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Key words: active plasticity, benefits, costs, passive plasticity, phenotypic plasticity, recombinant inbred lines, selection gradient analysis.

Letters

The sunshine-mediated trigger of synchronous flowering in the tropics: the rubber tree as a study model

Synchrony of flowering is important for outbreeding trees to maximize the chances of successful pollination. This is particularly crucial for species such as the rubber tree, *Hevea brasiliensis*, which has a naturally low rate of fruit-set (Warmke, 1951; Rao, 1961) even with artificial pollination (Ghandimathi & Yeang, 1984). *Hevea* flowering promodia are formed 2–3 months before blooming (Dornelas & Rodriguez, 2005). An environmental stimulus subsequently triggers the rapid and synchronous development of preformed floral meristems to the stage of flower maturity. In Malaysia, which lies close to the equator (*c.* 3°N), the main flowering season is from February to April, while a secondary season takes place during August and September (Yeang & Ong, 1988).

The celestial trigger for synchronous flowering at the equator

If a physiological episode in a perennial plant occurred consistently at the same time every year, it is likely to be linked to some recurrent meteorological event. In the case of the rubber tree, this consistency is maintained across different rubber-growing regions with varying climatic patterns, from the humid tropics to the monsoonal subtropics that experience marked wet and dry seasons (Yeang, 2007). The signal for synchronous flowering must therefore be one that largely transcends such environmental disparities: some form of celestial cycle, for instance. One meteorological factor that escapes the influence of localized seasonal climatic conditions (other than cloud cover) is sunshine. There is a reasonable likelihood, therefore, that that synchronous flowering in the rubber tree (and other tropical trees sharing similar flowering characteristics) is connected with some aspect of solar radiation arising from the movement of the earth around the sun.

The best researched aspect of light-mediated stimulus for flowering is the photoperiod. Long-day (short-night) plants and short-day (long-night) plants flower when their photoperiod requirements are met. While these are established norms in temperate regions, photoperiod control of flowering faces a problem at the equator where day length does not vary from 12 h year-round. More than that, a stimulus 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), the rubber tree being one such example.

The trigger that is sought for equatorial synchronous flowering must therefore be not only a sunshine-mediated factor that is independent of day-length variation, but also bimodal in its cycle. The search for such an environmental stimulus has yielded two candidates: the bimodal advance in sunrise–sunset times measured against the chronometer, and the bimodal variation in solar radiation intensity.

Bimodal cycles of sunshine at the equator

The tilt of the earth's axis relative to the sun gives rise to a seasonal photoperiod variation that regulates flowering in many temperate plant species. Unlike in temperate regions where incoming solar radiation (insolation) is dependent on both the day length and the radiation intensity, insolation at the equator is due entirely to the latter. At the equator, insolation peaks twice a year at the equinoxes, when the midday sun is directly overhead. In my previous paper in *New Phytologist* (Yeang, 2007), I noted that rubber trees growing near the equator and in the subtropics flowered when solar radiation intensity was high. I inferred from this that the cycle of solar radiation intensity was responsible for synchronous anthesis and blooming in *Hevea* and some other tropical trees.

When the earth's elliptical orbit around the sun is superimposed on to the tilt of the earth, the cyclical change in sunshine becomes even more complex. A discrepancy from chronometer time arises in the time-keeping that is determined from the position of the sun. One such effect is the bimodal variation in sunrise–sunset times that forms the basis of another hypothesis to explain synchronous flowering at the equator. Borchert *et al.* (2005) proposed that the seasonal shifts in sunrise–sunset times as a result of the earth's axial tilt and its elliptic orbit provided meteorological signals for flowering at the equator. By the sunrise–sunset advance hypothesis, tropical plants are triggered to flower around the time the sunrise or sunset advances are fastest in spring and autumn.

The discussion that follows looks at how each hypothetical sunshine-mediated signal might function to induce synchronous flowering in the tropics.

Character of the light signal in the sunrise–sunset time-shift model

Whatever the nature of the light signal that regulates flowering, the plant has first to detect some facet of the sunshine that it receives. The classic phytochrome photoreceptor has been used to explain light signalling while cryptochromes and phototropins are other classes of photoreceptors that have emerged more recently (Briggs & Olney, 2001; Mockler *et al.*, 2003). Light-activated genes in plants typically respond to some qualitative aspect of the light signal, such as its spectral composition (e.g. red: far-red light, blue light), or to a quantitative aspect, such as the duration or intensity (Searle & Coupland, 2004; Ausín *et al.*, 2005). Unlike seasonal photoperiod change in temperate regions, the sunrise–sunset time-shift model does not invoke change to the 12 h photoperiod at the equator. Neither does it involve change to any other qualitative or quantitative aspect of the light signal, such as its duration, intensity, direction and spectral quality. The only change is to its timing. Hence, the difference in light signal that the plant perceives would be neither qualitative nor quantitative in its nature. It would be essentially temporal. The photoreceptor does not sense what has changed or how much has changed, but when the change (sunrise or sunset) takes place.

The light signal might act directly to induce gene transcription on its own, or indirectly as a trigger to set off a cascade of reactions in the flowering pathway. Direct action seems unlikely, given that time shift of an otherwise unaltered light signal would not provide the same opportunity as a qualitative or quantitative change to induce substantial gene transcription. If the light signal were a trigger that facilitated or favoured certain cell reactions in a manner comparable to the photoperiod control of flowering (Putterill *et al.*, 2004; Ausín *et al.*, 2005; Bäurle & Dean, 2006; Zhou *et al.*, 2007), the plant would need to integrate the sunrise or sunset advance into its endogenous circadian cycle. Indeed, the sunrise–sunset hypothesis proposes that the plant measures sunrise and sunset times against its circadian clock to trigger flowering (Borchert *et al.*, 2005). In this connection, therefore, it is pertinent to examine how the circadian clock might operate at the equator.

To set and regulate its innate circadian cycle, the plant takes its cues from the solar day. Essentially, the circadian clock entrains itself to solar time. Since day length does not change at the equator, the intervals between sunrise, noon and sunset are constant year-round. Thus, even as the timing of noon drifts forward or backwards seasonally relative to chronometer time, sunrise and sunset move in tandem. It does not matter at which instant in the solar day (whether it is sunrise, noon, sunset or any point in between) that the plant uses as the reference for the entrainment of its circadian cycle, because there is only one solar clock running at the equator. While solar time is conventionally measured by the passage of the sun across the meridian at noon, it is equally well defined at the equator by the timing of sunrise on the eastern horizon or sunset on the western horizon.

Yet if the shifts in sunrise–sunset, on the one hand, and the plant's circadian clock, on the other, are both referenced against solar time, they cannot be out of phase and cannot be discrepant with each other. How, then, might a time shift in sunrise or sunset superimpose on the plant's circadian clock to register a signal for flowering? At the equator, the sunrise-sunset cycle *is* the circadian cycle.

In formulating the sunrise-sunset advance hypothesis for synchronous flowering, the notion of chronometer time is brought into the picture. The plant is thought to detect small cyclical discrepancies that arise between solar time and chronometer time. Since sunrise and sunset at the equator lie in the same time-frame as noon, which defines solar time, that obliges the plant's circadian cycle to follow chronometer time for the discrepancy to exist and for the hypothesis to stand. This rather untenable proposition prompted my earlier comment (Yeang, 2007) that 'gradual time shifts are meaningful only when measured against an external reference chronometer'. Chronometer time is a concept of anthropogenic engineering. Plants do not have an awareness of the precise chronometer time integral to the hypothesis (until the 18th century, neither did people).

Character of the light signal in the solar radiation intensity model

As the solar radiation intensity hypothesis of flowering provides for quantitative changes to the light signal that the plant perceives, functionality of the signal is not necessarily dependent on an interaction with its circadian cycle. Strong sunshine may play a more direct role in the transcription of genes that either promote floral development or relieve its inhibition.

If high solar radiation induced synchronous flowering, might there be a threshold intensity that is reached and exceeded before the trigger is actuated? Alternatively, might an increasing trend in solar radiation intensity be the critical criterion, analogous to the increasing or decreasing photoperiods reported for various tropical and subtropical plant species (Rivera & Borchert, 2001; Rivera *et al.*, 2002; Borchert *et al.*, 2005)?

In temperate regions, there is an almost 6-month increasing trend in the light photoperiod culminating in the summer solstice, followed by a 6-month decreasing trend towards the winter solstice. Therefore, when long-day plants flower before the summer solstice, it is always when day length is ascendant. Similarly, short-day plants typically flower when day length is on a declining trend. But at the equator, each period of solar radiation increase or decrease is only half as long since the annual cycle is bimodal. Thus, there are two 3-month periods of increase in sunshine intensity, culminating in the equinoxes, and two 3-month periods of decrease, culminating in the two solstices. The argument against the requirement of an increasing solar radiation trend is that the flowering season of species such as *H. brasiliensis* straddles the insolation peak. In Malaysia, *Hevea* flowering commences in February when solar radiation is on the increase. However, new floral buds continue to emerge and develop to anthesis even in April, after the equinox, when insolation is, in fact, decreasing. These observations are therefore more consistent with the explanation of a threshold insolation having been reached or exceeded.

The overhead sun makes the case for flowering being induced by high solar radiation intensity at the equator. Yet the variation in seasonal radiation need not necessarily be entirely quantitative in nature; it could be qualitative as well. When the midday sun is directly overhead, it passes through a relatively thin layer of the earth's atmosphere and the sunlight that reaches the ground is close to full-spectrum white light. Sunlight that is beamed in at an angle (e.g. at sunrise and sunset) and has thus to pass through a thicker layer of atmosphere is subjected to a greater degree of Rayleigh light scattering by gaseous molecules in the air. Such light scattering loss is more severe for the shorter wavelengths, blue, indigo, violet and ultraviolet. Besides the diurnal variation, there is also a seasonal cycle of spectral difference in light scattering at the equator since the midday sun is directly overhead only at the equinoxes. Therefore, the rubber tree flowers at the time it receives the full dose of blue-UV light from the overhead sun, and when the blue : red light ratio is maximal. There should also be a discrepancy between red and far-red light, although this would be relatively smaller because the difference in wavelengths is less. (Rayleigh scattering intensity is inversely proportional to the fourth power of the wavelength.) Future work might therefore take into account both the quantitative aspect of solar radiation (its total intensity) and the qualitative aspect (its spectral composition) in view of important roles that red light and blue light play in the flowering process (Bagnall & Hangarter, 1996; Guo *et al.*, 1999; Mockler *et al.*, 2003).

Timing of synchronous flowering with increasing latitude

Hevea brasiliensis demonstrates extraordinary robustness and adaptability that allows its cultivation to span more than 20° in latitude from the equator. Although there have been recent germplasm introductions, almost all the world's established plantings of rubber can be traced to a small number of seeds from the original collection by Wickham in 1876 (Tan, 1987). Not only is rubber that is cultivated in diverse regions generally derived from the same gene pool, but the clones grown at the equator are frequently the same ones planted in the subtropics. Therefore, flowering of the rubber tree at the extremities of its cultivated range offers an uncommon opportunity to learn how synchrony in this regard is achieved.

As already noted, synchronous flowering near the equator occurs around the equinoxes when the midday sun is directly overhead. Observations on the rubber tree indicate that flowering is delayed with increasing latitude from the equator (Yeang, 2007). This is consistent with the solar radiation intensity hypothesis, as it allows for the time lapse the sun takes to migrate from the equator to the Tropic of Cancer to the north and the Tropic of Capricorn to the south. In making a similar observation of flowering delay with latitude, van Schaik *et al.* (1993), noted that flowering in various plant species growing in locations between 20–25° north and south of the equator 'closely tracked the march of the sun'.

The difference in latitudes between a rubber planting area close to the equator (e.g. Kuala Lumpur, Malaysia, 3°N) and one close to the Tropic of Cancer (e.g. Hainan, China, 20°N, or Tripura, India, 24°N) would predict a delay of *c.* 2 months using the latitudinal position of the midday sun as the reference. Why, then, is the observed delay only 1–1.5 months (Yeang, 2007), local environmental influences notwithstanding? It should be remembered that, at the equator, seasonal variation in solar radiation is dependent entirely on the angle of the sun, with the day length playing no role. For this reason, the seasonal curves for noon insolation (Fig. 1a) and total day insolation (Fig. 1b) are identical at

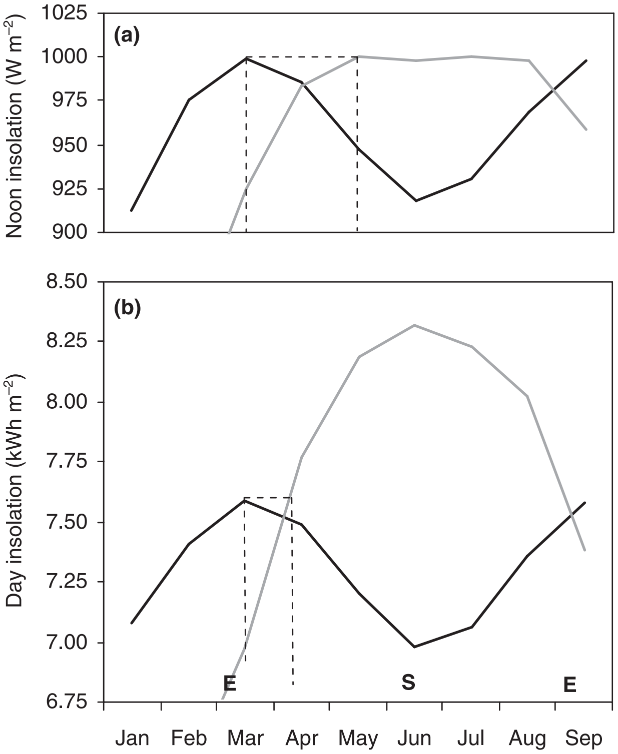

Fig. 1 Seasonal variation in solar radiation at the equator and at 20°N. Noon insolation (a) and total day insolation (b) at the equator (black line) and at 20°N (grey line) are calculated for the middle of the months as described previously (Yeang, 2007). The broken lines show insolation peaks at the equator, and the times when similar amounts of insolation are experienced at 20°N. The equinoxes (E) and the summer solstice (S) are indicated.

the equator. With increasing latitudes, however, day length begins to exert its influence and contributes to the total solar radiation received. While maximum noon insolation at the equator and at the Tropic of Cancer is essentially identical at the respective times of the year when the sun is directly overhead (Fig. 1a), total day insolation in the latter rises much higher with the advent of summer (Fig. 1b). Hence, comparable amounts of total day insolation at the equator and the tropics of Cancer and Capricorn are experienced ahead of comparable amounts of noon insolation (comparing Fig. 1a and b). This explains why flowering in the higher latitudes occurs ahead of predictions based strictly on the latitudinal position of the sun. Nevertheless, it does not necessarily mean that the entire extended photoperiod contributes towards the flowering trigger at the higher latitudes. As prolonged but weak sunshine may be ineffective in inducing flowering (Yeang, 2007), the added impact may only come from the portion of the extended day length when the sunshine is sufficiently strong. Hence, the discrepancies between the timing of flowering at the equator and at higher latitudes probably lie between what is shown in Fig. 1(a) and (b).

With the sunrise–sunset advance hypothesis, latitude increase is also expected to affect the predicted timing of synchronous flowering. Flowering at the equator is observed around the time that the rate of sunrise–sunset advance is at its peak. The maximal rate of advance, *c.* 20 s d^{-1}, is attained towards the end of March for the spring flowering. With increasing latitude, however, this same rate of advance occurs earlier (see Fig. 1 in Brochert *et al.*, 2005). Reading from the sunrise tables of the US Naval Observatory (2006) for latitude 20°N, the sunrise advance of 20 s d^{-1} would have been attained between late January and early February, well ahead of the March–April main *Hevea* flowering season in Hainan or Tripura. Thus, whereas the sunrise–sunset time-shift hypothesis predicts an advance in synchronous spring flowering with increasing latitude, a delay is in fact observed within the species, as for *Hevea*, or among various species (van Schaik *et al.*, 1993).

The sunrise–sunset time-shift hypothesis can be considered not just from the aspect of sunrise time shifts, but also from sunset time shifts (Brochert *et al.*, 2005). As already mentioned, any time advance or delay in sunrise at the equator would be accompanied by a corresponding advance or delay in sunset. Hence, there is essentially no difference whether it is the sunrise or sunset that is being monitored for the time-shift hypothesis at the equator, as they shift in tandem by equal intervals. However, this is no longer the case at the higher latitudes when day length is taken into account. It might be pertinent to recapitulate that even at locations close to the equator where day-length variation just begins to be perceptible, the photoperiodic cycle is unimodal. The longest duration of daylight falls on the summer solstice, just as it does in temperate regions.

At 20°N, the effect of increasing day length is quite significant by March and April, when rubber trees growing at this latitude flower. Even as sunrise continues to advance (i.e. the sun rises progressively earlier), the increasing light duration between sunrise and sunset means that sunset is increasingly delayed. Unlike at the equator, sunrise and sunset no longer shift in the same direction. Thus, whereas the sunrise–sunset time-shift hypothesis predicts a rapid advance in the time of sunset when the rubber tree flowers, this occurs only near the equator, but not at higher latitudes. In the latter, a delay in sunset is observed instead during the main *Hevea* flowering season in spring.

Comparing the sunrise–sunset time-shift model with the solar radiation intensity model, it can be seen that the former explains synchronous flowering near the equator, but not at the higher latitudes. The problem here lies with day-length variation at the higher latitudes. The increasingly early sunrise and the increasingly late sunset that is experienced as summer approaches confounds the prediction of flowering time. In comparison, the solar radiation hypothesis accommodates day-length variation and is operational both at the equator and in the subtropics. Indeed, prediction of flowering time is improved in the subtropics when the day length is factored into the calculation.

Perceiving degrees of bright sunshine

While delving into how plants might sense seasonal changes in sunshine, it is also of interest to consider how the same changes are observed, or not observed, from the perspective of the researcher.

Sunrise and sunset times vary by up to 30 min over the course of the year at the equator. However, since synchronous flowering at the tropics occurs not when the sunrise–sunset advance is greatest, but when the advance is fastest, the difference between the timing of sunrise–sunset at flowering and the maximum extent of the sunrise–sunset time shift is only *c.* 15 min. This difference (1% over 24 h) is understandably difficult for the observer to notice. In comparison, the levels of noon solar radiation intensity between the minima at the solstices and the maxima at the equinoxes are of the order of 10% at the equator. Shouldn't that discrepancy have been easier to spot?

There are various explanations as to why synchronous flowering at the equator has not previously been linked to seasonal solar radiation, chief among them the contemporary temperate bias in plant physiology research (Renner, 2007). In temperate regions, seasonal differences in temperature and day length are marked, and they determine the planting cycle in agriculture. In these regions, the equinox is when the durations of day and night are equal. In the tropics, on the other hand, the planting cycle tends to be synchronized with the rains, as neither temperature nor sunshine is limiting. Equality of day and night attracts no attention where there is hardly any day-length variation to begin with. The true significance of the equinox for equatorial regions is that it is the time when there is a peak in sunshine intensity. However, that sunshine intensity varies at all over the year may not even be obvious to the casual observer at the equator.

With the five human senses at our disposal, we do not hear, taste or smell sunshine. We feel the warmth of sunshine, but not its brightness. That leaves us with the sense of sight. However, we have difficulty differentiating between degrees of bright sunshine because our eyes are equipped with a light-compensating mechanism to optimize sight in dim or bright light. When light is limited, the iris of the eye dilates the pupil fully to maximize the entry of light. As it becomes brighter, the iris constricts the pupil progressively, and in the process makes it difficult to distinguish between 'bright' sunshine and 'very bright' sunshine.

Without the aid of instrumentation set up for the purpose, the human eye may not readily discern that, at the equator, the equinox is the brightest time of the year. Plants lack eyes (although irises are found in the plant kingdom!), but they have evolved various photoreceptors capable of perceiving a broad range of light qualities and intensities. Compared with humans, plants probably do a better job of perceiving the fine degrees of bright sunshine. It could be this ability that facilitates the induction of flowering when the threshold brightness is attained.

Acknowledgements

I thank Dr David Rainwater, University of Rochester, for sharing his insights on light scattering in the atmosphere.

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Key words: pollination, rubber tree, solar radiation intensity model, sunrise-sunset times-shift model, synchronous flowering, tropics.

Meetings

Functional genomics and ecology – a tale of two scales

Linking physiological ecology, evolutionary biology and functional genomics for understanding biotic responses to a changing environment and Mechanistic underpinnings of ecological processes: scaling from genes to ecosystems

Symposium and Organized session at the Ecological Society of America (ESA) 92nd Annual Meeting, San Jose, California, USA, August 2007

Science moves forward in small steps, punctuated by an occasional leap. Many believe that the advent of high-throughput sequencing of plant and animal genomes, coupled with the development of microarrays for transcript profiling, may prove to be such a leap for the biological sciences. Molecular biologists are currently using these technologies to reveal the dynamic nature of cells and organisms (Colebatch *et al.*, 2002). These advances hold equal promise for the ecologist who is willing to extend the use of these tools into the natural environment (Jackson *et al.*, 2002). Such efforts could lead to an improved understanding of how genes shape the structure and function of terrestrial ecosystems and how those insights could help us better predict the response of plants and animals to biotic and abiotic stresses in a rapidly changing world.

Two symposia were recently held at the 2007 meeting of the Ecological Society of America to evaluate the current use of functional genomics in the ecological sciences. One symposium focused on linking physiological ecology, evolutionary biology and functional genomics for understanding biotic responses to a changing environment. A second symposium addressed the mechanistic underpinnings of ecological processes with a special emphasis on scaling relationships from genes to ecosystems. The co-organizers of these symposia sought to tackle three cross-disciplinary objectives.
(1) How do we identify genes that underlie ecologically important adaptive traits?
(2) What climatic and edaphic forces will drive evolution in future, novel, environments?
(3) How do we scale from genotype to phenotype and beyond, to ecosystems?

> *'It is true that the ecologist will frequently have to work at the suborganismal level. The stated goal, however, should remain both integrative and extrapolative.' (Boyd Strain, Duke University, NC, USA)*

Identifying genes responsible for natural variation in adaptive traits

A central challenge in evolutionary and ecological genomics has been to identify the genetic basis of adaptive traits that allow an organism to survive and reproduce in natural environments (Feder & Mitchell-Olds, 2003). This challenge has been made less daunting by the increasing number of genome sequences and genetic resources that have become available in recent years. Investigators are constructing genetic linkage maps for species of interest, establishing