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Climatic factors responsible for triggering phenological events in *Manilkara hexandra* (Roxb.) Dubard., a canopy tree in tropical semi-deciduous forest of Sri Lanka

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Abstract: Vegetative and reproductive phenological events of *Manilkara hexandra* (Roxb.) Dubard. were studied in a tropical semi-deciduous forest at Bundala National Park, Sri Lanka, in relation to climatic factors. Twenty one individuals of *M. hexandra* were observed for phenological studies for four years at fortnightly intervals. *M. hexandra* is a leaf-exchanging species which shows synchronous phenological events. Rainfall played a key role in major leafing events. However, leaf shedding also took place in the middle of the major rainy season (late November-December). Flower buds initiated immediately after leaf shedding and leaf bud breaking but blooming took place towards the end of the major rainy season. High soil moisture and relative humidity due to heavy rainfall, low air and soil temperatures, low wind velocity and low solar radiation levels provided optimal external environmental conditions for flowering. However, triggering of flowering took place due to the sudden drop of solar radiation and subsequent drop in air and soil temperatures which was maintained for more than 36 hours. Abortion of flowers and young fruits occurred due to sudden climatic variations such as drought or heavy rains. In the absence of such adverse environmental conditions, a large number of fruits may be produced, resulting in a mass fruiting event.

Resumen: Los eventos fenológicos vegetativos y reproductivos de *Manilkara hexandra* (Roxb.) Dubard. fueron estudiados en un bosque tropical subcaducifolio en el Parque Nacional Bundala, Sri Lanka, en relación con factores climáticos. Veintiún individuos de *M. hexandra* fueron observados para el estudio fenológico durante cuatro años a intervalos quincenales. *M. hexandra* es una especie que recambia su follaje y que muestra eventos fenológicos sincrónicos. La precipitación jugó un papel clave en los eventos principales de foliación. No obstante, también hubo caída de hojas a la mitad de la estación lluviosa principal (finales de noviembre-diciembre). El inicio del desarrollo de botones florales ocurrió inmediatamente después de la caída de las hojas y el inicio del desarrollo de las yemas foliares, pero la floración tuvo lugar hacia el final de la estación lluviosa principal. Valores altos de humedad del suelo y de humedad relativa debido a las lluvias intensas, temperaturas bajas del aire y del suelo, una baja velocidad del viento y niveles bajos de radiación solar proporcionaron las condiciones ambientales externas óptimas para la floración. Sin embargo, la inducción de la floración se debió a un descenso repentino de la radiación solar y la disminución subsecuente en las temperaturas del aire y del suelo, las cuales se mantuvieron durante más de 36 horas. Algunas flores y frutos jóvenes fueron abortados debido a variaciones climáticas repentinas tales como una sequía o lluvias intensas. En ausencia de tales condiciones ambientales adversas se puede producir un gran número de frutos, lo cual resulta un evento de fructificación en masa.

Resumo: Eventos fenológicos vegetativos e reprodutivas, na *Manilkara hexandra* (Roxb.)

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Dubard. em relação a fatores climáticos foram estudados numa floresta semi-decídua tropical no Parque Nacional de Bundala, Sri Lanka. Estudos fenológicos em vinte e um indivíduos de *M. hexandra* foram efectuadosdurante quatro anos, em intervalos quinzenais. A *M. hexandra* é uma espécie semicaducifólia o que mostra eventos fenológicoss íncronos. A queda de chuvas desempenhou um papel fundamental nos principais eventos folheares. No entanto, a queda de folhas também ocorreu a meio da principal estação de chuvas (final de novembro-dezembro). Os botões florais iniciaram-se imediatamente após a queda de folhas e a rebentação do gomo folhearmas a floração ocorreu no final da temporada da principal estaçãode chuvas. A alta humidade do solo e a humidade relativa devido às fortes chuvas, as baixas temperaturas do ar e do solo, baixavelocidade do vento e baixos níveis de radiação solar proporcionaram condições ambientais externas óptimas para a floração. No entanto, o desabrolhar da floração ocorreu devido à queda repentina da radiação solar e queda subsequente das temperaturas do ar e do solo as quais se mantiveram por mais de 36 horas. O aborto de flores e frutos jovens ocorreu devido a variações climáticas bruscas, como secas ou fortes chuvas. Na ausência de tais condições ambientais adversas, um grande número de frutos podem ser produzidos, de que resulta um evento de frutificação em massa.

Key words: Climatic factors, *Manilkara hexandra*, phenological events, reproductive phenology, Sri Lanka.

Introduction

Phenological studies are important for conservation of tree genetic resources and management of forests (Kikim & Yadava 2001). Such studies are essential in understanding the pattern of plant growth and development as well as revealing the influence of the environment on flowering and fruiting behaviour (Zhang *et al.* 2006). Among the various factors that affect the phenological events of tropical plants, climatic factors are of prime importance. Changing climate may alter patterns in plant populations by impacting the phenological events of tropical forest species (Borchert 1998; Corlett & Lafrankie 1998).

Several studies have revealed that rainfall and soil moisture content are the most important climatic factors that affect vegetative phenological events (Elliot *et al.* 2006; Lieberman 1982; Lieberman & Lieberman 1984; Loomis & Connor 1992; Reich & Borchert 1984; Yadav & Yadav 2008). For instance, leaf fall in many tropical deciduous species is reported to take place during the dry period (Lieberman 1982; Reich & Borchert 1982; Singh & Singh 1992) while the leaf bud breaking and formation of young foliage take place during high rainfall period (Lieberman & Lieberman 1984; Reich & Borchert 1984).

The reproductive phenology of tropical plants also depends on several abiotic factors, of which rainfall is the most important (Elliot *et al.* 2006; Lieberman 1982; Lieberman & Lieberman 1984; Reich & Borchert 1984). Flowering and fruiting of many tropical dry forest species take place during rainy season (Lieberman 1982; Opler *et al.* 1976, 1980). Moreover, high solar radiation has been reported to trigger the flowering event among many plants in the tropics (van Schaik 1986; van Schaik *et al.* 1993; Wright & van Schaik 1994). Photoperiod or day length has been reported to induce flowering in subtropical dry and arid environments (Bowers & Dimmitt 1994; Humphrey 1975; Turner 1963; Sloan & Zimmerman 2007; Yadav & Yadav 2008).

Many researchers have correlated flowering events with change in temperature in many tropical environments (Ashton *et al.* 1988; Lyndon 1992; Marques *et al.* 2004; Stevenson 2004) but Stevenson *et al.* (2008) attributed the actual trigger of flowering to a sudden drop of solar radiation and subsequent drop of air and soil temperatures. However, the effects of various climatic factors and their threshold levels on phenological events of threatened tropical tree species that grow in dry seasonal environments have not adequately been studied. This study deals with *Manilkara hexandra* (Roxb.) Dubard. which is a dominant canopy tree species in tropical seasonal forests of Sri Lanka (Gunarathne & Perera 2009). The population of *M. hexandra* has been dying out due to both natural and anthropogenic causes (Gunarathne & Perera 2009). As such, the natural regeneration of this species is reported to be very poor (de Rosayro 1961; Holmes 1956; Perera 1998, 2001).

The present study aimed at evaluating: (1) the phenological patterns of a tropical tree *M. hexandra*, (2) abiotic factors affecting the phenological events of the species, and (3) the threshold levels of important climatic parameters for flowering of the species.

Materials and methods

Study site

The study was carried out in Bundala National Park (BNP) situated along the south coast of the Hambantota district in the low country dry zone of Sri Lanka (6° 08'- 6° 14' N, 81° 08'.- 81° 18' E) (Fig. 1). The Park is spread over an area of 3698.01 ha and the natural forest type of the park is tropical semi-deciduous forest. The climate of the study area is hot and dry, and the rainfall pattern is related to monsoon periods. The area receives the highest rainfall around November from North-East monsoon. The distribution of rainfall in the area is bimodal (Fig. 2), having a minor rainy season from April - May and a major rainy season from September or October to January. Consequently, there are two distinct dry seasons; a minor dry period that occurs from February to March and the major dry period which occurs from June to September or October. The mean annual temperature and the mean annual rainfall of the area for the period from 1995 - 2008 is 27.8 °C and 1059 mm, respectively.

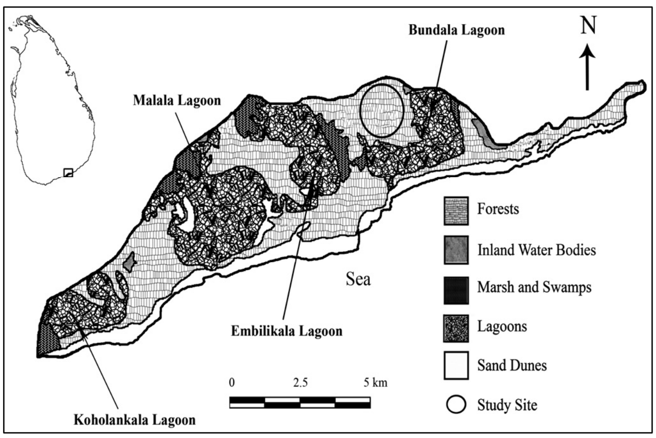

Fig. 1. A map of Bundala National Park and the location of the study site.

Most of the Park area has been disturbed in the past (before early 1990s) by shifting cultivation and selective logging which have led to a vegetation comprised of thorny shrub species such as *Atalantia ceylanica, Flueggea leucopyrus, Psilanthus wightianus, Ziziphus oenoplia,* with scattered *M. hexandra* trees. The present study was conducted in such a scrub forest located in the north central part of the Park. *M. hexandra* is a tree which grows up to 20 m in height with a large spreading crown with dark green foliage. Leaves are leathery in texture and oblong-obovate or elliptic in shape. Flowers are white in colour and are arranged in small clusters of 1-3 flowers at leaf axils. Its ripe fruit is a small sweet berry with a thick pulp and latex which is yellow in colour and ovoid in shape (Verdcourt & Meijer 1995).

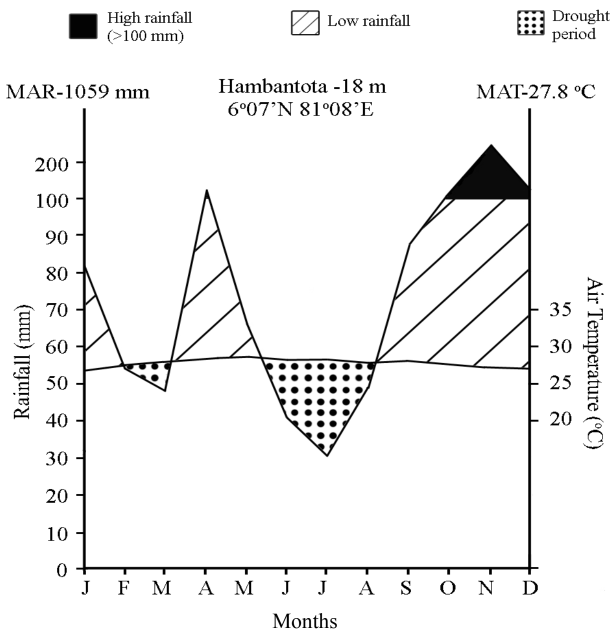

Fig. 2. Climate diagram for the study area. Rainfall and temperature data were collected from meteorological station at Hambantota (4 km away from Bundala National Park) over a period of 13 years from 1995 to 2008.

Recording the phenological events

Twenty one healthy and mature individuals of *M. hexandra* in the north central part of BNP were selected for observations on vegetative phenology (leaf flushing and leaf shedding) and reproductive phenology (flowering and fruiting). A binocular (x10-20 magnification, Nikon Action Series®) was used for observing these phenological events at every fifteen days interval over a period of four years from January 2006 - December 2009. To record leaf flushing, flowering and fruiting events, the proportions of crown cover with young leaves, flowers or fruits were noted respectively, while for leaf shedding, the percentage of crown cover without leaves was considered. To monitor the leafing patterns of *M. hexandra*, three healthy twigs from five healthy and mature trees were tagged and closer observations were made at a 15 day interval over a period of one year, from October 2008 to December 2009.

In addition, four twigs were sampled from the periphery of each selected individual and in each twig, the leaf area (the total surface area of the leaf in cm^2) of the first 10 leaves was measured using a leaf area meter (CI-202, CID, Inc.®) six times over a period of thirteen months. Whether or not pollinators are attracted to flowers of *M. hexandra* during the flowering season was examined with the aid of a binocular (x10-20 magnification).

Recording the climatic and micro- climatic data in the study area

A mini weather station was installed (WatchDog™ Weather Station, 900ET; Spectrum Technologies, Inc.) at the study site in February, 2007. The rainfall, air temperature and solar radiation data were collected at one hour interval over a period of two and half years. As the experiment was started in January, 2006, the climatic data from 2006 to 2007 were collected from the meteorological station at Hambanthota, situated about 5 km away from the park. Ecologically effective rainfall was determined by calculating the running mean of daily total rainfall over a period of seven days by assuming the amount of rain water received in a given day is available for plants only for the consecutive seven day period due to heavy evapo-transpiratory loss.

To measure the soil temperature, a Tinytag® Ultra 2 temperature data logger was established in BNP and the temperature measurements were obtained at every half an hour from December, 2006 to January, 2008. The soil moisture content was determined by considering the weight difference between fresh and oven dried soil samples as a proportion of the fresh weight of the soil sample. This procedure was repeated during wet and dry seasons from September, 2007 to September, 2009.

Impact of primates on flowers and fruits

Primates who damage flowers and young fruits were examined while the population density of primates inhabiting the park was estimated by line transect method described by Buckland *et al.* (1993). Then, individuals were counted once in three months over a period of two years in two selected 50 m line transects.

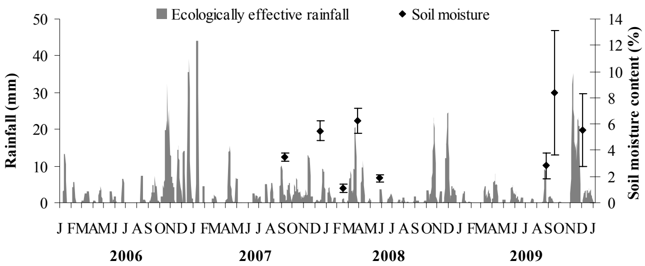

Fig. 3. Ecologically effective rainfall (7 day running mean) and plant available soil moisture contents at Bundala National Park.

Results

Climatic conditions

The rainfall pattern in Bundala is seasonal and the mean annual rainfall of the area varied from 1000 to 1300 mm. The highest monthly rainfall was received in November during the North-East monsoon period (Fig. 2). The water was available to the plants in most part of the year except towards the middle parts of the two drought periods (Fig. 3). This pattern is much similar to the pattern of variation of daily total rainfall (Fig. 4). Fig. 3 further indicates that in dry periods, the moisture content at the surface soil (up to 10 cm) was below 3 percent but in wet periods it was greater than 6 percent.

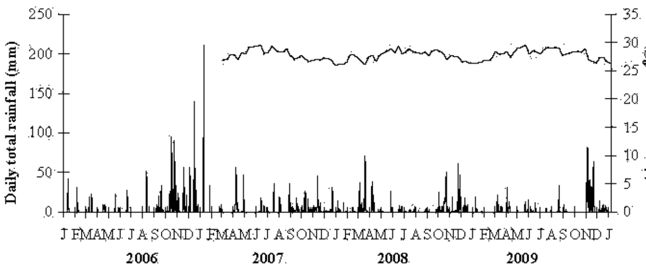

Fig. 4. Daily total rainfall and average air temperature (average of 10 days) in Bundala National Park.

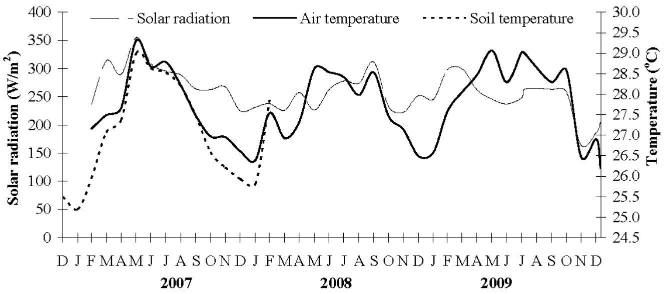

Fig. 5. Variations of monthly solar radiation and monthly air temperature over a period of 35 months (from February 2007 to January 2010) and monthly mean soil temperature over a period of 13 months (from December 2006 to January 2008) at Bundala National Park.

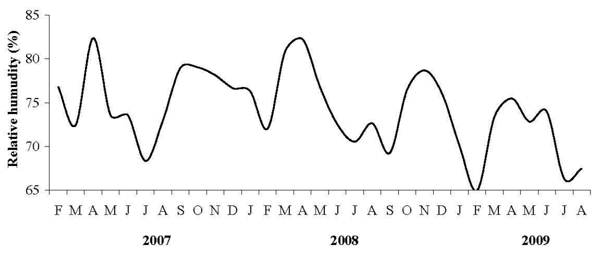

Fig. 6. Variations of relative humidity values over a period of 31 months (from February 2007 to August 2009) at Bundala National Park.

The amount of solar radiation received was low in November - January months of the year when there were heavy rainfall events (Fig. 5). The air temperature and soil temperature at the site were also low during this period (Fig. 5). The average relative humidity in the atmosphere was higher than that in the drought periods (Fig. 6). The mean annual relative humidity for the area (from 2007 - 2009) varied between 54.6 - 91.9 percent but it was higher than the annual average (75.9 percent) during the major rainy season. The monthly average wind velocity also varied within a year and it was usually low in the months of November to February (2 - 3 km hr^{-1}) i.e., during the major rainy period but higher than 5 km hr^{-1} from May to September (Fig. 7). Sometimes especially during the major rainy season, the solar radiation suddenly drops due to thick cloud cover and simultaneously, the air and soil temperatures show minimum values. For instance, solar radiation and the air and soil temperatures were lower than the annual average values in some parts of the year (in late November or December) during the study period (Table 1). However, a similar condition occurred in late April as well.

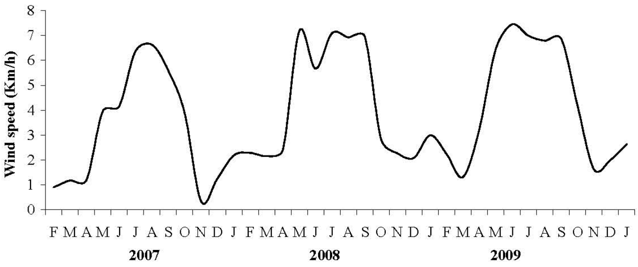

Fig. 7. Variations of wind speed over a period of 36 months (from February 2007 to January 2010) at Bundala National Park.

Vegetative phenology

Leaf flushing and leaf shedding in all individuals of the population of *M. hexandra* were synchronous. Vegetative phenological observations as well as the observations made on tagged twigs revealed that the leaf flushing in *M. hexandra* mainly occurs as major and minor flushing events (Fig. 8a). In addition to these two flushing events, a few new leaves did arise during other times of the year, but did not exceed 20 percent of the crown cover. The major leaf flushing event coincides with the major rainy season (Figs. 3, 4 & 8a) and proceeds over a period of 8 - 10 weeks. Leaf buds initiated in the early part of the major rainy season remained without expanding for few weeks, then expanded immediately; severe leaf shedding occurred in late November or early December. This pattern resulted in a rapid increase in average leaf area but the leaves reached the maximum size by the end of the major rainy season. However, the average leaf area does not vary significantly throughout the dry season (Fig. 9). During this period 100 percent crown is filled with young foliage. Young leaves are produced by both terminal and axillary buds and, 3 - 6 new leaves arise from every bud. Leaves are spirally arranged but clustered at shoot apex. The minor flushing event starts within 2 - 3 weeks after the end of the major leafing event and proceeds up to about six weeks and produces only a few young leaves. However, in 2009, the minor flushing event was not prominent.

Table 1. Average air temperature, soil temperature and solar radiation at possible flower bud triggering days in each flowering occasion.

Possible triggering dates	Average air temperature (°C)			Average soil temperature (°C)			Average solar radiation (Wm^{-2})	
	Day	Night	Annual	Day	Night	Annual	Day	Annual
08/12/2007	29	26	28	28	26	27	234	286
09/12/2007	26	24		26	25		75	
10/12/2007	29	26		27	25		208	
27/04/2008*	29	26	28	-	-	-	290	258
28/04/2008	26	26		-	-		83	
29/04/2008	29	27		-	-		254	
23/11/2008	29	25	28	-	-	-	218	258
24/11/2008	26	26		-	-		44	
25/11/2008	29	26		-	-		318	
22/12/2009	27	24	28	-	-	-	108	248
23/12/2009	25	24		-	-		67	
24/12/2009	28	25		-	-		211	

*unusual fruiting season due to the abortion of flowers and fruits in early 2008.

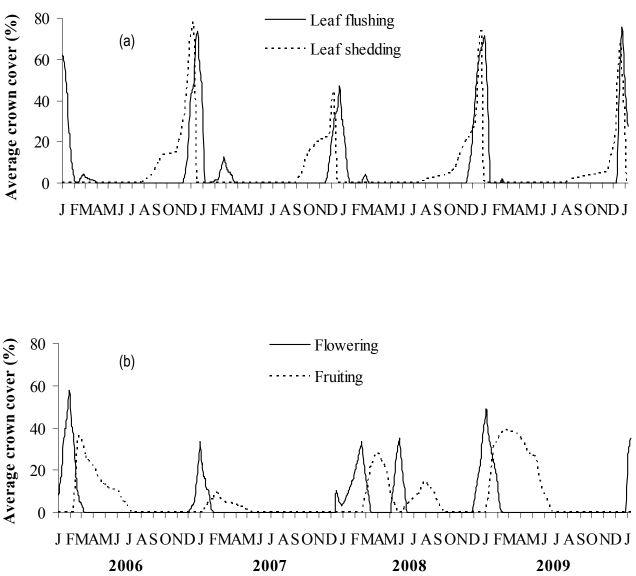

Fig. 8. (a) Vegetative phenology, (b) Reproductive phenology of *M. hexandra* in Bundala National Park. [Percentage values given in Fig. 3(b) are the fraction of individuals in the population with fruits].

Leaf shedding starts in the major dry season and proceeded until the later part of the major rainy season (till the end of December) (Fig. 8a) with a peak of leaf shedding in mid November-December, when the monthly average rainfall was high. When a crown of a given tree is observed, it appears that the leaf flushing takes place simultaneously with leaf shedding. However, when individual twigs were tagged and observed, it was clear that leaf shedding results into bare shoots at least for a few days and subsequently the twigs get filled up with leaf buds or young leaves.

Reproductive phenology

Flowering and fruiting in all individuals of the population of *M. hexandra* were synchronous. The flowers were produced every year but the duration of flowering period varied from year to year (Fig. 8b). In general, the flowering starts in December and continues till February or March in the following year. However, in 2008, the flowering season continued up to June but it occurred in two flushes. During this year, the flowers produced in December - February were aborted before fruits set, and trees bloomed again in May. It was noticed that, at both occasions, all the individuals of the population produced flowers.

During the years 2006, 2007 and 2009, all the individuals produced fruits but the number of fruits produced in 2007 was lower than that in 2006 and 2009. In 2008, although all the individuals had

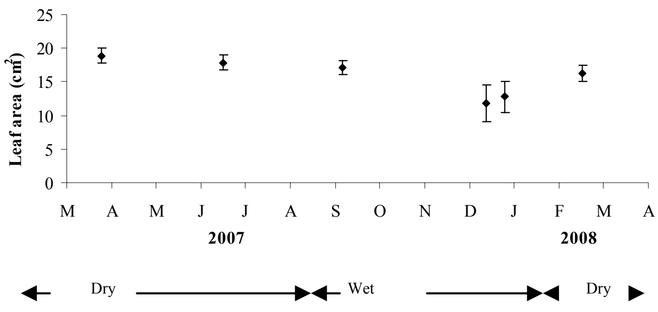

Fig. 9. Changes of leaf area of the selected individuals of *M. hexandra* in Bundala National Park at different times over a period of 13 months (from March 2007 to April 2008).

produced flowers after the first flowering peak, fruits appeared only on about 80 percent of the individuals. All individuals had produced flowers in the second flowering peak in 2008 but fruits occurred in about 70 percent of these individuals. As seen in Fig. 8b, it was clear that the duration of the fruiting season also varied from year to year. In 2006, the fruiting season extended from February to the end of June while in 2009, it was extended from January to mid June (Fig. 8b). Thus mature fruits were available from April to July. However, in 2007 and 2008, the fruiting periods were much shorter as young fruits were either predated by animals or aborted before ripening. In 2008, fruits occurred in two instances with respect to the two flowering events, despite that almost all of these fruits were destroyed before ripening.

Climatic factors and phenological events

It appears that phenological events of *M. hexandra* are influenced by various climatic factors. Mass scale leaf flushing always takes place during the middle of the major rainy season (at least four weeks after the beginning of heavy rains) (Figs. 4 & 8a). The ecologically effective rainfall together with the soil moisture levels (Fig. 3) acts as an indicator of the availability of water for plants and the data clearly show that plants have adequate amount of water when leaf flushing and flowering take place (Figs. 3, 8a & 8b). The wind velocity is comparatively low for the period from November to April (Fig. 8) when the important phenological events such as leaf bud breaking, leaf flushing, flower bud breaking, flowering and fruit set take place.

Careful examination of the average daily solar radiation and day- and night- air and soil temperatures for the dates prior to blooming proved that flowering was initiated within 5 - 7 days of a sudden drop of solar radiation (below 85 W m^{-2}) which was maintained for more than 36 hours and consequent drop of air and soil temperatures (below 26 ºC). These values are significantly lower than the average annual values of the respective parameters (t test: for solar radiation, $P < 0.001$; for day time air temperature, $P < 0.003$ and for night time air temperature, $P < 0.014$; Table 1). Both solar radiation and the day and night air temperatures increased again by the middle of January and these values were more or less similar to the respective annual average values (Fig. 5). The average atmospheric relative humidity was higher during the period from October to early January when leaf bud breaking, leaf flushing and flowering of the species took place (Fig. 6).

Flowers and young fruits of *M. hexandra* were aborted due to unfavourable climatic conditions. For instance, the heavy rainfall during the later part of the major rainy season in December 2006 and January 2007, aborted most of the flower initiation and fruit development. A severe drought prevailed at the early part of the fruiting season in Februay 2008 which led to the abortion of young fruits. However, another flowering session started during the subsequent short rainy season from April to June, 2008.

Biotic factors affecting leaves, flowers and fruits

Grey langur (*Semnopithecus entellus*) and Toque macaque (*Macaca sinica*) were the major pre-dispersal seed predators of *M. hexandra*. Around 300 primates per km^2 inhabit BNP. These primates regularly stay and/or visit the trees of *M. hexandra* and make a considerable impact on trees by cosuming young leaves, flowers and fruits.

Discussion

Vegetative phenological events

M. hexandra is a leaf exchanging species where the leaf bud breaking takes place simultaneously with leaf shedding. Subsequently, the leafless shoots get filled up with young leaves. Mass scale leaf bud breaking in *M. hexandra* may induce abscission of older leaves after resorption of nutrients which could be useful in the production of large amounts of new leaves. Kramer & Kozlowski (1979) observed that nutrient resorption or the withdrawal of nutrients from senescing leaves and their storage in perennial woody parts is a common phenomenon in forest trees. Borchert *et al.* (2002) have also reported such leaf exchanging species in tropical semi-deciduous forests in Costa Rica where mass scale leaf shedding takes place during the dry season. Drought-induced water stress is found to be the major cause of leaf shedding in tropical dry forests (Justiniano & Fredericksen 2000; Holbrook *et al.* 1995; Lieberman 1982; Lieberman & Lieberman 1984) and leaf shedding during the drought period potentially improves the moisture balance of trees (Borchert 1994a, b; Kozlowski 1973). However, unlike in many dry forest tree species, leaf shedding of *M. hexandra* peaked during the middle part of the major rainy period (late November - December).

Lieberman & Lieberman (1984) and Reich & Borchert (1984) have stated that bud breaking and young foliage formation are governed by a threshold level of soil moisture determined by the occurrence of adequate rainfall. Stem rehydration which results due to heavy and prolonged rainy period is also reported as a prerequisite for the vegetative bud breaking (Borchert 1996; Rivera *et al.* 2002). Presence of adequate amount of soil moisture and dissolved nutrients during the rainy season would support the plants to produce leaf flush. A high humidity (around 80 %) and low wind velocity (around 2 km h^{-1}) during this period may reduce evapotranspiration from young leaves and help in maintaining turgidity and growth. Thus, this study supports other research works conducted in tropical and sub tropical dry forests, which concluded that rainfall plays a major role in determining the vegetative phenology (Bowers & Dimmitt 1994; Elliot *et al.* 2006; Lieberman 1982; Lieberman & Lieberman 1984; Murali & Sukumar 1993; Opler *et al.* 1976, 1980; van Schaik *et al.* 1993).

M. hexandra shows a synchronous leaf flushing as do many other plants that grow in seasonally dry forests (Borchert 1980; Daubenmire 1972; Frankie *et al.* 1974; Hopkins 1970; Lieberman 1982; Njoku 1963; Reich & Borchert 1982, 1984). Young leaves are normally succulent and rich in nutrients (Feeny 1976) and hence, these are easily susceptible to herbivore damage. Synchronous flushing helps in minimizing the acute herbivore damage to plants (Aide 1988; Lieberman & Lieberman 1984; Rockwood 1974). Further, since young foliage is also available on other plant species in the rainy season, predation pressure by Toque maccaque and Grey langur on the foliage of *M. hexandra* in BNP is reduced.

Reproductive phenological events

As in many other tree species in tropical dry forests (Yadav & Yadav 2008), *M. hexandra* shows synchronous flowering. Such a flowering pattern provides some adaptive advantages to trees (Alder & Kielpinski 2000) like attracting pollinators (Marquis 1988). The initiation of flowering in *M. hexandra* takes place during the later half of the major rainy season (Late December or January).

The present study clearly shows that factors such as rainfall, soil moisture, air temperature, relative humidity and wind velocity were related to the flowering of *M. hexandra*. Once the heavy rainfall adequately moistens the subsurface soil (at least over a period of about 30 days) and the trees are free from stresses (reduced transpiration due to low wind velocity, and high day time relative humidity), trees achieve optimal conditions for blooming. However, our study indicates that the actual trigger of flowering is related to a sudden drop of solar radiation and subsequent drop in air and soil temperatures. This is in agreement with the findings of Stevenson *et al.* (2008). It appears that the subsequent gradual increase in solar radiation and air temperature may have affected to sustain mass flowering and may possibly support the pollination by insects.

In *M. hexandra*, the initiated flower buds spend a dormant period of 2 - 3 weeks till the young leaves are fully expanded. This could be due to the fact that more energy is required for flower development than initiation and newly expanded leaves produce adequate amount of energy and nutrients for the development of flowers (Dick 1995). As in *M. hexandra*, flowering immediately after leaf flushing has been recorded for many other plant species in tropical dry forests of Mudumalai Wildlife Sanctuary in Southern India (Murali & Sukumar 1994). However, if heavy rains occur towards the later part of the flowering season (early fruiting season), it may prevent a successful fruit set as flowers of *M. hexandra* are aborted due to heavy rains. Moreover, heavy rains may limit the activities of insect pollinators and may directly affect the fruit production.

Our study indicated that all flowering periods ended with fruit production and trees should be free from stresses for a successful fruit production. Especially, soil moisture should be sufficiently available throughout the fruiting season and if not, young fruits may get aborted as observed in February, 2008. Thus, this study agrees with David *et al*. (2012) who pointed out that the rainfall correlates positively in the production of non-fig fleshy fruit species in tropical dry evergreen forests at the Sriharikota island, Southern India.

Smythe (1970) stated that synchronous fruiting may be an adaptation to attract frugivores that play a major role in seed dispersal. In BNP, many bird species such as Red-vented Bulbul (*Pycnonotus cafer*) feed on the fruits of *M. hexandra* and act as seed dispersal agents. In addition, synchronous fruiting would also be helpful in reducing the impact of seed predators.

Conclusions

M. hexandra is a leaf-exchanging species which shows synchronous vegetative and reproductive phenological events. Leaf flushing mainly takes place during the major rainy season (September or October - January) when there are heavy rains. Leaf shedding and leaf bud breaking mainly take place in the middle of the major rainy season (late November - December) which is immediately followed by flower bud breaking. Flower buds remained dormant for a few weeks and blooming takes place towards the later part of the major rainy season once the leaves are fully expanded. High soil moisture and relative humidity due to heavy rainfall, low air and soil temperatures, low wind velocity and low solar radiation levels provided optimal external environmental conditions for flowering. However, the triggering of flowering took place due to the sudden drop of solar radiation and subsequent drop in air and soil temperatures which was maintained for about 36 hours. Abortion of flowers and young fruits occur due to sudden climatic variations but if the environmental factors remain favourable towards flower and fruit production, mass fruiting takes place.

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