

Commentary

Synchronous flowering linked to changes in solar radiation intensity

Using flowering data from rubber tree (*Hevea brasiliensis*; Fig. 1) plantations in Malaysia, Thailand, Indonesia, India, Sri Lanka, Vietnam, China, Nigeria, Cote d'Ivoire and Brazil, Yeang (this issue; pp. 283–289) takes a fresh look at the question of what signal tropical trees might use to synchronize their annual cycles of flowering. The external time giver proposed by Yeang is a meteorological event, namely the annually repeated cycles in incoming solar radiation and the associated changes in daily insolation. Why should these cycles, which after all are experienced by all organisms on Earth, be of special biological significance in the tropics? And just as curious, why should they have been overlooked as a time giver for rubber tree flowering until now?

The answer to the first question lies in a crucial difference between the temperate zone and the tropics. Everywhere on Earth, the amount of solar radiation that reaches the atmosphere is dependent on (i) the intensity of sunshine and (ii) its duration. Intensity is determined by the angle at which the sun's rays strike the surface of the Earth. In temperate latitudes, day length and irradiation intensity both contribute to the daily insolation, and the concurrent annual cycles in these two parameters are additive. Maximum radiation intensity



Fig. 1 Flowering *Hevea brasiliensis*. (Figure kindly provided by Kazuo Yamasaki).

– when the noon sun is at its highest above the horizon – and maximum day length occur on the same day, the summer solstice. Near the equator, however, seasonal change in insolation is dependent *entirely* on solar radiation intensity, as variation in day length is minimal. The seasonality is a result of the Earth's path around the sun and its tilt, with the sun passing directly over all tropical localities twice a year (Fig. 2 shows the latitudinal variation in the time course of insolation in the northern hemisphere from the equator to 50°N). The symmetric seasonal changes in insolation around the summer solstice (Fig. 2, vertical line) are the result of the declining (spring) and increasing (autumn) distance of the sun from its position at the summer solstice. In the equatorial belt proper, there are two distinct annual maxima of insolation, corresponding to the equinoxes (Fig. 2).

'Changes in radiation intensity as the explanation for how a tropical tree manages to synchronize its flowering may not convince everyone.'

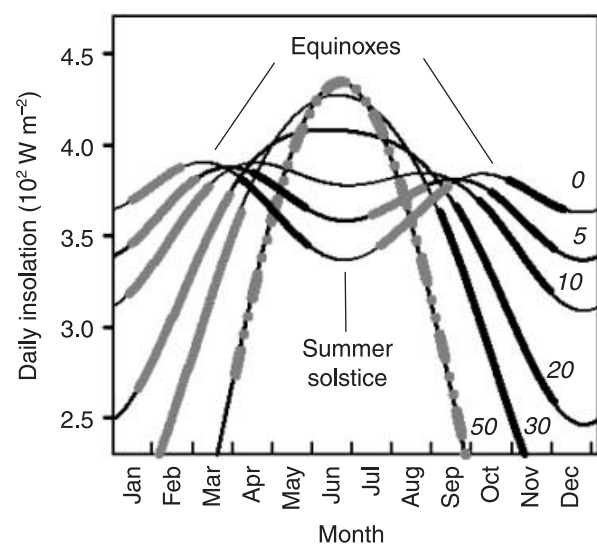


Fig. 2 The latitudinal variation in the time course of insolation in the northern hemisphere from the equator to 50°N. (figure kindly provided by R. Borchert).

What is the evidence that annual changes in insolation provide the external cue that synchronizes flower bud break in *H. brasiliensis*? First, rubber trees start flowering at the same time every year, making it unlikely that temperature, rainfall, cloud cover, or periods of drought could be the triggers as they do not occur with sufficient regularity. Secondly, data from rubber plantations in the northern and southern subtropics of South America, Africa and Asia show that flowering coincides with high insolation, not temperature or rainfall. The third line of evidence is the fit between the bimodal peak in incoming solar radiation (above and Fig. 2) and the bimodal flowering in *H. brasiliensis* in some localities (cf. Yeang's table 1). Most *H. brasiliensis* populations, however, flower only once a year, around the spring equinox (Yeang, this issue).

As proposed by Yeang, high solar radiation intensity, and in particular bright sunshine (as distinct from prolonged diffuse radiation), induce flowering in *Hevea*, and he considers whether average radiation, very high radiation on a cloud-free days, or hours of high daily sunshine might be decisive. This fails to make explicit that bud break is not induced by some threshold value *per se*, but by the increase in daily insolation that precedes the two maxima in March and September (Fig. 2).

Changes in radiation intensity as the explanation for how a tropical tree manages to synchronize its flowering may not convince everyone. First, given the large diurnal and day-to-day fluctuations of cloud cover, how can seasonal variation in insolation be a trigger for precisely timed flowering? Yeang elegantly refutes this argument with data on insolation near the ground that show that there is a consistent correlation with insolation above the atmosphere, such that one is a proxy for the other. Secondly, does Yeang's hypothesis obviate or refute the idea of Borchert *et al.* (2005), who linked the flowering times of 84 tropical tree species to the four annual periods at which changes in sunset times are greatest (as a result of the earth's tilt and elliptic orbit, the times of sunrise and sunset near the equator vary by 30 min over the course of the year)? Yeang argues (i) that the gradual time shifts of less than 1 min a day are too small to be perceived by plants, (ii) that they are 'meaningful only when measured against an external reference chronometer', and (iii) that a trigger linked to changes in day length would imply a single annual flowering (because no plant is simultaneously a long-day plant and a short-day plant). The first of Yeang's arguments is plausible, although the minimum change in day length required for flower induction is not yet known. The second does not hold, as there is 80 years' worth of work (Bünning, 1936) showing that plants can perceive changes in light rhythms with the help of endogenous circadian clocks. The third argument, that photoperiodic control implies a single annual flowering, is unconvincing as some species could use the periods of advancing day length to flower, and others those of receding day length. Even

individual trees that flower bimodally, as in some populations of *Hevea* (as mentioned above), do not present a problem for the hypothesis of Borchert *et al.* (2005) because each year there are two periods of receding and two periods of increasing day length.

What are needed to resolve the relative roles of changes in insolation and day length as cues for the induction of flowering in tropical plants are more data on widespread species, such as *H. brasiliensis*, ranging from the equator to > 10°N. This will permit us to distinguish whether latitudinal changes in flower bud break *in the same species* parallel latitudinal changes in daily insolation or day length.

Yeang's is among the few studies to have made use of the vast amount of phenological data available for commercially important tropical species. Besides rubber, these include durian (*Durio zibethinus*), mangosteen (*Garcinia mangostana*), rambutan (*Nephelium lappaceum*), avocado (*Persea americana*) and many others, and the obvious question now is to what extent their flowering also coincides with the yearly peaks in maximally changing daily insolation. Earlier studies of tropical phenology instead analysed natural communities (e.g. Opler *et al.*, 1980; Wright & van Schaik, 1994) or species in a range of genera (Borchert *et al.*, 2005). These studies show that synchronous flower bud break *with minimal interannual variation* characterizes not just *H. brasiliensis* but hundreds of tropical tree species in many different families, with some species flowering near the spring equinox, others near the autumn equinox, and a few bimodally (Spruce, 1908; Opler *et al.*, 1980; van Schaik *et al.*, 1993; Borchert *et al.*, 2005). Given that van Schaik *et al.* (1993) and Wright & van Schaik (1994) explicitly drew attention to the annual cycle of insolation as a potential time giver for tropical trees (stressing that predictable irradiance seasonality occurs throughout the tropics), why did changing insolation receive so little attention before Yeang's investigation? One reason may be the temperate bias of plant physiology, especially modern Arabidopsis-centred work on the proximate mechanisms behind phenological changes (Simpson *et al.*, 1999; Yanovsky & Kay, 2003). Other reasons may be that cloud cover and water stress were played up as modifiers or alternative triggers, and that irradiance was seen as a limiting factor (hence 'insolation-limitation hypothesis'; van Schaik *et al.*, 1993; Wright & van Schaik, 1994), rather than a precise external cue that allows tropical plants to synchronize their reproduction. Such synchronization must be under strong selection because stigmas and/or pollen are only viable for relatively short times, and successful reproduction therefore depends on the exact timing and synchronization of flowering.

How trees perceive daily changes in insolation is not yet clear. Ultimately, the interaction of light absorbed by the various photoreceptors with the expression of circadian clock-dependent transcription factors must determine flowering (Simpson *et al.*, 1999; Yanovsky & Kay, 2003).

Yeang's study points to the need for experiments that address the effects of irradiance *per se*, independent of day length.

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Key words: flowering, *Hevea brasiliensis*, phenology, photoperiodic control, solar radiation.

Blowin' in the wind – the transition from ecotype to species

Adaptive divergence is generally regarded as of central importance to the process of speciation. One way in which such divergence may proceed is via the evolution of genetically different forms of a species – ecotypes (Turesson, 1922) – that are adapted to different environmental conditions or habitats. The recognition that many plant species are likely to exhibit ecotypic variation triggered a large number of studies of this type of variation in the 20th century (Clausen *et al.*, 1948; Heslop-Harrison, 1964). Although much was learnt

about morphological, physiological and life history differences, few studies examined the nature and level of reproductive isolation between different ecotypes of a given species. Because many ecotypes occur in habitats geographically separated from other ecotypes, reproductive isolation because of geographical distance is likely to be important in preventing interbreeding and the erosion of ecotypic variation within a species. But what about situations where different ecotypes occur in habitats that are geographically close or even adjacent to each other? How might an ecotype originate and/or be maintained under these conditions in the face of potentially large amounts of gene flow from another ecotype of the same species? Does selection under these conditions favour the evolution of traits that reduce gene flow between different ecotypes? These are some of the questions that needed answering if it were to be demonstrated that ecotypic differentiation is indeed an important step in the speciation process. Because direct measures of gene flow only became possible in most species following the development of molecular polymorphisms in the 1990s by the polymerase chain reaction, researchers were prevented until recently from answering these key questions.

In this issue, Foster *et al.* (pp. 370–380) report a study of ecotypic divergence in the tree species *Eucalyptus globulus*. Using chloroplast and nuclear DNA markers, they present evidence for the parallel and parapatric evolution of a dwarf ecotype from the normal (tall) form of the species at different locations. Then, using a set of nuclear microsatellite markers, they show that no pollen-mediated gene flow occurs from the tall to the dwarf ecotype in a situation where the two ecotypes grow in close proximity. Such reproductive isolation is attributed to a difference in flowering time in addition to some spatial separation.

'... the publication by Foster et al. is the first to report that an ecotype of a sexually outcrossing plant species is not subjected to pollen-mediated gene flow from another adjacent ecotype ...'

The recurrent and independent origin of a particular ecotype within a species has been reported previously in both plant and animal kingdoms (e.g. Schluter & Nagel, 1995; Rajakaruna *et al.*, 2003). However, conclusive evidence, either (phylo)genetic or otherwise, in support of parallel or incipient parallel speciation (Rundle *et al.*, 2000; Johannesson, 2001) is more difficult to obtain (see below, under 'Issues to be

resolved'). One difficulty, of course, is to prove that the divergent ecotypes (incipient species) are reproductively isolated from each other. A recent study, using genetic markers, demonstrated that levels of gene flow (measured indirectly from F_{ST} values) between adjacent divergent ecotypes can be low and associated with a difference in flowering time in a sexually outcrossing plant species (Silvertown *et al.*, 2005). However, the publication by Foster *et al.* is the first to report that an ecotype of a sexually outcrossing plant species is not subjected to pollen-mediated gene flow from another adjacent ecotype, based on progeny tests utilizing genetic markers. This finding is important in regard to how ecotypes might evolve into species.

Ecotypic differentiation in response to variation to wind exposure

Although it is frequently reported that genetically dwarf and tall forms of a species occur in sites exposed to strong winds and relative shelter, respectively, no studies, to date, have proved that such variation is adaptive. Such proof requires a demonstration (e.g. by reciprocal transplant analysis) that dwarf types have the highest relative fitness in exposed sites where they grow, whereas tall types have the highest relative fitness in more sheltered sites. The best evidence that such genetic divergence is of adaptive significance comes from a study by Aston & Bradshaw (1966) on the wind-pollinated grass species *Agrostis stolonifera*. If the study by Foster *et al.* on *E. globulus* is compared with that by Aston & Bradshaw (1966) on *A. stolonifera*, the following similarities and differences are noted: (i) in each case there is evidence that 'dwarfism/smallness' is an inherited trait; (ii) some evidence is presented for smallness being adaptive in *A. stolonifera*, whereas dwarfism is assumed to be adaptive in *E. globulus*; (iii) molecular evidence is presented for the recurrent and independent origin of the dwarf ecotype of *E. globulus* at different sites, whereas no such evidence is available for *A. stolonifera*; and (iv) the dwarf ecotype of *E. globulus* is shown to be isolated from pollen-mediated gene flow from the tall ecotype, based on genetic marker evidence, whereas in *A. stolonifera* indirect evidence was used to suggest the same form of isolation.

Reproductive isolation between ecotypes and speciation

Previous studies of reproductive isolating barriers between plant ecotypes have mainly focused on ecotypes adapted to different soil type (McNeilly & Antonovics, 1968; Silvertown *et al.*, 2005). The classic work on heavy metal tolerance in plants in the 1960s revealed that plants growing on mine spoil containing high levels of a heavy metal, flower earlier and exhibit a higher level of self-fertility relative to nontolerant plants from the surrounding pasture area (Antonovics, 1968;

Box 1 A model for parapatric speciation via ecotypic divergence after McNeilly & Antonovics (1968).

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| Stage 1. A population occupies a new habitat and exhibits no breeding barriers and no divergence in adaptive characters relative to adjacent progenitor material. |
| Stage 2. The population exhibits divergence in adaptive characters, but no breeding barrier, and can be considered to be an ecotype. |
| Stage 3. The ecotype becomes discontinuous from adjacent parental material with partial breeding barriers existing; divergence increases. |
| Stage 4. Two isolated populations are recognised that are reproductively isolated and independent of each other. These can be considered as two different species. |

McNeilly & Antonovics, 1968). This difference in flowering time was recently shown to have persisted over a period of 40 yr at one mine/pasture site (Antonovics, 2006).

Based on this research, McNeilly & Antonovics (1968) proposed a four-stage model of parapatric speciation via ecotypic divergence (Box 1). Although the final stage of this model (i.e. complete reproductive isolation from an adjacent ecotype), has yet to be reached in the mine material studied, McNeilly & Antonovics (1968) pointed out that 'some serpentine species are isolated from what appear to be their immediate counterparts on normal soils'. In this regard, Kruckeberg (1986) put forward a similar model of speciation for the evolution of serpentine endemics, but with greater emphasis on the need for some degree of tolerance within normal populations of a species, so as to allow initial colonization of serpentine soils. Furthermore, Macnair & Gardner (1998) made the point in a review of the evolution of edaphic endemics that 'the crucial step differentiating an ecotype from an endemic is likely to be the acquisition of partial or complete reduction in gene flow between the normal, ancestral population and ecotype, allowing an independent gene pool to develop.

The study by Foster *et al.* strongly suggests that this step has been reached in the dwarf ecotype of *E. globulus*, which is shown to be completely isolated from pollen-mediated gene flow from the tall ecotype. Thus, the conditions of the 'biological species concept' (BSC, after Mayr, 2002) appear to be fulfilled by the dwarf ecotype, although recognition by the BSC would require that independently evolved ecotypes of the same kind are reproductively compatible.

'But proving parallel speciation is a daunting task with four criteria needing to be satisfied.'

Issues to be resolved

Is the recurrent origin of the dwarf phenotype an example of incipient parallel speciation in parapatry?

An important aspect of the publication by Foster *et al.* is the possible incipient parallel speciation seen in the recurrent and independent origins of the dwarf ecotype of *E. globulus*. Rundle *et al.* (2000, p. 306) define parallel speciation as 'a special form of parallel evolution in which traits that determine reproductive isolation evolve repeatedly in independent, closely related populations as a by-product of adaptation to different environments.... The outcomes are reproductive compatibility between populations that inhabit similar environments and reproductive isolation between populations that inhabit different environments'. An implicit significance of parallel speciation thus lies in its contribution to falsifying genetic drift as the alternative interpretation to ecological selection, because observing a consistent correlation of the same evolutionary transitions with environmental change renders drift unlikely (Schluter, 2004). Following the ground-breaking work on sticklebacks (*Gasterosteus*) (e.g. Schluter & Nagel, 1995; Rundle *et al.*, 2000; McKinnon *et al.*, 2004; Schluter, 2004), numerous other examples of (incipient) parallel speciation have been discovered in animals, aided by combining research on molecular phylogeny and ecology (Johannesson, 2001). However, detailed studies of parallel speciation in plants have lagged behind, despite the wealth of information available on ecological plant races and species that occupy different habitats (Levin, 2001). This is why the study of Foster *et al.*, along with similar research on edaphic races in *Lasthenia* (Asteraceae; Rajakaruna *et al.* 2003), is important. Together, they cast new light on the question of how common incipient parallel speciation might be in plants. But proving parallel speciation is a daunting task with four criteria needing to be satisfied (Schluter & Nagel, 1995; Levin, 2001). First, populations that inhabit similar environments must be phylogenetically distinct. Second, their shared characteristics must be shown to have evolved by natural selection, and third (and fourth), populations that inhabit similar (different) environments must be reproductively compatible (isolated). Except for sticklebacks, none of the current examples of parallel speciation, either in animals or in plants, strictly satisfy all of these criteria. Foster *et al.* provide evidence to satisfy the first and fourth criterion in their study of *Eucalyptus*, but additional work is required to satisfy the remaining two criteria.

Another key point that often remains to be fully established in studies of parallel evolution is whether the divergent ecotype/species did indeed originate in parapatry. Some authors have argued that parallel speciation is a compelling signature of nonallopatric (i.e. parapatric or sympatric) divergence (e.g. Johannesson, 2001). However, recent work on sticklebacks has revealed that the expected outcomes of parallel

speciation (as mentioned in the previous paragraph) can also result from allopatric divergence followed by multiple invasions, secondary contact, hybridization and reinforcement (Taylor & McPhail, 2000; Schluter, 2001). In phylogenetic terms, perhaps the biggest problem afflicting nonallopatric interpretations is that gene exchange after secondary contact can yield the misleading conclusion that different ecotypes in the same area are sister taxa (Johannesson, 2001; Coyne & Orr, 2004). As a case in point, initial evidence in sticklebacks for parallel speciation in sympatry, based on mitochondrial DNA, evaporated when multiple nuclear markers were also studied (Taylor & McPhail, 2000; Schluter, 2001). However, in the case of *E. globulus*, the data are suggestive of incipient parallel speciation in parapatry as both molecular data sets indicate that nearby populations of the two different ecotypes are the closest relatives in two of the three different locations analysed.

Does reproductive isolation evolve to reduce gene flow or in response to other factors?

Selection might lead to the origin of reproductive isolation during diploid parapatric speciation in three different ways. (i) There may be direct selection for reproductive isolating characters, such as differences in flowering time and increased self-fertility, to prevent maladaptive hybridization. Alternatively, reproductive isolation may arise as a by-product of ecological adaptation, either owing to (ii) selection of characters that adapt ecotypes to their respective habitat, or (iii) pleiotropic effects of genes for the divergently selected character(s), or closely linked genes.

One of the few well-established cases of direct selection for reproductive isolation is the evolution of flowering-time differences between metal-tolerant and metal-susceptible populations of *Agrostis tenuis* and *Anthoxanthum odoratum* (McNeilly & Antonovics, 1968). Probably more common is indirect selection (Coyne & Orr, 2004), which actually forms part of the definition of parallel speciation of Rundle *et al.* (2000) (see the previous section). For instance, metal- or serpentine-tolerant ecotypes of *Mimulus* spp. that have diverged from neighbouring nontolerant populations not only flower earlier (because of drier and less nutritious soils), but also self-pollinate more frequently, assuring reproduction when pollinators could be scarce or absent (Macnair & Gardner, 1998). Although in most of these instances the genetic basis of both characteristics remains unknown, they probably contribute to genetic isolation because of their ecological role, rather than being the immediate target of selection for reproductive isolation. Finally, there is good evidence in *Mimulus guttatus* that pleiotropy or linkage is responsible for the association between ecological adaptation and postzygotic reproductive isolation. Here, genetic analyses revealed that the gene for copper tolerance (or an allele at a closely linked locus) was responsible for the low viability of hybrids

between a copper-tolerant and a nontolerant population of this species (Macnair & Christie, 1983; Christie & Macnair, 1987). In the case of *E. globulus*, it is not yet known whether early flowering of the dwarf ecotype is genetically controlled or is a plastic response to local conditions. Until this is determined, a discussion of possible evolutionary causes of the temporal ecological isolation observed would be premature.

Future work

The article by Foster *et al.* brings into sharp focus the importance of studying ecotypic variation within species to obtain a better understanding of the process of parallel adaptive divergence and speciation. If appropriate ecotypic material is chosen, the 'toolbox' of environmental/evolutionary genomics could be used to examine all stages of ecotypic differentiation leading to speciation. We expect therefore that recurrently formed ecotypes will be used increasingly in future research aimed at isolating genes which control traits important in adaptation (Bouck & Vision, 2007) and, particularly, genes controlling characters that determine reproductive isolation. This should lead to major advances in our understanding of the genetics of parallel speciation.

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Key words: ecotypes, eucalyptus, parallel speciation, parapatry, reproductive isolation, wind pollination.