Synchronous flowering of the rubber tree (*Hevea brasiliensis*) induced by high solar radiation intensity

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Summary

• How tropical trees flower synchronously near the equator in the absence of significant day length variation or other meteorological cues has long been a puzzle. The rubber tree (*Hevea brasiliensis*) is used as a model to investigate this phenomenon.
• The annual cycle of solar radiation intensity is shown to correspond closely with the flowering of the rubber tree planted near the equator and in the subtropics. Unlike in temperate regions, where incoming solar radiation (insolation) is dependent on both day length and radiation intensity, insolation at the equator is due entirely to the latter.
• Insolation at the upper atmosphere peaks twice a year during the spring and autumn equinoxes, but the actual solar radiation that reaches the ground is attenuated to varying extents in different localities. The rubber tree shows one or two flowering seasons a year (with major and minor seasons in the latter) in accordance with the solar radiation intensity received.
• High solar radiation intensity, and in particular bright sunshine (as distinct from prolonged diffuse radiation), induces synchronous anthesis and blooming in *Hevea* around the time of the equinoxes. The same mechanism may be operational in other tropical tree species.

Key words: equinox, *Hevea brasiliensis* (rubber tree), insolation, meteorological factors, solar radiation intensity, synchronous flowering, tropical trees.

Introduction

In temperate regions, the change in day length induces seasonal flowering in many plants. Day length does not change appreciably close to the equator, and yet many tropical rainforest trees flower synchronously in the absence of marked climatic changes or obvious meteorological cues (Holtum, 1931). Other major climatic factors do not seem to play an obvious role in triggering synchronous annual flowering. The temperature in the humid tropics is so uniform throughout the year that it has little bearing on the phenology of trees. Indeed, diurnal temperature variation can exceed the seasonal range. While a dry spell often precedes flowering in many tropical species, trees growing close to the equator can have one or two flowering periods even when a distinct dry season is lacking. For example, Singapore (1°N) and peninsular Malaysia (e.g. Kuala Lumpur, 3°N) do not experience any distinct period of dryness. Yet the seasonal fruit trees in this region, such as the durian (*Durio zibethinus*, the mangosteen (*Garcinia mangostana*) and the rambutan (*Nephelium lappaceum*), have two flowering seasons in March and September, corresponding to spring and autumn in the northern hemisphere (Holtum, 1931).

More recently, Borchert *et al.* (2005) proposed that the seasonal shifts in sunrise-sunset times in an annual cycle as a result of the Earth's tilt and elliptic orbit acted as meteorological cues for flowering at the equator. However, it may be argued that gradual time shifts (less than 1 min a day) are meaningful only when measured against an external reference chronometer. If the day length from one day to the next remained essentially unchanged, it would be a challenge for any organism – not just trees – to have an awareness of a 1 min

advance or retreat in sunrise or sunset. There is, moreover, no obvious mechanism by which trees have a memory of previous sunrise or sunset times with which to compare the current times.

Previous studies on synchronous flowering of tropical forest trees have looked at a variety of species growing in selected field localities. Such an approach is subject to the confounding effects of the heterogeneous tree population. Even where flowering were induced in the different forest species by the same environmental stimulus, the degree or the timing of the resulting response might differ between species, thereby complicating data interpretation. In the present study, a single species, *Hevea brasiliensis*, is used as a model to study synchronous flowering in tropical trees. Originating from the Amazonia, the rubber tree is an outbreeding forest species (Simmonds, 1986) for which flowering synchrony is important. The floral shoot of this monoecious tree terminates in a vegetative whorl and several flower panicles bearing male and female flowers develop from the internodal buds or axillary buds of the more basal leaves (Yeang & Ong, 1988). The rubber tree has one main flowering season annually, although in some locations there can be minor secondary flowering as well.

The advantage of studying cultivated rubber trees over trees in their forest habitat is also that the incidence of flowering is easily tracked and recorded continuously over any period of time. Such records from rubber plantations are likely to be more detailed and accurate because thousands of trees are continually in full view to the observer year-round, whereas locating and revisiting scattered trees in the forest may involve trekking considerable distances through the forest. A further advantage in adopting *Hevea brasiliensis* as a study model is the wide geographical range over which the tree is planted. The rubber tree it is today cultivated in many parts of the world, mainly within 10° north and south of the equator. Because of its economic value, the range of rubber cultivation has been extended to the subtropics, up to 20° north and south. In focusing on *Hevea*, therefore, its flowering behaviour when planted in different localities – near the equator or outside its natural range in the subtropics – can be compared. These observations might provide further clues concerning the nature of the flowering stimulus.

Materials and Methods

Information on the timing of *Hevea brasiliensis* (A. Juss.) Müell. Arg. synchronous flowering (published and unpublished) was collated for various rubber-growing localities in Malaysia, Thailand, Indonesia, India, Sri Lanka, Vietnam, China, Nigeria, Cote d'Ivoire and Brazil. These are representative of the major areas of rubber cultivation, straddling three continents (Asia, Africa and South America), and lie both north and south of the equator. The reference towns in these regions shown in Table 1 are generally where the centres for rubber research (and the source of most of the data on flowering) are located.

Insolation (I) at the time of *Hevea* flowering in these different localities was calculated as $I = S \cos Z$ according to Lambert's cosine law, where S, the clear day insolation on a surface perpendicular to incoming solar radiation, was approximated as 1000 W m^{-2}, and Z, the zenith angle, was calculated as arccos (sin(latitude)sin(solar declination angle) + cos(latitude)cos(solar declination angle)cos(hour angle)), and where solar declination angle = 23.45(sin((Julian day + 284) × 360/365)) and hour angle = 15° × (hour from midnight – 12).

Day lengths were calculated from the sunrise and sunset times obtained from the internet site of the US Naval Observatory (http://aa.usno.navy.mil/data/docs/RS_OneYear.html). Ground solar radiation data were obtained from different published sources as shown in Table 2. Rainfall data for the reference towns or locations nearby were obtained from the internet at the WorldClimate website (www.worldclimate.com). For the purpose of this study, a seasonal dry spell is defined as < 50% average monthly rainfall occurring 1 or 2 months preceding commencement of the flowering period.

Results and Discussion

The photoperiod is a key stimulus for flowering in many plants growing in temperate regions, but day length as the explanation in the tropics faces two immediate inconsistencies. Firstly, day length does not change appreciably at the equator. Even allowing for cases where induction of flowering in the tropics has been attributed to very slight day length changes (Dore, 1959; Rivera & Borchert, 2001), a trigger linked to the change in day length (either long or short day) would imply a single annual flowering. However, flowering in tropical trees near the equator is frequently bimodal (Holtum, 1931; Borchert *et al.*, 2005), as it is for *Hevea brasiliensis* in several localities where the tree is planted (Table 1).

Other than the photoperiod, a dry season and/or seasonal leaf change are among the factors most frequently associated with the induction of flowering or the induction of anthesis in tropical trees (Daubenmire, 1972; Mori & Kallunki, 1976; Opler *et al.*, 1976; Borchert, 1983). Hence, the possible involvement of these factors should be considered as possible triggers in *Hevea* synchronous flowering. Leaf-shedding ('wintering') of the rubber tree occurs to varying degrees annually. In some regions, it coincides with a seasonal dry spell at the end of which flowering occurs when the canopy refoliates with the advent of rain (Table 1). Nevertheless, wintering also occurs in other locations without a distinct dry spell, as in Malaysia. Nor does flowering always coincide with the onset of rain that breaks the dry season. In Belem (Brazil), the months preceding flowering are very wet, while in nearby Tracuateua, flowering actually occurs during the dry season itself (P. d. S. Goncalves, pers. comm.). Similarly in Vietnam, *Hevea* flowering initiates in the midst of the dry season (N. A. Nghia, pers. comm.). Hence, while the dry season or the transition from the dry to the wet season are relevant factors that

Table 1 *Hevea brasiliensis* synchronous flowering and related factors in various localities of rubber cultivation

Location	Latitude	Months of highest average solar radiation[a]	Flowering months		Distinct dry spell preceding flowering	
			Main season	Secondary season	Main season	Secondary season
Northern hemisphere, subtropical						
Agartala, Tripura state, north-east India	24°N	–	Mar–Apr (9)[b]	Aug–Sep (9)	Yes	No
Danxian, Hainan Island, China	20°N	–	Mar–Apr (10)	May–Jul, Aug–Sep (10)	No	No
Northern hemisphere, equatorial						
Ho Chi Minh City, Vietnam	11°N	Feb–Apr (1)	Feb–Mar (11)	Jun–Jul (11)	Yes	Yes
Hat Yai, Songkhla province, south Thailand	7°N	Feb–Apr (2)	Mar (12)	Sep–Oct (12)	Yes	No
Agalawatta, Sri Lanka	7°N	Mar–Apr (3)	Feb–Apr (13)	–	Yes	–
Igbotako, Nigeria	6°N	Feb–May (4)	Feb–Apr (14)	–	Yes	–
Abidjan, Cote d'Ivoire	5°N	Feb–May (5)	Feb–Mar (15)	–	Yes	–
Kuala Lumpur, Malaysia	3°N	Feb–Apr (6)	Feb–Apr (16)	Aug–Sep (16)	No	No
Southern hemisphere, equatorial						
Belem, Para state, Brazil	1°S	Aug–Oct (7)	Jul–Aug (17)	–	No	–
Bogor, Java, Indonesia	7°S	Aug–Oct (8)	Jul–Sep (18)	–	Yes	–
Southern hemisphere, subtropical						
Votuporanga/Piracicaba, São Paulo state, Brazil	20°S/23°S	–	Aug–Nov (9, 19, 20)	Apr–May (9, 19)	Yes	No

[a]Based on monthly solar radiation measured at the ground for equatorial locations (which experience two annual insolation peaks during the solstices). Readings were taken at reference locations in Column 1, or at nearby locations.
[b]References (in brackets): 1, Long (2005); 2, Exell (1976); 3, Renné *et al*. (2003); 4, Akpabio & Etuk (2003); 5, Eldin *et al*. (1976); 6, Chuah & Lee (1981); 7, da Rocha *et al*. (2004); 8, Morrison & Sudjito (1992); 9, Priyadarshan *et al*. (2001); 10, Huang & Hao (1998); 11, N. A. Nghia (pers. comm.); 12, P. Jewtragoon (pers. comm.); 13, Sedgley & Attanayake (1988); 14, Omokhafe (2004); 15, A. Clement-Demange (pers. comm.); 16, Yeang & Ong (1988); 17, Warmke (1952); 18, Madjid *et al*. (1976); 19, P. d. S. Goncalves (pers. comm.); 20, Dornelas & Rodriguez (2005).

Table 2 Day length, insolation and solar radiation measured at the ground during *Hevea brasiliensis* flowering

Location	Main flowering season			Secondary flowering season		
	Day length (h)	Insolation[a] (kWh m^{-2} d^{-1})	Ground solar radiation (kWh m^{-2} d^{-1})	Day length (h)	Insolation (kWh m^{-2} d^{-1})	Ground solar radiation (kWh m^{-2} d^{-1})
North-east India	12.4 [102][b]	7.24 [96]	5.5 [111] (21)	12.6 [104]	7.62 [101]	4.6 [92]
Hainan, China	12.3 [102]	7.40 [98]	3.7 [74] (22)	13.3 [110]	8.29 [110]	5.4 [108]
				12.6 [104]	7.70 [102]	4.6 [92]
South Vietnam	12.2 [101]	7.72 [102]	5.1 [102] (1)	12.8 [105]	7.22 [96]	4.6 [92]
South Thailand	12.1 [100]	7.47 [99]	5.1 [102] (2)	12.1 [100]	7.44 [99]	4.4 [88]
Sri Lanka	12.1 [100]	7.48 [99]	5.0 [100] (3)	–	–	–
Nigeria	12.1 [100]	7.48 [99]	4.0 [80] (4)	–	–	–
Cote d'Ivoire	12.0 [99]	7.31 [97]	5.0 [100] (5)	–	–	–
Malaysia	**12.1 [100]**	**7.55 [100]**	**5.0 [100]** (6)	12.1 [100]	7.61 [101]	4.6 [92]
Belem, Brazil	12.1 [100]	7.32 [97]	4.6 [92] (7)	–	–	–
Java, Indonesia	11.9 [98]	7.68 [102]	4.2 [85] (8)	–	–	–
Sao Paulo state[d], Brazil	12.3 [102]	7.34 [97]	4.8 [96] (23)	11.3 [94]	5.82 [77]	4.0 [80]

[a]Insolation readings for the peak flowering periods are taken as the midpoints of the flowering months shown in Table 1. Ground solar radiation readings are the mean of readings for the flowering months given in Table 1, and were taken at reference locations in column 2 of Table 1, or at nearby locations.
[b]Figures in square brackets are percentages of the corresponding values (bold) for the main flowering season in Kuala Lumpur, Malaysia.
[c]References (in round brackets): 1, Long (2005); 2, Exell (1976); 3, Renné *et al*. (2003); 4, Akpabio & Etuk (2003); 5, Eldin *et al*. (1976); 6, Chuah & Lee (1981); 7, da Rocha *et al*. (2004); 8, Morrison & Sudjito (1992); 21, Islam (2002); 22, Michalk *et al*. (1993); 23, Codato *et al*. (2004).
[d]Latitude in between Votuporanga and Piracicaba (Table 1).

may accentuate flowering in *Hevea*, they are not primarily responsible for the induction of synchronous flowering. The same can be said of leaf canopy refoliation. In localities that experience a secondary flowering season, leaf fall does not normally precede floral initiation. Hence, leaf shedding and subsequent canopy refoliation are similarly not essential pre-requisites to synchronous flowering of the rubber tree; the trigger responsible for this phenomenon lies elsewhere.

Since rubber trees growing near the equator flower synchronously at the same time every year, the external stimulus for this occurrence is likely to be linked to a meteorological event. What significant meteorological event occurs at the equator at the time the rubber tree flowers? In the northern hemisphere, the main flowering season of the rubber tree is around March, with a secondary season in some localities falling around August/September (Table 1). In the southern hemisphere, *Hevea* flowers from July to September. Where the equatorial region is concerned, the obvious major meteorological events in March and September are the equinoxes. At the equator, radiation intensity peaks when the sun passes directly overhead at the spring and autumn equinoxes, and wanes towards the solstices.

It needs to be appreciated, firstly, that the nature of solar radiation at the equator is dissimilar to that in the temperate regions. Incoming solar radiation (insolation) that reaches the Earth's upper atmosphere is dependent on the duration of sunshine as well as its intensity, the latter being determined by the angle of incidence of the sun (the angle at which the sun's rays strike the surface of the Earth). In temperate latitudes,

both day length and solar radiation intensity contribute to the daily insolation, but changes in these two parameters are concurrent and additive. Maximum radiation intensity – when the noon sun is highest above the horizon – and maximum day length occur at the summer solstice, whereas radiation intensity and day length are minimal at the winter solstice (Fig. 1).

At the equator, however, seasonal change in insolation is dependent *entirely* on solar radiation intensity. Day-length variation plays no part, since deviation from the 12 h day length is minimal. The sun passes directly over the equator twice a year, resulting in a bimodal cyclical change in incoming solar radiation (insolation) experienced in the equatorial regions (Fig. 1). The two solar radiation intensity maxima experienced at the equator are 3 months out of phase with maximum and minimum insolation in the temperate latitudes. At latitudes further from the equator, the two radiation intensity peaks gradually merge (Fig. 1).

Table 1 shows the flowering seasons of *Hevea brasiliensis* near the equator and in the subtropics on three continents, South America, Africa and Asia. In all cases, day length during the main flowering season is close to 12 h. Near the equator, the major flowering event occurs in the spring (around March in the northern hemisphere and July/August in the southern hemisphere), close to the time of the equinox when the sun is directly overhead. In comparison, the main flowering seasons in the subtropical regions are delayed by 0.5–1.5 months. By this time, the sun would have moved such that insolation (noon insolation and total daily insolation) are more similar
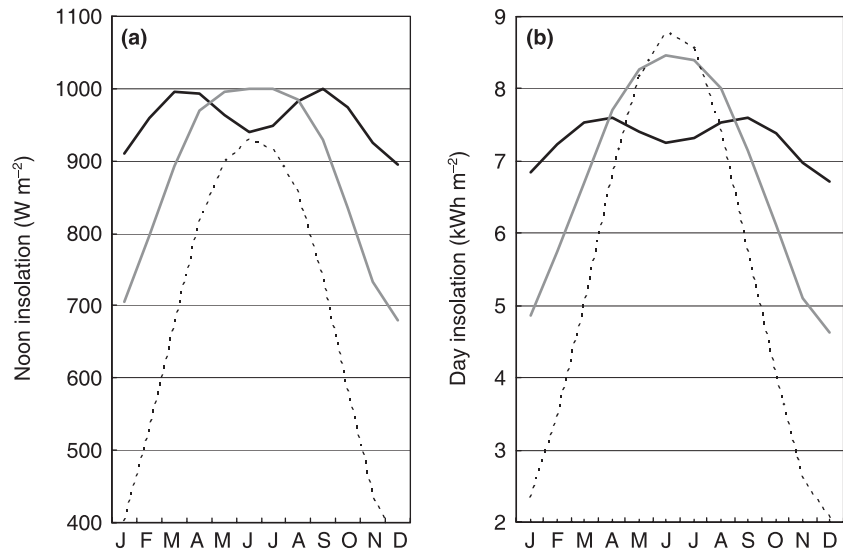
Fig. 1 Annual insolation for locations at equatorial, subtropical and temperate latitudes. Insolation at noon (a) and total day insolation (b) are calculated for an equatorial location (Kuala Lumpur, Malaysia, 3°8′N, black line) and a subtropical location (Agartala, India, 23°50′N, grey line) of rubber planting. A typical temperate latitude (45°N, dotted line) is also shown for comparison. The total day insolation is the hourly insolation summed for the daylight hours.

to that experienced at flowering in the equatorial regions. Thus, while *Hevea* flowering in the northern hemispheric equatorial latitudes commences mainly from February, it begins only in March in Tripura State, India (24°N), and in Hainan Island (20°N), China (Table 1). In Taiwan and many parts of mainland China (Fujian, Guangdong, Guangxi and Yunnan, stretching to 25°N), flowering can be delayed until May (Li, 2003). A similar trend is seen in the southern hemisphere where flowering near the equator in Belem and in Java begins in July. Further south in São Paulo State, blooming does not commence until August or later (Table 1).

The delay in principal flowering in the subtropics with increasing latitudes from the equator can be evident even over relatively small distances. For example, flowering in Votuporanga (20°25′S) in Brazil may occur 20–30 d earlier than in Campinas (22°54′S) (P. d. S. Goncalves, pers. comm.). Near the Tropic of Cancer and Tropic of Capricorn, where high insolation is maintained from spring to autumn (Fig. 1), two or even three consecutive cycles of flowering can take place over this extended period. Thus, even when the rubber tree is relocated from its native rainforest habitat to the subtropics, the timing of its flowering remains closely linked to high solar radiation intensity.

Notwithstanding the evidence suggesting that high solar radiation is the cue for synchronous flowering, a question concerning the seasonality of *Hevea* flowering needs to be resolved. If there are two equal equinoxes annually, why is there only one main *Hevea* flowering season in a year, and why does it fall around the spring equinox and not the autumn equinox? The basic reason there aren't two equal flowering seasons a year is that solar radiation received at the ground is unequal for the two equinoxes. Solar radiation is substantially reduced by light scattering and absorption by cloud cover and aerosols, etc. as it passes through the Earth's atmosphere. The attenuation of insolation in its passage through the atmosphere

may vary at different times of the year for a given location. It is hence arguable that actual solar radiation readings at the ground should have greater relevance than insolation values predicted by latitude. However, reported readings of the former at different localities may not be readily comparable because of dissimilarities in measurement instrumentation and calibration procedures. Therefore, both the calculated insolation and measured ground solar radiation at the time of flowering are presented in Table 2.

Terjung (1970) used data from over 1000 sampling points to construct a classification of world seasonal solar radiation patterns. The proposed association between solar radiation and *Hevea* flowering is in agreement with Terjung's radiation map, which shows that most rubber-growing areas of the world experience the principal peak in ground solar radiation in the spring, with the autumn peak being much smaller, or absent altogether. In Peninsular Malaysia, for example, Wycherley (1967) reported that 'the hours of bright sunshine and estimated solar radiation are maximal in February to April (with) a tendency towards a second smaller peak in August and/or September'. These periods match exactly the major *Hevea* flowering season in the spring and the minor flowering period in the autumn (Table 1). Where there is only a single *Hevea* flowering season in other equatorial areas such as in Cote d'Ivoire, Nigeria and Sri Lanka to the north of the equator, or in the Amzaonia and Java to the south, the principal peak of solar radiation is similarly experienced around the spring equinox (Table 1). *Hevea* flowering months generally coincide with the months of the highest average solar irradiation measured at the ground for all the equatorial locations examined (Table 1).

A requirement for adequate rest between sequential flowering seasons might be an additional explanation as to why flowering in spring is favoured over flowering in the autumn. The equinoxes are separated by 6 months at locations exactly

on the equator. However, much of commercial rubber cultivation is not sited *exactly* on the equator. With increasing latitudes from the equator, the insolation peak in spring is delayed, occurring only after the equinox, whereas the second peak is advanced, occurring before the autumn equinox. The intervening rest period from the spring peak to the autumn peak that is thus decreased may result in the latter period being less conducive to intense flowering. For locations that are not directly on the equator, flowering in the spring confers an advantage to the tree since fruit formation (a major carbon sink) takes place in the summer when insolation is higher than in late autumn (Fig. 1) when fruits from the secondary flowering develop.

The specific attributes of high solar radiation that are critical to synchronous flowering still need to be determined: whether it is the average solar radiation received that is important or if it might be, for example, very high radiation on a few cloud-free days, or the hours of high daily sunshine that are also relevant. In this connection, the observation that *Hevea* flowers unusually early in the year in north-east Thailand provides some clues.

In south Thailand (Songkhla province, 7°N), *Hevea* flowers around March (Table 1) when average solar radiation is highest (Exell, 1976) and when the hours of strong sunshine are also the longest (Thailand Meteorological Department, 2007). In the north-eastern region (15–18°N) in comparison, the timing of synchronous flowering is not delayed despite its latitude, but is in fact advanced by *c.* 1 month to around February (P. Jewtragoon, pers. comm.). The reason for this seeming anomaly may lie in the fact that north-east Thailand has a very pronounced monsoonal climate with distinct wet and dry seasons. In the equatorial rubber-growing regions where rainfall (and hence cloud cover) is more evenly distributed throughout the year, daily global (total) radiation is concurrent with the hours of bright sunshine. In north-east Thailand, on the other hand, the marked wet season is characterized by overcast skies, whereas the skies are more likely to be clear in the dry season. The highest global radiation is experienced in the rainy season in May, but a large component of this is in the form of diffuse radiation (Exell, 1976). When solar radiation is considered in terms of hours of strong sunshine rather than global radiation, a different picture emerges. The duration of strong sunshine in north-east Thailand peaks in the dry season around January, *c.* 1 month ahead of south Thailand (Thailand Meteorological Department, 2007). It would appear therefore that not only is high average solar radiation important to the induction of synchronous flowering, but sufficient hours of strong sunshine are also crucial. These observations suggest that a threshold solar radiation intensity may have to be reached or exceeded before flowering is triggered. The threshold need not be the insolation at the equinox, but could be a lower value that is already attained earlier (e.g. in February in Malaysia). By this hypothesis, perhaps sufficient intense sunshine is required to set off cellular reactions essential to flowering.

The stage of *Hevea* flower development at which high solar radiation intervenes to induce synchronous flowering may be surmised from available information on flower bud development. In many locations of rubber cultivation (e.g. Malaysia), seasonal leaf fall precedes the main *Hevea* flowering season (although not generally the secondary flowering season) and flowers reach anthesis as the canopy begins to refoliate. These are recognized characteristics of proleptic floral bud development (Borchert, 1983) where there is discontinuous development of a meristem into an inflorescence, with a rest period between early flower development and anthesis (Hallé *et al.*, 1978; Borchert, 1983). The occurrence of prolepsis in *Hevea* is supported by a study on the expression of the *HbFLY* gene that regulates *Hevea* vegetative and reproductive development. Activation of the *HbFLY* 'flowering' gene that is expressed selectively in *Hevea* reproductive tissue is detected in floral meristems 2–3 months before anthesis when solar radiation is still low (Dornelas & Rodriguez, 2005). Hence, it would appear that increased solar radiation intensity in the spring induces synchronous flowering by stimulating rapid development of the preformed floral meristems to the stage of anthesis. It is unlikely that a period of low solar radiation intensity is required to initiate the floral meristem itself because secondary flowering cycles still occur at subtropical latitudes even when there is no preceding period of low solar radiation.

The concept that flowering (and leaf flushing) in tropical forests might be linked to high solar radiation was earlier raised by van Schaik *et al.* (1993), who found insolation seasonality 'largely ignored by ecologists' as a possible phenological factor. In a subsequent study, Wright & van Schaik (1994) noted a coincidence between leaf and flower periodicity with peak irradiance in widely disparate tropical forests where water was not limiting. The analysis in this paper strongly suggests that the annual solar radiation cycle is indeed closely linked to synchronous flowering of the rubber tree. One reason why the solar radiation intensity cycle in the tropics has not been more commonly linked to flowering may be that researchers expect tropical plants to behave like temperate plants, that is being sensitive to day length. It may not have been fully appreciated that even at the equator, where day length does not count, there is still an annual cycle of solar radiation intensity, except that its peak is not in the (equivalent of) summer, but at the equinoxes that occur 3 months out of phase with the solstices.

The same mechanism that synchronizes *Hevea* flowering at the two equinoxes may be operational in other tropical tree species. For example, many Malaysian seasonal fruit trees, such as the durian, mangosteen and rambutan, flower at approximately the same time as the rubber tree.

Acknowledgements

References

Akpabio LE, Etuk E. 2003. Relationship between global solar radiation and sunshine duration for Onne, Nigeria. *Turkish Journal of Physics.* **27**: 161–167.

Borchert R. 1983. Phenology and control of flowering in tropical trees. *Biotropica* **15**: 81–89.

Borchert R, Renner SS, Calle Z, Navarrete D, Tye A, Gautier L, Spichiger R, von Hildebrand P. 2005. Photoperiodic induction of synchronous flowering near the equator. *Nature* **433**: 627–629.

Chuah DGS, Lee SL. 1981. Solar radiation estimates in Malaysia. *Solar Energy* **26**: 33–40.

Codato G, Oliveira APD, Escobedo JF. 2004. Comparative study of solar radiation in urban and rural areas. *Anais do XIII Congresso Brasileiro de Meteorologia, Fortaleza, Brazil.* http://www.iag.usp.br/meteo/labmicro/Georgia_CBMet2004.pdf

Daubenmire R. 1972. Phenology and other characteristics of tropical semi-deciduous forest in northwestern Costa Rica. *Journal of Ecology* **60**: 147–170.

Dore J. 1959. Response of rice to small differences in length of day. *Nature* **183**: 413–414.

Dornelas MC, Rodriguez APM. 2005. The rubber tree (*Hevea brasiliensis* Muell. Arg.) homologue of the LEAFY/FLORICAULA gene is preferentially expressed in both male and female floral meristems. *Journal of Experimental Botany* **56**: 1965–1974.

Eldin M, Monteny B, Cardon D. 1976. Solar radiation extinction by a wet tropical atmosphere – Incidence on evapotranspiration and photosynthesis of plant canopies. Abidjan, Cote d'Ivoire: ORSTOM. http://horizon.documentation.ird.fr/exl-doc/pleins_textes/pleins_textes_5/b_fdi_06-07/08459.pdf

Exell RHB. 1976. The solar radiation climate of Thailand. *Solar Energy* **18**: 349–354.

Hallé F, Oldeman RAA, Tomlinson PB. 1978. *Tropical trees and forests. An architectural analysis.* Berlin, Germany: Springer-Verlag.

Holtum RE. 1931. On periodic leaf-change and flowering of trees in Singapore. *Gardens' Buletin (Straits Settlements)* **5**: 173–211.

Huang W, Hao Y. 1998. Morphology, growth, habit and environmental requirements of the rubber tree. In: Pan Y, ed. *Tropical crops cultivation in China.* Beijing, China: China Agriculture Press, 13–23.

Islam M. 2002. Assessment of renewable energy resources of Bangladesh. http://www.sdnpbd.org/sdi/issues/energy/publications/shakti-ebook1.pdf

Li P-T. 2003. (ed.) *Flora Republica Sinicae Vol. 44/1.* Beijing, China: Science Press.

Long NT. 2005. Country paper: solar energy development in Vietnam. Paper presented at the Workshop on information for the commercialisation of renewables in ASEAN, Vientiane, Lao PDR, 7–9 April 2005. http://www.ptm.org.my/icra/ICRA%20papers/Bangkok_Laos/icra_papers/wshop_laos/Papers/Vietnam_PV.doc

Madjid A, Maslichah Saleh D, Bunyamin. 1976. Experiment of flower induction in *Hevea* rubber. *Paper presented at the Symposium of the International Rubber Research and Development Board, 8–9 November 1976, Bogor, Indonesia.* Bogor, Indonesia: Indonesian Biotechnology Research Institute for Estate Crops.

Michalk DL, Fu N-P, Zhu C-M. 1993. Improvement of dry tropical rangelands in Hainan Island, China: 1. Evaluation of pasture legumes. *Journal of Range Managment* **46**: 331–339.

Mori SA, Kallunki JA. 1976. Phenology and floral biology of *Gustavia superbea* (Lechythidaceae) in Central Panama. *Biotropica* **8**: 184–192.

Morrison GL, Sudjito. 1992. Solar radiation data for Indonesia. *Solar Energy* **49**: 65–76.

Omokhafe KO. 2004. Interaction between flowering pattern and latex yield in *Hevea brasiliensis* Muell. Arg. *Crop Breeding and Applied Biotchnology* **4**: 280–284.

Opler PA, Frankie GW, Baker HG. 1976. Rainfall as a factor in the release, timing, and synchronization of anthesis by tropical trees and shrubs. *Journal of Biogeography* **3**: 231–236.

Priyadarshan PM, Sasikumar S, Goncalves PDS. 2001. Phenological changes in *Hevea brasiliensis* under differential geo-climates. *Planter* **77**: 447–459.

Renné D, George R, Marion B, Heimiller D. 2003. *Solar resource assessment for Sri Lanka and Maldives.* Golden, CO, USA: National Renewable Energy Laboratory.

Rivera G, Borchert R. 2001. Induction of flowering in tropical trees by a 30-min reduction in photoperiod: evidence from field observations and herbarium specimens. *Tree Physiology* **21**: 201–212.

da Rocha HR, Goulden ML, Miller SD, Menton MC, Pinto LDVO, De Freitas HC, Figueira AMES. 2004. Seasonality of water and heat fluxes over a tropical forest in eastern Amazonia. *Ecological Applications* **14**: S22–S32.

van Schaik CP, Terborgh JW, Wright J. 1993. The phenology of tropical forests: Adaptive significance and consequences for primary consumers. *Annual Review of Ecological Sysems* **24**: 353–377.

Sedgley M, Attanayake DPSTG. 1988. The breeding system of rubber (*Hevea brasiliensis*): an evaluation of controlled hand-pollination methods. *Euphytica* **39**: 83–91.

Simmonds NW. 1986. Theoretical aspects of synthetic/polycross populations of rubber seedlings. *Journal of Naural Rubber Research* **1**: 1–15.

Terjung WH. 1970. A global classification of solar radiation. *Solar Energy* **13**: 67–81.

Thailand Meteorological Department. 2007. Thailand weather data records. http://www.ourweb.info/01/weather

Warmke HE. 1952. Studies on natural pollination of *Hevea brasiliensis* in Brazil. *Science* **116**: 474–475.

Wright SJ, van Schaik CP. 1994. Light and the phenology of tropical trees. *American Naturalist* **143**: 192–199.

Wycherley PR. 1967. Climatological and phonological phenomena in Malaysia. In: Misra Royal, Gopal B, eds. *Proceedings of the Symposium on Recent Advances in Tropical Ecology, Part 1.* Varanasi, India: International Society for Tropical Ecology, 138–143.

Yeang HY, Ong SH. 1988. Low fruit-set from *Hevea* hand-pollination: a consideration of fruit load and the propensity of floral shoots to fruit-bearing. *Journal of Natural Rubber Research* **3**: 143–154.