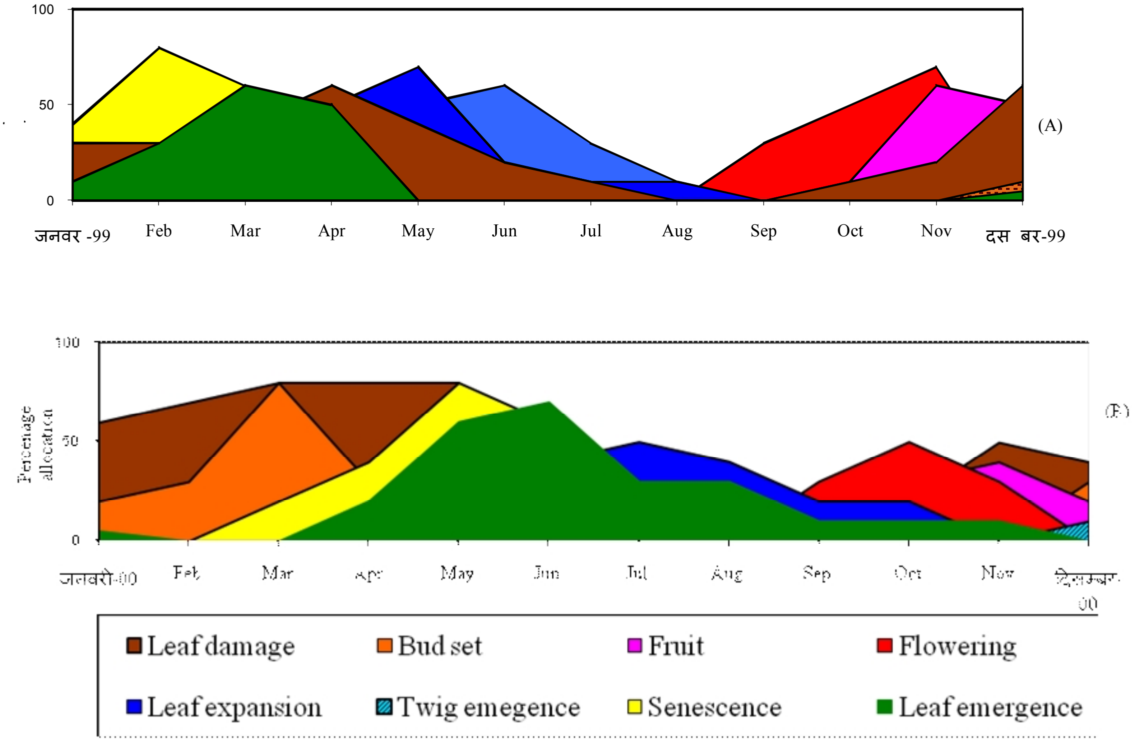

Figure 3:
Phenological spectrum of *Castonopsis indica* in 1999 (A) and 2000 (B)

Figure 3: Phenological spectrum of *Castanopsis indica* in 1999 (A) and 2000 (B)

RESULTS

Wood moisture percent

Wood moisture percent (W_C), density of wood (W_D) and water in wood per volume (W_W) showed significant variation among the months (W_C; $P = 0.02$, W_W; $P < 0.001$) except W_D; $P = 0.4$) (Table 1). Wood water properties showed a profound effect of precipitation and the effect was more pronounced in the first year of drought when mean soil water potential at 15 cm depth was less than -1.5MPa[12]. Mean wood moisture percent (W_C) was 73.1 % and showed significant variation in the months ($P = 0.02$) (Table 1). W_C in *C. indica* ranged from 54.4 % (May 1999) to 98.4 % (December 2000) and decreased from December 1998 till June 1999 in the first year of drought. Increase in W_C was observed in September 1999 when there was adequate amount of water in the soil. A gradual decline in W_C was observed in *C. indica* from November 1999 onwards when depletion in soil water availability started. However, in the third year, i.e. year 2000, observations showed an increase in W_C in November – December (Figure 1).

Density of wood (Dry wood)

Wood density did not follow a general seasonal trend and remained consistent throughout the observation period and showed significant variation with sampled years ($P < 0.001$) (Figure 1).

Water in wood per volume

Water in wood per volume (W_W) showed significant variation among the months studied ($P < 0.001$). Mean value of W_W was 0.39 g cm^3 (Table 1). ANOVA showed a significant variation of the species with the years observed ($P < 0.001$). During the three years of observations, mean W_W in 1st year was different from the third year's observation (Table 2). Seasonal effect of precipitation was reflected by W_W and ranged from 0.26 g cm^3 (March 1999) to 0.52 g cm^3 (September 1999). After receiving the monsoon rain W_W remained high till the beginning of dry months and high values were observed during winter months (Figure 1).

Starch Percentage

There was significant variation in starch percentage in zero-year twig ($starch_0$) among months ($P < 0.001$). A significant variation was observed in starch percentage in zero-year-old ($starch_0$) and one-year old twig ($starch_1$). Mean $starch_0$ was 64.1 % and $starch_1$ was 61.7 % (Table 1). $Starch_0$ ranged from 0 % (October and December 2000) to 100 % (January 1999) and $starch_1$ ranged from 5 % (October 2000) to 100 % (April 2000) (Figure 1). Increase in starch percentage just before the vegetative bud break and low value after leaf emergence and expansion or when there were not many phenological activities was observed.

Specific Leaf Mass

Specific Leaf Mass (SLM) showed insignificant variation with months ($P > 0.9$) and the years studied ($P = 0.92$). Mean SLM 0.94×10^{-2} g cm^{-2} (Table 1). SLM ranged from 0.68×10^{-2} g cm^{-2} (June 2000) to 1.53×10^{-2} g cm^{-2} (February 2001). SLM increased in April in all three years of observation which was the leaf expansion period while a decrease in SLM was observed from November or December when leaf senescence started with great damages in leaves (Figure 2).

Nitrogen

A non-significant variation was observed in nitrogen percentage content (N) showed variation among the months studied ($P > 0.4$). N was highest in March 1999 (2.68 %) and lowest in December 1998 (1.6 %). Except for the 1st year of observation a marginal decrease in N was observed from December to April which increased from June to November. There was a non-significant variation in nitrogen percent content (N) among the months studied ($P = 0.49$) and significant variation in the years studied ($P = 0.03$) and 1st year mean N differed from that of 2nd and 3rd year. Mean N was 1.98 % (Table 2).

Twig Starch

There was significant variation in starch percentage content in zero-year twig ($starch_0$) and one-year-old ($starch_1$) among months ($P < 0.001$). Increase in starch percentage was found just before the vegetative bud break and low value was observed after leaf emergence and expansion or when there were not many phenological activities (Figure 2). Mean $starch_0$ and $starch_1$ were 64.1 % and 61.7 % respectively and starch percentage content decreased with ageing i.e. $starch_0 > starch_1$ (Table 2).

Specific Leaf Mass

SLM showed non-significant variation with months ($P < 0.9$). SLM increased when leaves were fully developed and decreased when leaf senescence started with great damages in leaves (Figure 2). High SLM was observed in February during the three years of observation and it decreased when leaf emergence took place and the ratio of increase in SLM was related to leaf expansion.

Categorization of Phenological events

Leaf emergence, senescence, flowering and fruiting occurred during the dry months and a more or less phenological synchrony was observed in this ecosystem; i.e. same sized trees were in the same phenophase at the time of one observation while the smaller ones followed them immediately. The phenological processes were completed in single activity; i.e. leaf drop, leaf emergence, flowering and fruiting were accomplished in one episode. The studied species exhibited evergreen types of leaf exchange patterns with a concentrated leaf drop in a particular season (Figure 3).

Leaf drop or senescence pattern

Senescence started from January in the first year of observation while it was delayed by two months in 2000. However, in the third year of observation (2001), the severely damaged leaves started falling from February onwards only. In *C. indica* leaves were highly damaged long before senescence. The damages were mainly due to drying of leaves besides the necrotic patches and holes. During this study, senescence was confirmed when approximately 20 % of the leaves were shed off from the sampled as well as surrounding trees. Leaf drop period was lengthy, and it took more than two months to complete the process. Leaf drop occurred round the year but leafing was seasonal (evergreen with continual leaf drop type).

Leaf flush

C. indica exhibited single leaf flush and had an extended leaf flush period that lasted for almost two months. In general, leaf flushing showed a definite seasonal periodicity and leaf drop preceded leafing. Leaf life span was 12–13 months and leaf flush occurred from January in 1999 but was delayed in the next year and it started from April only while in the third year of observation, leaf emergence had not started till April and highly damaged leaves were present in the trees. However occasional leafing was observed till the beginning of winter season.

Flowering and fruit maturation

C. indica, a member of Fagaceae, showed a typical type of flowering and fruiting behavior. Flowering started from June and continued till September and seeds were set immediately thereafter, however fruits did not grow in size till next summer. In the following summer these fruits grew in size and led to maturation in the winter months. During this period acorns in catkins from the latest season were also present. Thus in this species fruits of one or other year's crop were present on the trees. The delayed senescence and leaf emergence showed no influence in the timing of flowering in the second year.

Twig emergence and shoot elongation

Twig emergence reflected the pattern of leaf flush – if the leaf flush was early, shoot elongation was also early and late in delayed leaf emergence. Young shoots were severely damaged by drying and dying and due to this shoot expansion could be observed in a very few branches in May (leaf flush period). Twig emergence started from March onwards in the first year. Due to the drying and dying of shoot tips, shoot expansion was observed in a very few branches from April in the next year (2001). However after the completion of the rainy season, an extensive shoot elongation was recorded in September-October 2000. Similarly as a result of severe leaf damage and a prolonged senescence along with drying of the shoot tips no shoot elongation was observed in the dry summer of 2001.

DISCUSSION

Wood moisture percent (W_C) decreased in dry summer months when leaf emergence took place thus indicating withdrawal of stored stem water for bud break as suggested by Borchert[15]. Wood water properties showed a profound effect of precipitation and the effect was more pronounced in the first year of drought when rainfall was 5.4 mm only for a period of five months and soil water potential at 15 cm depth and predawn water potential in *C. indica* was less than - 4.0 MPa and 1.6 MPa respectively[12]. W_W was high in winter months and low in dry summer months. W_W increases with the fraction of living parenchyma cells in the wood due to winter sapwood formation. Decrease in W_W during the dry summer months might be associated with high transpirational demand during these months and also with the low tree Ψ [12] which minimizes the temporal imbalance between water supply and demand. W_D showed a non-significant correlation with W_C (P = -0.05) which suggested that the presence of diffused and loosely aggregated metatracheal parenchyma separated by wider tracts of fibrous tissue might have reduced the significant space for water storage and hence resulted in a comparatively lower W_C and a non significant correlation with W_D. W_C ranged from 54.4 % (May 1999) to 98.4 % (December 2000). W_D ranged from 0.47 g cm^{-3} to 0.69 g cm^{-3}. A lower range has been reported in the lightwood and softwood evergreen trees with sclerophyllous and coriaceous leaves respectively in dry tropical forest in South America[14]. A comparatively high W_C was observed in the third year of observation (December 2000) which might be due to soil water replenishment by sporadic precipitation as well as low leaf conductance[12]. *C. indica* showed a close relationship between SLM and the developmental changes in leaf characteristics. Variations in SLM are caused by variations in leaf thickness or in leaf mass density[20] and are associated with the differences in both leaf anatomy and chemical composition[21]. SLM increased in late dry months when leaves expanded and decreased with the onset of senescence. Differences in SLM have been related to the differences in the proportion of photosynthetic tissues[22]. Thus increase in SLM as leaves expanded might be due to the increased thickness of palisade parenchyma. These tissues were responsible for the further increase in SLM, by accumulating dry matters till apposite conditions such as water availability, increased irradiance and developed stomata; lead to photosynthetic operation. Leaf expansion was very rapid and SLM increased only at the later stage of leaf expansion indicating that during the initial stage of leaf expansion, large epidermal cells were developed. These epidermal cells lack chloroplasts and have low mass density resulting low SLM. A significant negative correlation between SLM and leaf nitrogen in *C. indica* suggested development of larger number of tissues such as schelerenchyma or vascular tissue that are composed of nitrogen free or poor substances. SLM decreased at the time of senescence. Senescence was ensued by yellowing; drying up, damages and holes and such damages and drying of the leaves prior to senescence decreased the leaf density thus lowering SLM.

Leaf dynamics

Leaf life span was 12 – 13 months slightly higher than reported in Indian central Himalaya[23]. *C. indica* produced additional leaves in early winter months (October - November) having severely damaged leaves all through. This pattern fitted to the model constructed by Isawa and Cohen[24] for some temperate region plants which produce additional leaves by using photosynthates from the first formed leaves. In this way the species might compensate for the large proportion of leaf damaged throughout the year. A significant negative correlation between SLM and leaf nitrogen ($P > 0.01$) suggested development of large volume of tissues such as schelerenchyma or vascular tissue that are composed of nitrogen free or poor substances. High SLM and low N contents are related to leaf life longevity[25]. *C. indica* had higher leaf nitrogen content and lower SLM which lead to the formation of more productive leaves and a shorter life span. Leaf nitrogen content (N) increased during the leaf emergence and decreased at the time of senescence and ranged from 1.6 % to 2.68 %. Leaf N was at the crest of concentration during leaf initiation then declined either by resorption at the time of senescence or by dilution in the expanded leaves by increasing cell wall material. N content was high in September 1999, which suggests that this period was productive period for the expanded leaves and plants were rich in protein matter. Another parameter, which showed an apparent relationship with leaf phenology, was starch percentage content in twigs, produced in different years. High starch content was found in zero-year twigs at the time of leaf emergence e.g. February to May. Such high value was due to the accumulation of reserved carbohydrates. Mostly, higher starch staining was found in zero year twigs than in the previous year's twigs; which indicated the expeditious shift of such accumulates to the new shoots. Decrease in starch staining after leaf emergence indicated hydrolysis of photosynthates into soluble carbohydrates. However a substantial amount of starch was present in the twigs after leaf emergence. According to Larcher[26] about a third of the reserve material is utilized in the unfolding of leaves and flowers and developing fruits are then supplied preferentially. As flowering and fruiting take place immediately after leaf flush in *C. indica*, existing starch might be used for flowering and fruiting. Low starch staining during the dry winter months suggested the conversion of starch into soluble carbohydrates, which in turn might have acted as osmotic solutes and contributed to osmotic regulation during these months when plants were water stressed.

Adaptation to drought

Phenological activities are inhibited by moderate water deficits[3]. Thus, phenological activities that should be activated during early rainy season were not true in the present study. Phenological processes such as leaf drop, leaf emergence, flowering and fruiting occurred in the dry summer months as in the temperate trees of Indian Central Himalaya[27]. After the completion of leaf fall in mid-September, the soil dries out and water balance becomes negative as indicated by declining tree water potential from the beginning of winter months[12]. Senescence is a functional strategy of the plants to maintain a favourable tissue water status as the decreased leaf surface area eliminates higher fraction of water loss through transpiration. Other phenological events such as flowering, bud break and shoot elongation, occur simultaneously so that the same physiological and environmental factors promote both growth and reproduction and were not correlated with the seasonal pattern of precipitation. This might be due to the endogenous control of plants or interactions of factors like edaphic, photoperiod, and temperature suggested by Longman and Jenik[28]. *C. indica* showed an incessant senescence (November-April) in the third year with low osmotic potentials, in agreement to Nilsen and Muller's[29] findings; which state that leaf abscission is a morphological response to substantial drought. Early senescence was reported in the dry season to avoid large decrease in leaf Ψ_{30}. Lowering of osmotic potential at zero and full turgor in winter months and significant negative correlation with starch content in twigs in *C. indica* might be responsible for remobilization of sugars from senesced leaf back to the main stem and its additional leaf production in early winter months of October to November. Senescence was delayed by about two months in the second year of observation which could have been due to lower N retranslocation (> 10 %) in this year. Higher predawn water second year as compared to previous year could also have buffered the impact of water stress that might be responsible for the delayed senescence. In conclusion, wood water properties, SLM (related to the differences in the proportion of photosynthetic tissue as well as increased scelerophylly) and leaf N resorption showed close empathy with leaf phenology and developmental changes along the seasonal gradients. Stem water storage played an important role in rehydration of the twigs and also compensated the tranpirational loss. Individual shift in the timing of phenological events as a consequence of seasonal stress was very common in the present study. Sigdel and Ikeda[31] detected the year 1999 to be a winter drought year in Nepal, one of the six cases over a period of 33 years. Water stress was not as severe in the following years of observations as occasional replenishment was done by sporadic pre monsoon and winter precipitation. In recent years, due to the effect of climate change, some research suggests that drought in the future may be amplified in certain areas due to changes in climate variability and extremes resulting from global warming. Hence, as the geographic situation of Mahabharata range makes the recurrence of summer drought more likely, and drought may be more extensive as a consequence of climatic changes (global warming, altered precipitation), this evergreen species needs to exhibit a wide range of adaptational abilities to compete.

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