ROLE OF WOOD WATER PROPERTIES AND LEAF DYNAMICS IN PHENOLOGY AND RESPONSE TO DROUGHT IN EVERGREEN HIMALAYAN TREE SPECIES

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ABSTRACT

Five evergreen Himalayan trees namely C*astanopsis indica, Schima wallichii, Rhododendron arboreum, Quercus lanata* and *Q. semecarpifolia* were studied for their phenological responses to drought. Wood water properties (wood moisture percentage, wood density and water in wood per volume), starch percentage content, specific leaf mass, nitrogen content in leaves and phenological processes such as leaf emergence, senescence, flowering and fruiting were measured. Measurements were taken 28 times from December 1998 to April 2001 except for the monsoon months. There was significant variation in starch percentage in zero and one year old twigs. Mean starch percentage content ranged from 23% and 17.1% (*S. wallichii*) to 64% and 61.7% (*C. indica*) in zero year and one year old twig, respectively. Wood water properties were highest in *R. arboreum* and lowest in *C. indica*. SLM showed significant variation with sampled species and mean SLM was highest in *R arboreum* (1.6×10^{-2} g cm^{-2}) and lowest in *S. wallichii* (0.64×10^{-2} g cm^{-2}). Mean N ranged from 1.13% (*R arboreum*) to 1.98% (*C. indica*). 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.

Key words: *Castanopsis indica, Quercus lanata, Q. semecarpifolia, Rhododendron arboreum, Schima wallichii*, senescence, specific leaf mass.

INTRODUCTION

Phenological events of the plants are good indicator of climatic differences as leaf life cycle puts strong demands on plant water balance. The timing of leaf production can be predicted from seasonal pattern of rainfall and mechanism of drought resistance in tropical forest plants (Wright 1996). Phenological behaviors are generally affected by the interaction between water availability, stem water storage and sensitivity to water stress. Phenomorphological variations are observed by many researchers as a consequence of tree water status: leaf expansion (Meinzer *et al.* 1983), bud set and shoot elongation (Ritchie and

Shula 1984), premature leaf senescense (Kozlawaski *et al.* 1991), bud burst, shoot growth and flowering of trees (Borchert 1994 a, b, c).

Phenological behavior of Himalayan evergreen trees is of practical interest because they grow in a typical seasonality, where precipitation occurs during summer season only. There are a few informations 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 (Bhooj and Ramkrishan 1981, Ralhan *et al.* 1985, Ralhan and Singh (1987). Phenological process such as leaf emergence, expansion, flowering and fruiting occur before the onset of monsoon when trees still bear the old leaves unlike the deciduous trees where rehydration of leafless twigs becomes a prerequisite for initiation of new leaves (Borchert 1994 a, b, c) and the loss of parameters like nitrogen, specific leaf mass etc. begins when a subsequent decrease in soil water potential occurs. 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, leaf initiation, flowering and fruiting) would be helpful.

The present study is focused on the timing of leaf development, leaf dynamics (nitrogen content and specific leaf mass) and senescence associated with the seasonal changes in wood water reserve and starch content in leaves. For this purpose five evergreen angiosperm species- *Castanopsis indica* (Roxb.) Miq., *Quercus lanata*, *Q. semecarpifolia* Smith, *Rhododendron arboretum* Smith and *Schima wallichi* (DC) Korth. were selectected.

MATERIALS AND METHODS

Study sites
The study was carried out at Phulchowki Hill (27⁰33'N, 85⁰22'E), 10km SE of Kathmandu, Nepal. It is a part of sub-Himalayan Mahabharat region with an altitudinal range of 1400-2715 m with extensive diverse forests mostly dominated by broad-leaved evergreen trees. The general picture of the vegetation in Phulchowki is based on the altitudinal concept widely applied in the Himalayas (Stainton 1972, Hara *et al.* 1978). It covers an area of approximately 50 sqkm consisting of a vast range of flora. The natural vegetation of Phulchowki Hill is characterized by three distinct evergreen broad-leaved forests types: mixed *Schima- Castanopsis* forest at the base (1400–1800 m), Oak-Laurel forest (1800–2400 m) and evergreen oak forests (2000 m above). Three sites were selected for the study: *C. indica* and *S. wallichii* at 1400m, *Q. lanata* and *R. arboreum* at 2020 m and *Q. semecarpifolia*, the high altitude oak of Nepal, at 2130 m representing its lower elevation limit.

The study area has 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). There is no perennial source of water above 1600 m in Phulchowki Hill.

The area under present investigation does not have meteorological station of its own so climatic data were collected from Tribhuvan International Airport at 1350 m, 10 km NW of the study site. Mean long-term air temperature ranges between 2.6-18.7°C in winter and 15.8-28.2°C in summer. Temperature lapse rate in mountain ranges from 4-6°C with an increase of 1000m elevations. Thus *Q. semecarpifolia* site was cooler than *Schima-Castanopsis* site. Mean long-term annual rainfall is 1882 mm with about more than 80% of this occurring between mid-June and mid-September. Relative humidity at 6:30 AM is > 90% in July, with a minimum of 63% in April. The annual precipitation at Kathmandu for 1999 was 1729 mm and 1407 mm in 2000, 78-83% contributed by monsoon rains. Early winter had negligible rainfall in both years (Poudyal *et al.* 2003).

Measurements

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 for three representative trees of each species at monthly intervals, except for the monsoon months. Measurements were taken 28 times 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 for each species was determined from the sapwood of the marked trees and Specific Leaf Mass (SLM) was measured in five leaves from three branches of such sampled trees for each species of the marked trees Measurements were done according to Poudyal (2004). Percentage Nitrogen content in leaves was estimated by micro-Kjeldahl method in modified form (PCARR 1980).

Estimation of twig starch content was done according to Zobel (1996). 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).

Phenological observations were done in sampled trees of all species as well as in non-sampled ones for a general acuity. Three twigs were marked on each sampled tree and phenological events such as leaf senescence, leaf emergence, leaf damage, twig emergence, bud formation, flowering and fruiting were tabulated for each month of observation.

Analysis of variance (ANOVA) and least significance difference test (LSD) were done separately for all variables. Factors in the ANOVA were species, number and their interactions. Spearman rank correlation was used to express the relationship between the sampled variables. The statistical package used was StatGraphics Plus ver. 4.0 (Statical Graphics Corp., Rockville, MD, USA).

RESULTS

Wood water properties

Wood moisture percent (W_c), density of wood (W_D) and water in wood per volume (W_w) showed significant variation among the sampled species (W_c, W_D, W_w -$P < 0.001$) (Table 1). Mean values of all species exhibited similar pattern of W_c during three years of observation ($P \leq 0.4$) except C. indica, which exhibited different W_c in different year.

Wood water properties in most of the species showed a profound effect of precipitation and the effect was more pronounced in the first year of drought when soil water potential at 15 cm depth was less than -1.5MPa. However, *R. arboretum* showed consistently high W_c and wood water properties remained unaffected by seasonal changes (Figs. 1, 2 and 3).

Table 1. Mean values (± SE) of measurements for each species during all sampling dates; mean wood moisture percentage (W_c), wood density (W_D), and water in wood per volume (W_w). Units for W_D and W_w are g cm^{-3}. Within columns, different letters indicate significant differences (*P*=0.05, Fisher's multiple range test).

Species	W_c	W_D	W_w
C. indica	73.1±1.8a	0.53±0.01b	0.39±0.01a
S. wallichii	97.1±1.8b	0.52±0.01b	0.50±0.01c
R. arboreum	121.9±1.8c	0.48±0.01a	0.56±0.01d
Q. lanata	74.3±1.8a	0.65±0.01c	0.45±0.01b
Q. semecarpifolia	76.0±1.8a	0.68±0.01d	0.52±0.01c
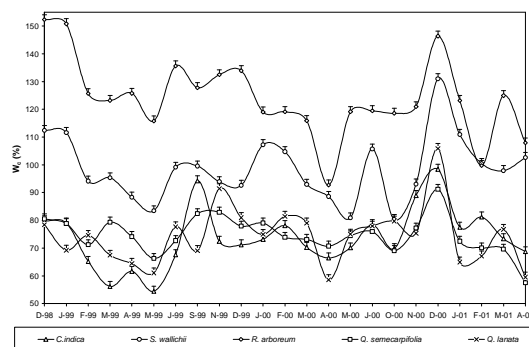
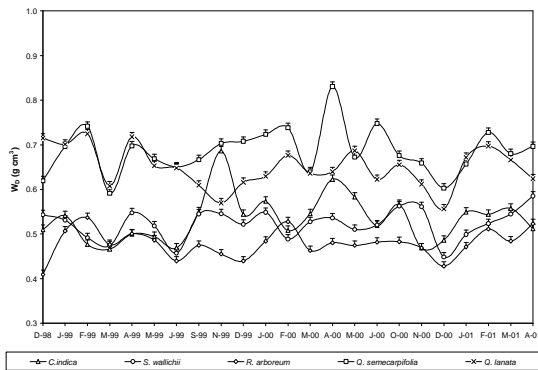**Fig. 1.** Wood moisture percent (W_c) in five species. The bars show one standard error of mean for each species.

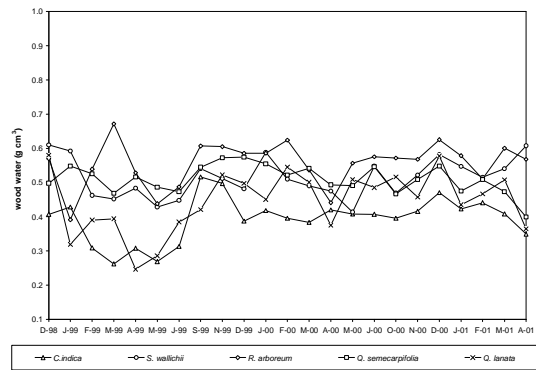Fig. 2. Wood dry wt. (W_D) in five species. The bars show one standard error of mean for each species.

Fig. 3. Water in wood in per volume (g cm^3) in five species.

Table 2. Mean values (± SE) of measurements for each species during all sampling dates. Mean starch percentage in zero year twig (starch$_0$), one-year old twig (starch$_1$), specific leaf mass (SLM), unit for SLM is g cm^{-2} and nitrogen content in percent (N). Within columns, different letters indicate significant differences (P = 0.05, Fisher's multiple range test).

Species	Starch$_0$	Starch$_1$	SLM	N
C. indica	64.1± 4.1 c	61.7 ± 3.4 c	$0.94 \times 10^{-2} \pm 0.06$ b	2.0 ± 0.04 d
S. wallichii	24.0 ± 4.3 a	17.1 ± 3.3 a	$0.64 \times 10^{-2} \pm 0.06$ a	1.8 ± 0.04 c
R. arboreum	38.8 ± 4.0 b	24.0 ± 3.3 b	$1.63 \times 10^{-2} \pm 0.06$ c	1.1 ± 0.04 a
Q. lanata	26.4 ± 4.0 a	23.7 ± 3.3 b	$1.52 \times 10^{-2} \pm 0.06$ c	1.7 ± 0.04 bc
Q. semecarpifolia	30.9 ± 4.0 a	28.1 ± 3.3 b	$1.33 \times 10^{-2} \pm 0.06$ b	1.7 ± 0.04 b

Table 3. Phenological activities: leaf emergence (E), leaf damage (ld), senescence (S), flowering (F), fruiting (I- immature and M - mature) during all sampling months in five species.

Species → Months↓	*C. indica* Leaf / flower / fruit	*S. wallichii* leaf / flower / fruit	*R. arboreum* leaf / flower / fruit	*Q. lanata* leaf / flower / fruit	*Q. semecarpifolia* leaf / flower / fruit
Jan-99	S	S		ld	
Feb-99	S E	S E		ld E	
Mar-99	S E	S E	S F	S E	E
Apr-99	E	S E F	S F	S E	E
May-99	E	F I	S E	E	S E
Jun-99		F I	S E	E F	S E
Jul-99		I	S E	E F	S E F
Aug-99		M	S	E F I	E F I
Sep-99	F	M		F	F I
Oct-99	ld F	M		S E F M	F M
Nov-99	ld I			E M	
Dec-99	ld M			E M	
Jan-00	ld			ld E	
Feb-00	ld	S		ld E	

|					
Mar-00	S	S E	F	ld E	E
Apr-00	S	S E F	F	S	E
May-0	S E	S E F	S E	E	S E
Jun-00	S E	F I	S E	E F	S E
Jul-00	E	F I	S E	E F	S E
Aug-00	E	F I		E F	E F
Sep-00	F	M		E F I	
Oct-00	ld F I	M		S E I	
Nov-00	ld F I	S M		S E I	
Dec-00	ld M	S	S	ld E	S
Jan-01	S	S	S	S E	S
Feb-01	S	S E	S	S E	S
Mar-01	S E	S E	S	S E	S E
Apr-01	S E	S E	S E	S E F	S E

Twig starch content

There was significant variation in starch percentage content in zero-year twig ($starch_0$) and one-year-old ($starch_1$) among species ($P < 0.001$) (Table 2).

Starch content increased in all species just before the vegetative bud break and decreased after leaf emergence and expansion or when there were not many phenological activities. Mean $starch_0$ and starch were highest in C. indica (64.1% and 61.7% respectively) and the lowest in S. wallichii (24.0% and 17.1%, respectively) (Figs. 4 and 5). Starch percentage content relatively decreased with ageing i.e. $starch_0 > starch_1$ in all sampled species.
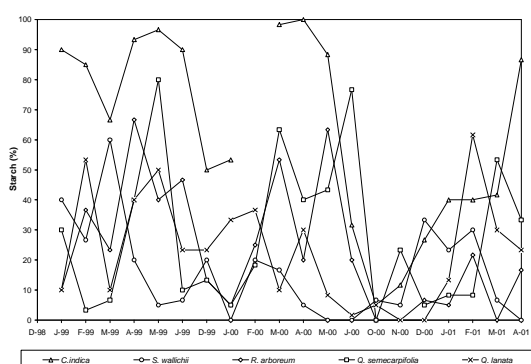
**Fig. 4. Starch content percentage in zero year twig ($starch_0$) in five species.**
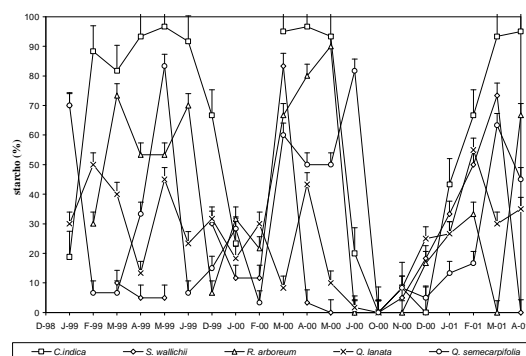
Fig. 5. Starch content percentage in one year twig ($starch_1$) in five species. The bars show one standard error of the mean for each species.

Specific leaf mass

Specific leaf mass (SLM) showed significant variation with sampled species ($P < 0.001$). Mean value showed significant difference among the sampled species. *S. wallichii* differed from all other species while *Q. lanata* and *R. arboreum* differed from *C. indica* and *Q. semecarpifolia* (Table 2).

In *C. indica* and *S. wallichii*, SLM increased when leaves were fully developed and decreased when leaf senescence started with great damages in leaves (Fig. 6). A consistent SLM was observed throughout the observation period in *R. arboreum*. High SLM was observed in the month of February

in all three years of observation and it decreased when leaf emergence took place. In *Q. lanata* an irregular pattern of SLM was observed while SLM in *Q. semecarpifolia* increased from the winter months till the completion of dry months i.e. from December to May (Fig. 6). In all species the ratio of increase in SLM was related to leaf expansion.
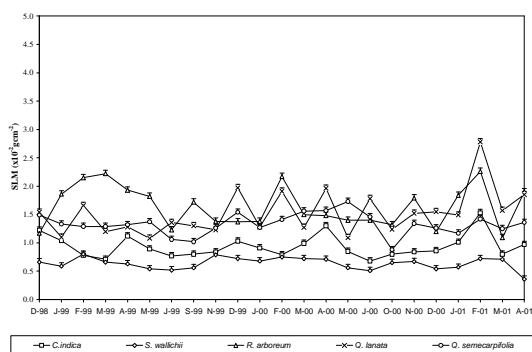

Fig. 6. **Specific leaf mass (SLM) in five species. The bars show one standard error of the mean for each species.**

Nitrogen content

A significant variation was observed in leaf nitrogen content (N) among the species (Table 2). Nitrogen content in C. indica 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 (Fig. 7). In S. wallichii N ranged from 1.4% (November 1999) to 2.18% (June 1999) and was high from January to June during the observation period, except for a sharp decline in April 1999, 2000 and a marginal decrease in April 2001. R. arboreum, however showed its ability to keep a consistent N during the winter months observed. The range of N in *R. arboreum* was 0.94% (June 2000) to 1.43% (February 2001). In *Q. lanata*, N observed was from 1.25% (December 1998) to 2.59% (March 1999). In *Q. lanata* N decreased from June till December with marginal increase in N from January to April in general. In

Q. semecarpifolia highest N observed was 2.2% in September 1999 and lowest, 1.34% in June 2000. In *Q. semecarpifolia*, N decreased from May to December in all three years of observation (Fig. 7).
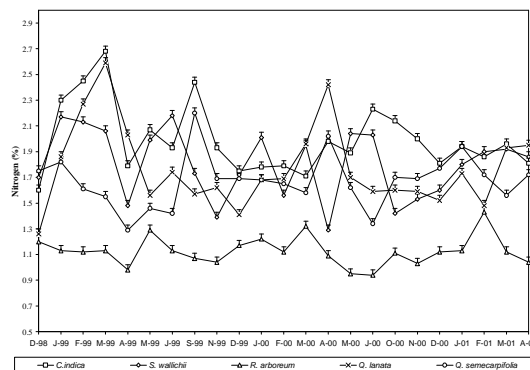
Fig. 7. **Nitrogen perentage content in leaves in five species. The bars show one standard error of the mean for each species.**

Phenology

Phenological events in most of the species, except *C. indica*, commenced mostly from the late winter months and ended before monsoon in the studied species and completed in single activity i.e. leaf drop; leaf emergence, flowering and fruiting were accomplished in one episode. The studied species showed single leaf flush except *Q. lanata* which showed multiple leaf flush and evergreen types of leaf exchange pattern with a concentrated leaf drop in a particular season but plants were not naked due to simultaneous leafing. In *C. indica* and *Q. lanata* leaves were highly damaged long before senescence with 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. During the period of leaf exchange two leaf cohorts were present on the same tree: one about 12 months old developed during the previous dry season (adult and old leaves) and the other new leaves developed in the current dry season (new young leaves). Leaf life span varied among the

species longest being in *R. arboreum* (18 months), *Q. lanata* (15-16 months but very few in numbers), *Q. semecarpifolia* (14 months), *C. indica* (12-13 months), and least in *S. wallichii* (about 12 months).

Phenolgy, among all sampled species was different for the years studied. In *C. indica*, leaf drop occurred round the year but leafing was seasonal (evergreen with continual leaf drop type). Leaf drop started from January-February and leaf flush occurred from February in the 1st year (1999) but in the next year both processes were delayed for a few months while in the 3rd year severely damaged leaves started falling from February onwards and leaf emergence started from March but highly damaged old leaves were present in the trees till April 2001. Occasional leafing was observed in *C. indica* till the beginning of winter season (November) throughout the observation. Twigs emergence and shoot elongation occured almost one month later but as a result of severe leaf damage and a prolonged senescence along with drying of the shoot tips no shoot elongation was observed in 2001 dry summer. *C. indica,* a member of Fagaceae, showed a typical type of flowering and fruiting behavior. In this species, flowering took place in September and seed were set immediately thereafter, but the fruits did not grow in size till next summer. In the following summer these fruits grew in size and lead to maturation in the winter months. During this period acrons 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.

S. wallichii showed concentrated leaf drop in the dry season of the year and leaf drop started from January. In the 2nd year, senescence was delayed by almost two months. However, in the 3rd year of observation, *S. wallichii* had an early senescence from November 2000, and senescence lasted for about four months (November-February). Leaf emergence occurred from January

onwards in the 1st year and was delayed by two months in 2000 while in the 3rd year, leaf flushing started from early February. In *S. wallichii* shoot elongation took place from April to May and cessation of shoot elongation occurred in June due to the bending of twigs. However some shoot expanded in winter month (December) also but the degree was lesser. Flowering lasted for two months (April-May) while fruiting was observed from May-September in the 1st year. Fruits, though less in numbers, were produced for an extended period of about six months (April-November) in the 2nd year.

In *R. arboreum*, senescence started from March and was concentrated during May-June after the completion of flowering. Next year it was delayed by a month while in the 3rd year early and extended senescence from December to April was observed. Leaf flush lasted for two months (May-June) while shoot elongation was slow and prolonged (January-June) (Table 3). Formation of buds started from September after the completion of monsoon period and buds were formed consistently but it was difficult to differentiate the vegetative bud from floral buds. *R. arboreum* bloomed in March-April with its large showy flowers but in the 3rd year there was almost no flowering in *R. arboreum* at the study site.

Q. lanata exhibited a different type of leaf drop pattern in which an incessant leaf senescence and simultaneous leaf flush occured (Table 3). Due to unremitting process of leaf drying and damage, *Q. lanata* could not exhibit a clear senescence pattern. Senescence was rapid and sometimes even one-month-old leaf dried and fell off. In *Q. lanata* though leaf emergence took place round the year leaf flushing was more prominent in dry summer season and leafing of this period produced more leaves than other flushing. Second flushing took after the rainy season while third flushing occurred in winter months. Shoot elongation and twig emergence were a continuous processes in

Q. lanata hence it was difficult to determine an exact period of its starting. However, shoot elongation was greater in winter months than in the dry summer months. Flowers appeared during June –July but early flowering was observed in April 2001. Fruits were set immediately after flowering but matured during the winter months

Leaf senescence in *Q. semecarpifolia* took place from May-June but in the 3rd year it showed early senescence that started from December (Table 3). In *Q. semecarpifolia* leaf flushing was longest of all the species and it took nearly 4 - 5 months to completely replace the old leaves. However, in this species, leaf emergence was delayed by one month in the 3rd year i.e. it started from April in 2001. In *Q. semecarpifolia* flowering took place in September - November while fruiting was typical of Fagaceae i.e. though set immediately after flowering but matured late afterwards.

DISCUSSION

Seasonal patterns among the species

Wood moisture percent (W_c) in all species decreased in dry summer months when leaf emergence took place thus indicating withdrawal of stored stem water for bud break as suggested by Borchert (1994 *c*).

Q. lanata with multiple leaf flush, did not show a regular pattern of wood moisture content. W_c depleted during the leaf flush of summer months only. In April 2000, this evergreen species exhibited an unusual foliar appearance as most of the trees became leafless with swollen buds just about to open. W_c in this month reached to a minimum value of 58.6% and a substantial decrease in hydraulic conductivity to 4.01 $\times 10^{-6}$ kg sec^{-1} MPa^{-1} m^{-1} (Poudyal *et al.* 2004) occurred due to cavitation as suggested by (Holbrook *et al.* 1995). Similarly high W_c in December 2000 when winter leaf emergence had just started was due to high hydraulic conductivity (24.2 $\times 10^{-6}$ kg sec^{-1} MPa^{-1} m^{-1}, Poudyal *et al.* 2004).

W_w was high in winter months in all studied species 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 and also to low tree Ψ during these months (Poudyal *et al.* 2003) minimizing the temporal imbalance between water supply and demand (Stratton *et al.* 2000). Tyree and Yang (1990) observed stem water to contribute < 6% of the daily transpirational water loss in *Thuja occidentalis*. W_w in *Q. lanata* did not decrease in summer months as in other species, which might be due to recurrent shoot emergence thus increasing the parenchymatous cells.

W_D showed a significant negative correlation with W_c (0.01 >*P*>0.001) in all species except *C. indica* which was in agreement to Schulze *et al.* (1988) and Borchert (1994 *a, b*). This suggested that these species had abundance of thin walled cells capable of elastic water storage (Carlquist 1988 and Borchert 1994 *a*). The presence of diffused and loosely aggregated metatracheal parenchyma separated by wider tracts of fibrous tissue in *C. indica* as described by Pearson and Brown (1932) 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.

Comparison among other species

W_c in the sampled species ranged from 73% to 130%. Schulze *et al.* (1988) reported 94% water content in evergreen trees and a higher range of 89% to 196% was reported by Borchert (1994 *c*) in different species of lightwood evergreen trees with mesic or scelerophyllous leaves. Bhattarai (2001) reported a lower W_c i.e. 80.5% in *S. wallichii* in Hetauda at 689m, a lower elevation part of the country.

In the studied species W_D ranged from 0.53 g cm^{-3} to 0.69 g cm^{-3}. Borchert (1994 *a*) reported a lower range in the lightwood evergreen trees with sclerophyllous leaves and evergreen softwood tree species with coriaceous leaves in dry tropical forest in South America at the time of active phenological periods indicating less non-lignified parenchymatous tissues in the studied species.

SLM in *R. arboreum, Q. lanata* and *Q. semecarpifolia* were in agreement to those regarded for scelerophyllous species by Daalen (1984) which was $\geq 1.4 \times 10^{-2}$ g cm^{-2}. Singh *et al.* (1994) reported a similar value in *R. arboreum* at 2600 m and a higher SLM in *Q. lanata* and *Q. semecarpifolia* at 2800 m in Indian Central Himalaya. Castro-Diez *et al.* (1997) also reported a higher SLM in two evergreen oaks, *Q. ilex* and *Q. coccifera* and a lower SLM for deciduous oak, *Q. faginea* in Spain along a rainfall gradient.

Leaf dynamics

Leaf life span was longest in *R. arboreum* (< 18 months) followed by *Q. lanata* (15-16 months), *Q. semecarpifolia* (14 months), *C. indica* (12-13 months) and least in *S. wallichii* (about 12 months) slightly higher than reported by Singh *et al.* (1994) in Indian central Himalaya. A greater leaf life span in *R. arboreum* and *Q. lanata* among the studied species may be attributed to their high SLM and low N contents as according to Reich *et al.* (1992). *C. indica* and *S. wallichii* had higher leaf nitrogen content and lower SLM which lead to the formation of more productive leaves and a shorter life span. Similar observation was made by Valentini *et al.* (1992) in *Q. pubscence. C. indica* produced additional leaves in early winter months (October - November) while *Q. lanata* had multiple leaf flushing, both species having severely damaged leaves all through. This pattern fitted to the model constructed by Isawa and Cohen (1989) for some temperate region plants which produce additional leaves by using photosynthates from the first formed leaves. In this way these species might compensate for the large proportion of leaf damaged throughout the year.

In *R. arboreum* there was almost no flowering in the third year of observation. Flowering requires a period of water stress followed by hydration (Crisosto *et al.* 1992) and full hydration of terminal branches is a prerequisite of dry season anthesis (Borchert 1994 *a, b*). Unlike 1st and 2nd year of observations there was an increase in wood water content in *R. arboreum* in March 2001, the flowering period. To add to it a lower soil Ψ than tree Ψ in the same month (Poudyal *et al.* 2003), indicated that there was not enough soil water available or stem water was not utilized to hydrate the apical meristem thus it could not support the floral expansion (Borchert 1994 *a, b*) because water stress inhibits meristem activity and rehydration only enables the expansion of resting flower buds. In *R. arboreum* formation of buds took place in September after the completion of monsoon when leaves were 4-5 months old. Resumption of growth in the shoot meristem as well as transition from vegetative to reproductive state initiates the flowering. Such type of phenological cycle was observed by Borchert (1995) in some neotropical dry forest species.

Relationship of wood moisture (W_c) with phenology

A pronounced relationship between W_c and leaf emergence was found in *S. wallichii*. W_c decreased from February onwards in the first year when leaf emergence started while in the 2nd year W_c depleted from March only and leaf emergence was delayed by a month. In 2001 W_c decreased from January when vegetative buds were fully developed and a further decrease was observed in the next month when leaf emergence started thus indicating the withdrawal of stem moisture for bud break. In *Cochlospermum* (with high water storage and low wood density), Choat *et al.* (2006) found

senescence early in the dry season to avoid large decrease in leaf Ψ.

The studied species showed a close relationship between SLM and the changes in leaf characteristics. Variations in SLM are caused by variations in leaf thickness or in leaf mass density (Witkowski and Lamont 1991) and are associated with the differences in both leaf anatomy and chemical composition (Lambers *et al.* 1998). Differences in SLM have been related to the differences in the proportion of photosynthetic tissues. Thus the increase in SLM as leaves expanded might be due to the increased thickness of palisade parenchyma. A significant negative correlation between SLM and leaf nitrogen in *C. indica* ($P > 0.01$) suggested development of large volume of tissues such as schelerenchyma or vascular tissue that are composed of nitrogen free or poor substances.

Positive correlation between SLM and Huber value ($P > 0.01$) in *C. indica* (Poudyal *et al* 2003) indicated that changes in SLM was related to the changes in leaf area. Senescence was ensued by yellowing; drying up, damages and holes (especially in *C. indica* and *Q. lanata*) and such damages and drying of the leaves prior to senescence decreased the leaf density thus lowering SLM. SLM in the studied species showed non-significant correlation with light in contrast to the findings of Lei and Lechowicz (1998), which might be because leaves were sampled from both sun-facing and dappled side.

Leaf nitrogen content (N) increased during the leaf emergence and decreased at the time of senescence in the species studied. N ranged from 1.7% to 1.98% in the sampled species. A similar range of 1.64-1.79% was reported by Zobel *et al.* (1995) in Himalayan oaks. Leaf N in the studied species was at the crest of concentration during leaf initation 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.

Of all the species studied *C. indica* showed highest proportion of nitrogen resorption from the senescing leaves (35%) followed by *S. wallichii* (28%), *Q. lanata* (22%), *Q. semecarpifolia* (20%) and least by *R. arboreum* (13%). Ralhan and Singh. (1987) reported 22-25% of nitrogen retranslocation from the senescing leaves of *Q. leucotrichophora*. Vitousek and Sanford (1986) reported $\approx$ 40% on average N resorption in tropical rain forest. Similarly Reich *et al.* (1995) found that 43% on average N was retranslocated in tree species in an oligotrophic Amazonian forest. *C. indica* and *S. wallichii* showed high leaf nitrogen resorption among the sampled species and were in agreement to the findings of Turner and Olson (1976) that plants with high leaf nutrient retranslocate larger proportion of their nitrogen than do plants with low nutrient status. A lower range of nitrogen retranslocation (28% in *C. indica* and 11% in *S. wallichii*) might also be responsible for the 2nd year's delayed senescence in these species.

Reduced nitrogen content in leaves was observed in *S. wallichii*, *R. arboreum* and *Q. lanata* more often after rainy season to early winter. Decrease in N during this period might be due to leaf senescence or due to low nitrogen availability in soil as well as absorption by other herbaceous crops (which grow copiously after the monsoon is over) or both. However, *C. indica* and *Q. semecarpifolia* showed high N content in September 1999, which suggests that, this period was productive period for the expanded leaves and plants are rich in protein matter. Likewise increase in leaf nitrogen in winter months was more foremost in *Q. semecarpifolia* and *Q. lanata* when leaves have attained their maximum expansion, which might be due to the formation of more proteins.

Another parameter, which showed an apparent relationship with leaf phenology, was starch percentage content in twigs, produced in different years. In all studied species high starch content was found in zero- year twig at the time of leaf emergence. Such high value was due to the accumulation of reserved carbohydrates. Mostly a higher starch staining was found in zero year twigs than in the previous year's twigs in these species, which indicated the expeditious shift of such accumulates to the new shoots. Zobel (1996) observed a correlation in the starch content of 1-year-old and 2- year-old twigs of pine and *Quercus leucotrichophora*. 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 in these species. According to Larcher (1995) 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*, *Q. semecarpifolia* and *Q. lanata*, existing starch might be used for flowering and fruiting by them. In *R. arboreum* as flowering precedes leaf emergence, substantial starch accumulation was found throughout the active phenological period though a higher value during leaf emergence. *Q. lanata* with its multiple leaf flushing behaviour showed an inconsistent starch staining but starch was not completely hydrolysed throughout the observation period. Starch staining was low during the winter months in all species. This suggests 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. Épron and Dreyer (1996) suggested that large increase in soluble carbohydrates contributes in the osmotic adjustment of oaks (*Q. petraea* Matt. Liebl.).

Adaptation to drought

Phenological activities are inhibited by moderate water deficits (Borchert 1994 a). Thus, phenological activities that should be activated during early rainy season were not true in the present study. In studied species, the 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 (Ralhan *et al.* 1985). After the completion of leaf fall in mid September, soil dries out and water balance becomes negative as indicated by declining tree water potential from the beginning of winter months (Poudyal *et al.* 2004). 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.

R. arboreum had consistently high W_c among the sampled species that remained high even during the dry months thus suggesting a sufficient amount of water stored to avoid severe water stress during the dry summer months. Low predawn Ψ (-1.5 MPa) and a low twig conductance (Poudyal *et al.* 2003) in April 2000 decreased W_c to 93%.

An unremitting leaf shedding shown by *Q. lanata* without little or no change in SLM during the dry period could be a way to recover its water status mainly by decreasing exposed leaf area rather than by leaf morphological changes. However *Q. semecarpifolia,* showed dimorphic leaves: one with entire margin and another with spiny leaves sometimes in same trees but spiny leaves were mostly found in young trees. Spiny leaves might be associated with their drought tolerant adaptations. Givnish and Vermeji (1976) and Givnish (1984) found dissected margins in leaves in drought tolerant tropical trees. As the root system in young trees is not capable of drawing water from deeper sources plant might have adapted this strategy which minimizes the vapour pressure gradient between the mesophyll cells and air.

Other phenological events such as flowering, bud break and shoot elongation in the studied species occur simultaneously so that the same physiological and environmental factors promote both growth and reproduction and were not correlated with seasonal pattern of precipitation. This might be due to the endogenous control of plants as suggested by Borchert (1992) or interactions of factors like edaphic, photoperiod, and temperature suggested by Longman and Jenik (1987). Of all the species studied *C. indica* and *S. wallichii* shed their leaves in January-February but had shoot elongation only a few months back while in high elevation species shoot expansion occurred much before leaf shedding which was similar to Borchert's (1998) findings which stated that increasing water stress at lower elevation accelerates leaf shedding and delays shoot elongation.

In the 1st year of observation when drought was severe, SLM increased at the time of senescence in *S. wallichii* (February), *R. arboreum* (February-May) and *Q. semecarpifolia* (April-May). This indicated that SLM increase in these species was not due to the thickness of parenchyma but increased schelerophylly of the leaves during the dry months and hence these species have a high energy cost (Griffin 1994) at this time. This also suggests that *Q. semecarpifolia* had a higher rate of dry matter accumulation, which increased the dry weight per unit leaf area.

In conclusion, wood water properties, SLM (related to the differences in the proportion of photosynthetic tissue as well as increased sclerophylly) and leaf N resorption showed close empathy with leaf phenologiacal and developmental changes along the seasonal gradients by our species. 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 these species. Hence, as the geographic situation of Mahabharat 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), these evergreens should show a wide range of adaptational ability to compete.

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