

19. Okanishi, M., Suzuki, K. and Umezawa, H., Formation and reversion of *Streptomyces* protoplasts: Culture condition and morphological study. *J. Gen. Microbiol.*, 1974, **80**, 389–400.
20. Ferenczy, L., *Symp. Soc. Gen. Microbiol.*, 1981, **31**, 1–34.
21. Hopwood, D. A. and Chater, K. F., *Streptomyces*. In *Genetic and Breeding of Industrial Microorganisms* (ed. Ball, C.), CRC Press, 1984, pp. 8–40.
22. Illing, G. T., Normansell, I. D. and Peberdy, J. F., Protoplast isolation and regeneration in *S. clavurigelus*. *J. Gen. Microbiol.*, 1989, **135**, 2289–2297.
23. Prescott, L. M., Harley, J. P. and Klein, D. A., *Microbiology*, 2nd edn, WCB Publ., 1993, pp. 123–124.
24. Hopwood, D. A. and Wright, H. M., Bacterial protoplast fusion: Recombination in fused protoplasts of *S. coelicolor*. *Mol. Gen. Genet.*, 1978, **162**, 307–317.

ACKNOWLEDGEMENTS. We thank Dr Morteza Azarnoush, Pasteur Institute of IRAN, Dr Nasrin Moazzami (Iranian Research Organization for Science and Technology) and heads and personnels of departments of these centers for their cooperation.

Received 7 October 2004; revised accepted 28 February 2005

Paradox of leaf phenology: *Shorea robusta* is a semi-evergreen species in tropical dry deciduous forests in India

K. P. Singh* and C. P. Kushwaha

Department of Botany, Banaras Hindu University, Varanasi 221 005, India

Shorea robusta*, widely distributed in moist and dry forests in the tropics, has been paradoxically described as deciduous, semi-deciduous or evergreen species. To assess this contradiction, quantitative documentation of leaf dynamics, flowering and fruiting (by monthly counts on tagged twigs) was made in marked individuals of *Shorea* in a tropical dry deciduous forest. Annual leaf exchange seems to be a survival strategy in *Shorea* during the period of seasonal drought; it replaces all old leaves of differing longevity with new leaves to reduce water loss due to transpiration, and simultaneously supports asynchronous flowering. During March (the transitional month for the leafing phenophase) four phenological variants, reflecting considerable functional diversity in conspecific trees, were recorded. These were: variant a, leaf fall completed and leaf flush begins; variant b, leaf fall and leaf flush overlapping; variant c, leaf fall completed but leaf flush delayed, short leaflessness; variant d, leaf fall incomplete (old leaves persist) and leaf flush delayed. Individuals of *Shorea

responded variously (leaf exchange or evergreenness to leaflessness or deciduousness, but ≤ 1 year leaf lifespan) to microsite conditions, making it essentially a semi-evergreen species. It is suggested that semi-evergreenness in *Shorea*, an indicator of high adaptability, permits its extensive distribution in the tropics, from moist to the dry regions.

SHOREA robusta Gaertn. f. (sal) is one of the dominant tree species in tropical deciduous forests (moist as well as dry types) in India¹. The nature of *S. robusta* in terms of leaf phenology has been questionable due to evergreen vs deciduous paradox². While some workers have described *S. robusta* as a deciduous species^{3–5}, or semi-deciduous species⁶, others have viewed it as an evergreen species^{7–9}. Joshi¹⁰ has variously described *S. robusta* as deciduous or as border line between evergreen and deciduous. The lifespan of leaves is important in that it reflects several eco-physiological attributes¹¹. For example, compared to deciduous species, evergreen species generally show longer leaf lifespan, deeper root system, earlier leaf flushing during the dry season, higher stem water potential and greater ability to rehydrate the stem during the dry season, lower resource requirement to support leaf turnover, and longer duration of photosynthetic activity at lower rates^{12–15}. Thus, the phenological terms ‘deciduous’ and ‘evergreen’ have different connotations in tree physiology and should be applied to a species with great care.

In tropical trees, leaf phenology is important because it reflects the influence of evolution and environment on plant characteristics, and in turn has substantial implications for plant functioning¹⁶. Contrary to the deciduous tree species which are generally summer-flushing (vegetative bud breaks in hot-dry summer, May–June), *S. robusta* is a spring-flushing species (vegetative bud breaks around spring equinox, March–April) in Indian dry tropical forests¹⁷. The period around spring equinox is important because of the overlap of leaf fall, leaf flushing, and flowering/fruiting in *Shorea*. Occurrence of annual leaf exchange in *Shorea* in tropical dry deciduous forests raises several questions. Whether this species is evergreen or deciduous? Why does leaf exchange occur always during the mid dry season? Whether conspecific trees show similar phenological response? There is a need to precisely document the time and duration of various phenological events (like leaf flush and leaf fall) in this species and to quantify the extent of leafless period, if any, in conspecific trees. The objectives of the present quantitative phenological study on *S. robusta*, carried out in a tropical dry deciduous forest in the Vindhyan region, were to document the seasonal pattern of phenological events, especially the leaf dynamics, flowering and fruiting, including conspecific asynchrony, with a view to determining the leaf phenological nature of the species.

This study was carried out in Hathinala Forest (24°18'N, 83°6'E; elevation 315–485 m asl), spread over the Vindhyan plateau (ca. 150 km away from Varanasi), in the Sonbhadra

*For correspondence. (e-mail: kps@bhu.ac.in)

district of Uttar Pradesh, India. Based on interpretation of satellite imagery support and with field observations, the site can be described as the least-disturbed forest stand in the region. The Hathinala series of rocks is composed of haematitic slates or schists together with banded jaspers and quartzites, hornblende and limestones. According to the VII approximation of the USDA soil nomenclature, the soils are part of the hyperthermic formation of typical plinthustults with ustorthents.

Climate is characterized by three seasons: warm-wet rainy (mid June–September); cool-dry winter (November–February); and hot-dry summer (April–June); October and March are the transition months between seasons. Temperature and rainfall data, obtained from the State Irrigation Department, show that the mean maximum day temperature varies from 20°C in January to 42°C in May, and the minimum night temperature from 10°C in January to 24°C in May. About 85% of the annual rainfall is received in the rainy season, and 7–8 dry months occur during the annual cycle. Long-term annual rainfall varies between 850 and 1300 mm. During the study period, extending through two annual cycles (May 2001 to June 2003), the annual rainfall was 1410 and 1125 mm respectively (Figure 1).

The vegetation in the Hathinala forest belongs to the Northern Tropical Dry Deciduous Forest type (subgroup 5-B of Champion and Seth¹). The top-storey trees in the forest form a nearly continuous 15–20 m high canopy, underlain by a discontinuous lower storey of trees, a thin shrub layer and a seasonal herb layer which includes several grasses. *S. robusta* is a dominant tree species, co-existing with several associates (e.g. *Acacia catechu*, *Anogeissus latifolia*, *Diospyros melanoxylon*, *Hardwickia binata*, *Lagerstroemia parviflora*, *Lannea coromandelica* and *Terminalia tomentosa*). *S. robusta* occurs at relatively moist microsites (from hill base to mid-slope). In the rainy season, the forest becomes lush green due to the presence of fully expanded leaves of trees and shrubs and a dense herbaceous layer. The summer aspect is pale and parched because of the leafless trees and shrubs and a dried-up herb layer.

In a 2-ha permanent plot established at the Hathinala site, four twigs (currently growing shoots of last-order branches) on each of the four major branches (one in each direction) were marked with metal tags on ten adult individuals (> 30 cm GBH) of *Shorea*. Monthly counts of leaf, flower and fruit were made from May 2001 to June 2003 on the marked twigs. The following phenological events were derived from the monthly leaf, flower and fruit counts: initiation of leaf flush, completion of leaf flush, initiation of leaf fall, completion of leaf fall, flower initiation, completion of flowering, and duration of fruiting phenophase. Leaf flush period of an individual is the duration (days) from the first leaf flush to the last one. Leaf-fall period of an individual represents the time duration from the estimated first leaf fall to the last one.

Synchrony indices for leaf flushing, leaf fall, flowering, fruit flush and fruit fall phenophases of *Shorea* were calculated as the ratio between the marked individual's mean duration of a phenological phase and the overall duration of the phase¹⁸. The higher the ratio, greater the coincidence between different individuals of a species (i.e. at ratio 1.0 perfect synchrony will occur, and as the ratio decreases from 1.0 asynchrony will increase). Value of synchrony index was subtracted from 1.0 to get the asynchrony index.

Shorea trees maintained significant foliage (reflected by leaf number) well beyond the rainy season (Figure 2). Seasonal reduction in foliage occurred during the period February–April, and minimum foliage (ca. 30% of the peak leaf number) was recorded in March in individuals which did not become leafless. New leaf formation began during the mid-dry season (March–April), and >75% of total new leaves were produced during hot-dry summer, i.e. before the onset of rainy season (July). Leaf flushing, however, continued until October or November (following the rainy season, i.e. early winter season). Four phenological variants of *Shorea* were distinguished on the basis of contrasting leaf phenological events during March (Figure 2). During this month: (i) 40% individuals (located at lower slope of hills) showed completion of leaf fall and beginning of leaf flush

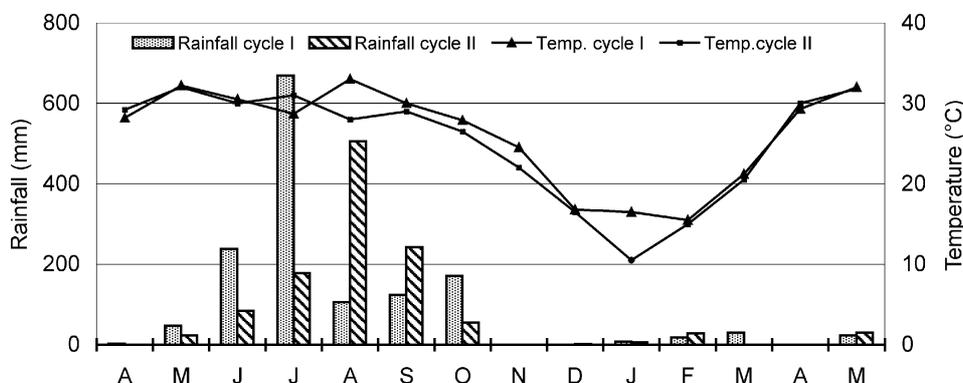


Figure 1. Climatic conditions at the Hathinala site in the Vindhyan region.

in March, variant (a); (ii) 30% individuals (located at hill base) showed overlapping in leaf fall and leaf flush, variant (b); (iii) 20% individuals (located at mid slope) showed a time gap between completion of leaf fall and initiation of production of new leaves, leaf fall phase was completed but the process of production of new leaves did not set in by the end of March, variant (c); and (iv) 10% individuals (located at mid slope) retained some old leaves and did not show production of new leaves by the end of March, variant (d). It is interesting to note that in both annual cycles the entire population of *Shorea* never became leafless, only about one-fifth individuals (variant c), situated in relatively dry and shallow soil, became leafless for a short period in March. Flowering began in winter and continued until early summer (January–April); this corresponds to the period of leaf fall (Figure 2). Greater flowering and fruiting occurred during the annual cycle I (being the mast year).

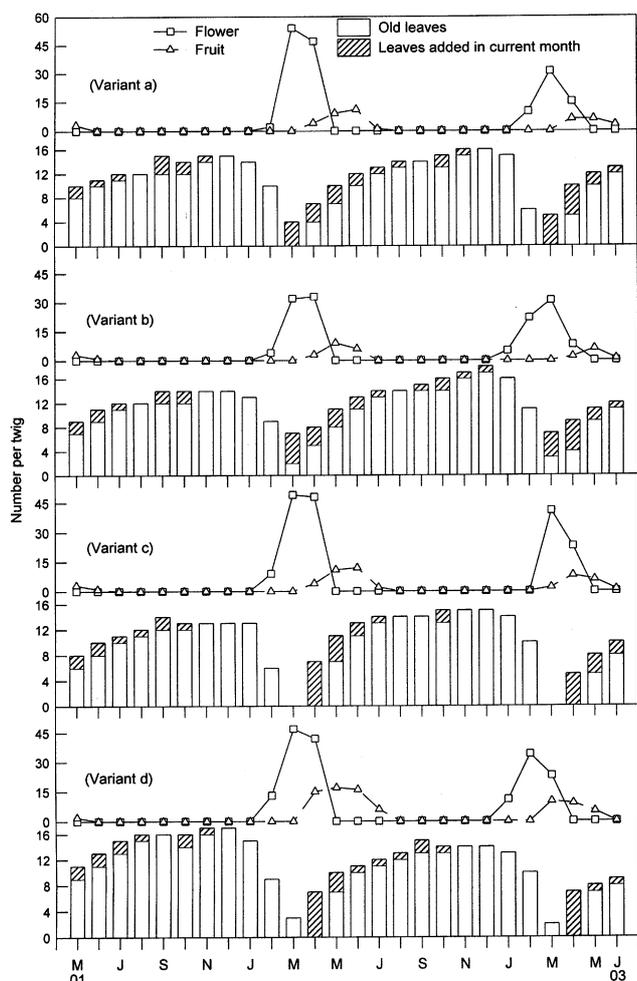


Figure 2. Seasonal patterns of dynamics of leaf, flower and fruit in four phenological variants of *Shorea robusta* through two annual cycles (May 2001 to June 2003) in tropical dry deciduous forest in the Vindhyan region.

Conspecific trees of *Shorea* growing in the same environment showed different phenological patterns with respect to leafing, flowering and fruiting (Figure 3). In contrast to long duration of leaf flush (March–November), leaf fall duration (January–March) was much shorter. Thus, concentrated fall of leaves of varying longevity occurred during the mid-dry season, resulting in turnover of the total foliage annually. Shedding of old leaves was either accompanied or followed by leaf flush around spring equinox (March–April). Variants a and b (representing majority, 70% individuals) initiated leaf flush in March and variants c and d (30% individuals) did so in April (Figure 3). Except variant c during annual cycle I, in all variants leaf fall started in January during both annual cycles. Completion of leaf fall in variants a and c (60% individuals) occurred within February, and in variants b and d (40% individuals) in March. A small fraction of leaves was shed in October. In all phenological variants, flowering was initiated with the onset of leaf fall in winter, and the duration of flowering coincided with the leaf transitional state (leaf fall and leaf flush initiation, Figure 3). Variant c continued flowering and initiated fruit formation during the leafless period. Thus, both reproductive phase (flowering and fruit development) and leaf initiation were supported at the same time.

Asynchrony amongst individuals for different phenological events varied between years (Table 1). During both annual cycles, leaf flushing was relatively more synchronous in conspecific trees (indicated by lower asynchrony index) compared to other phenological events. Among different phenological events, fruit fall was least synchronous in conspecific trees. During the mast year (annual cycle I), flowering, fruit initiation and fruit fall were highly synchronous compared to the annual cycle II.

Phenology of trees in dry tropics is mainly determined by the duration and intensity of seasonal drought. The degree of drought to which trees are exposed varies widely, depend-

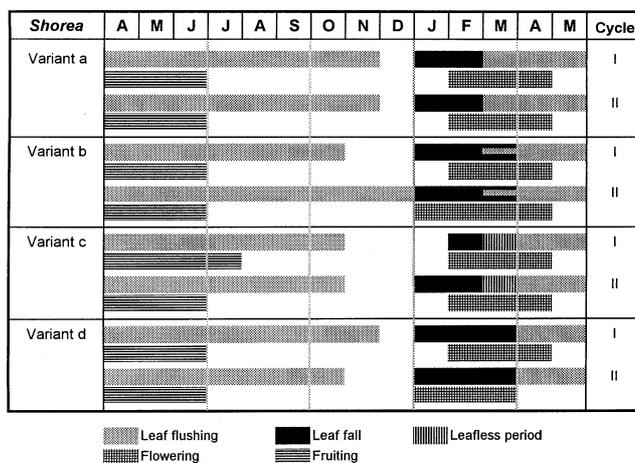


Figure 3. Diversity in seasonal durations of leafing, flowering and fruiting phenophases in four phenological variants of *S. robusta* in tropical dry deciduous forest in the Vindhyan region.

Table 1. Asynchrony index for different phenological events in *Shorea robusta* in tropical dry deciduous forest in Vindhyan region

Phenological event	Asynchrony index	
	I annual cycle	II annual cycle
Leaf flushing	0.08	0.13
Leaf fall	0.20	0.15
Flowering	0.03	0.36
Fruit initiation	0.04	0.34
Fruit fall	0.30	0.42

ing on temperature and availability of soil water, and also tree characteristics such as rooting depth¹⁹. *Shorea* changes foliage in the middle of the dry season around spring equinox, contrasting with the co-existing deciduous tree species producing new leaves after varying leafless periods during the dry-hot summer (May–June), shortly before the beginning of the rainy season¹⁷. While evergreen species generally show leaf flush in the mid dry season, the deciduous species leaf out just before or with the onset of the rainy season¹⁴. In view of its spring leaf flushing, predominant leaf exchange and substantial re-establishment of canopy during the hottest and driest period of the year (March–June), *Shorea* cannot be designated as a deciduous species. Occurrence of leaf flushing and flowering in *Shorea* during the mid dry period of the annual cycle reflects its ability, like many evergreen species, to quickly rehydrate the stem during the dry season. Leaf fall and a high water potential of twigs are prerequisites for subsequent leafing¹². Leaf-exchanging species (like *Shorea*) are restricted to relatively moist sites and maintain a high water potential during the dry season²⁰. *Shorea* shows deep root system, enabling access to sub-soil water¹⁰. Detection of four leaf phenological variants in *Shorea* in our study shows considerable functional diversity among conspecific trees. Individuals of *Shorea* respond variously (leaf exchange or evergreenness to leaflessness or deciduousness, but ≤ 1 year leaf life span) to microsite conditions, making it essentially a semi-evergreen species. In drier microsities, short leaflessness imposed on few individuals may be due to longer stem rehydration duration and consequent delayed leaf flushing. Semi-evergreen species are hardly ever without green leaves, and if so only for a relatively short period^{21,22}.

Annual leaf exchange in *Shorea* seems to be a survival strategy during the period of seasonal drought. It replaces all old leaves of different longevity with new leaves to reduce water loss due to transpiration. In deep-rooted *Shorea*, flowering and leaf flushing are probably dependent on prior leaf fall and the availability of sub-soil water reserves, both promoting water status of the trees. *Shorea* shows opportunistic leaf phenological nature, its individuals being able to tolerate (evergreenness) or avoid (deciduousness) drought depending upon microsite conditions; most of the individuals tolerate drought, but few (about one-fifth)

avoid drought for a short period. Occurrence of four phenological variants indicates that semi-evergreen *Shorea* can leaf out whenever trees or branches have become fully hydrated, i.e. their opportunistic phenology is mainly determined by seasonal variation in tree water status at a given microsite. Based on qualitative visual observations, Singh and Singh²³ reported that in dry tropics *Shorea* does not become leafless on the moist site, but on the dry site, most of the individuals become leafless for a week or so in March. However, in moist Central Himalaya, *Shorea* is a dominant evergreen species with concentrated early summer leaf fall and simultaneous leafing⁹. We suggest that wide leaf phenological response in *Shorea* due to its semi-evergreen nature helps in its extensive distribution in the tropics, from the moist regions (e.g. Central Himalaya) to the dry regions (e.g. Vindhyan). Functionally, *S. robusta* is the only semi-evergreen tree species in the presently studied dry deciduous forest, and semi-evergreenness might be an indicator of its high adaptability.

Plants can increase their plasticity through phenological asynchrony among individuals¹⁸. In the present study, conspecific asynchrony for various phenological events varied between the two annual cycles. Variation in the date of onset of monsoon and the amount and distribution of rainfall during the annual cycle may affect factors regulating the soil-plant-atmosphere water continuum. In dry environments, heterogeneity and periodicity of water availability have been demonstrated as being crucial factors in phenological rhythms of tree populations²⁴. Borchert²⁵ hypothesized that in dry forests, within-species asynchrony in tree phenology is guided by differences in water availability and hence tree water status is likely to cause the observed variation in *Shorea* phenology. Conspecific asynchrony in phenological behaviour is also a functional attribute that contributes to species dominance over a range of micro-environmental conditions.

Atluri *et al.*²⁶ reported that flowering in *Shorea* commences during late February, while trees are leafless with little asynchrony among individual trees. In contrast, in the Vindhyan region, conspecific trees of *Shorea* begin highly asynchronous flowering along with initiation of leaf fall during winter season, and flowering coincides with the leaf transitional stage (leaf fall and leaf initiation). Thus, drought-induced leaf shedding seems to act as a flowering cue. In many species, flower bud expansion and anthesis are triggered during the dry season by rehydration of twigs caused by leaf shedding⁷. Soil water status seems to substantially modulate the reproductive phase as well as leaf-shedding in semi-evergreen species^{24,27}. Intra-species asynchrony at the time of flowering induced by drought-induced leaf shedding varies in a landscape with differences in soil water storage¹². Presence of semi-evergreen winter flowering *Shorea* in tropical dry forests indicates the presence of microsities with reliable, large sub-soil water reserves, from which deep-rooted trees can extract water during the dry season.

There is increasing evidence that global climatic change is affecting species physiology, distribution and phenology²⁸. Phenology displayed at present in tropical forest trees will shift towards forest of lesser or greater moisture balance, in roughly direct proportion to the way in which any global change element changes moisture balance²⁹. India may experience between 5 and 25% decline in winter-time rainfall³⁰, severely affecting tree species like *Shorea*, which show critical phenological events (leaf exchange and flowering) at the end of winter. Even a moderate decline in annual rainfall in combination with increasing evapotranspiration resulting from predicted increase in temperature, may deplete soil water reserves, thereby further marginalizing the distribution of the semi-evergreen *Shorea* in the tropical dry deciduous forest region.

1. Champion, H. G. and Seth, S. K., *A Revised Survey of the Forest Types of India*, Manager of Publications, Government of India, New Delhi, 1968, p. 404.
2. Troup, R. S., *The Silviculture of Indian Trees*, Clarendon Press, Oxford, 1921, vol. I, p. 336.
3. Kirtikar, K. R. and Basu, B. D., *Indian Medicinal Plants*, Jayyed Press, New Delhi, 1975, vol. I, p. 838.
4. Cooke, T., *Flora of Bombay*, Botanical Survey of India, Calcutta, 1958, vol. I, p. 632.
5. Tiwari, D. N., *A Monograph on Sal (Shorea robusta Gaertn. f.)*, Vedams eBooks (P) Ltd, New Delhi, 1995, p. 277.
6. Bor, N. L., *Manual of Indian Forest Botany*, Oxford University Press, Bombay, 1953, p. 441.
7. Borchert, R., Organismic and environmental controls of bud growth in tropical trees. In *Dormancy in Plants: From Whole Plant Behavior to Cellular Control* (eds Viemont, J. D. and Crabbe, J.), CAB International, Wallingford, 2000, pp. 87–107.
8. Krishnaswamy, V. S. and Mathauda, G. S., Phenological behaviour of a few forest spp. at New Forest, Dehra Dun. *Indian For.*, 1954, **80**, 3–4.
9. Singh, J. S. and Singh, S. P., *Forests of Himalaya*, Gyanodaya Prakashan, Naini Tal, 1992, p. 257.
10. Joshi, H. B., *The Silviculture of Indian Trees*, Controller of Publications, New Delhi, 1980, p. 471.
11. Reich, P. B., Walters, M. B. and Ellsworth, D. S., Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecol. Monogr.*, 1992, **62**, 365–392.
12. Borchert, R., Rivera, G. and Hagnauer, W., Modification of vegetative phenology in a tropical semi-deciduous forest by abnormal drought and rain. *Biotropica*, 2002, **34**, 27–39.
13. Eamus, D. and Prior, L., Ecophysiology of trees of seasonally dry tropics: Comparisons among phenologies. *Adv. Ecol. Res.*, 2001, **32**, 113–197.
14. Medina, E., Diversity of life forms of higher plants in neotropical dry forests. In *Seasonally Dry Tropical Forests* (eds Bullock, S. H., Mooney, H. A. and Medina, E.), Cambridge University Press, Cambridge, 1995, pp. 221–242.
15. Chapin, F. S., Bret-Harte, M. S., Hobbie, S. and Zhong, H., Plant functional types as predictors of the transient response of arctic vegetation to global change. *J. Vegetation Sci.*, 1996, **7**, 347–357.
16. Reich, P. B., Uhl, C., Walters, M. B., Prugh, L. and Ellsworth, D. S., Leaf demography and phenology in Amazonian rain forest: A census of 40000 leaves of 23 tree species. *Ecol. Monogr.*, 2004, **74**, 3–23.
17. Kushwaha, C. P. and Singh, K. P., Diversity of leaf phenology in a tropical deciduous forest in India. *J. Trop. Ecol.*, 2005, **21**, 47–56.
18. Devineau, J.-L., Seasonal rhythms and phenological plasticity of savanna woody species in a fallow farming system (south-west Burkina Faso). *J. Trop. Ecol.*, 1999, **15**, 497–513.
19. Van Schaik, C. P., Terborgh, J. W. and Wright, S. J., The phenology of tropical forests: Adaptive significance and consequences for primary producers. *Annu. Rev. Ecol. Syst.*, 1993, **24**, 353–377.
20. Rivera, G., Elliott, S., Caldas, L. S., Nicolossi, G., Coradin, V. T. R. and Borchert, R., Increasing day-length induces spring flushing of tropical dry forest trees in the absence of rain. *Trees*, 2002, **16**, 445–456.
21. De Bie, S., Ketner, P., Paase, M. and Geerling, C., Woody plant phenology in the West African savanna. *J. Biogeogr.*, 1998, **25**, 883–900.
22. Gerhardt, K. and Hytteborn, H., Natural dynamics and regeneration methods in tropical dry forests – An introduction. *J. Vegetation Sci.*, 1992, **3**, 361–364.
23. Singh, J. S. and Singh, V. K., Phenology of seasonally dry tropical forest. *Curr. Sci.*, 1992, **63**, 684–688.
24. Konate, S., Leroux, X., Tessier, D. and Lepage, M., Influence of large termitaria on soil characteristics, soil water regime, and tree leaf shedding pattern in a West African savanna. *Plant Soil*, 1999, **206**, 47–60.
25. Borchert, R., Induction of rehydration and budbreak by irrigation or rain in deciduous trees of a tropical dry forest in Costa Rica. *Trees*, 1994, **8**, 198–204.
26. Atluri, J. B., Ramana, S. P. V. and Reddi, C. S., Explosive pollen release, wind-pollination and mixed mating in the tropical tree *Shorea robusta* Gaertn. f. (Dipterocarpaceae). *Curr. Sci.*, 2004, **86**, 1416–1419.
27. Seghier, J. and Simier, M., Variations in phenology of a residual invasive shrub species in Sahelian fallow savannas, south-west Niger. *J. Trop. Ecol.*, 2002, **18**, 897–912.
28. Borchert, R., Responses of tropical trees to rainfall seasonality and its long-term changes. *Climatic Change*, 1998, **39**, 381–393.
29. Reich, P. B., Phenology of tropical forests: Patterns, causes and consequences. *Can. J. Bot.*, 1995, **73**, 164–174.
30. Pandey, D. N., Global climatic change and carbon management in multifunctional forests. *Curr. Sci.*, 2002, **83**, 593–602.

ACKNOWLEDGEMENTS. We thank the Head, Department of Botany and the Coordinator, Centre of Advanced Study in Botany, BHU, Varanasi for laboratory and library facilities. Financial support was provided by the Council for Scientific and Industrial Research, New Delhi, in form of Research Associateship to C.P.K.

Received 17 September 2004; revised accepted 28 February 2005