

# Flowering while leafless in the seasonal tropics need not be cued by leaf drop: evidence from the woody genus *Brachychiton* (Malvaceae)

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**Background and aims** – A suite of woody plants inhabiting the seasonally-dry tropics flower while leafless during the dry season. A functional hypothesis for this phenomenon is that leaf drop early in the dry season pre-empts dehydration, and that flowering is triggered by the improved water status caused by leaf drop. If true, this would strongly constrain adaption to optimise flowering times.

**Methods** – I examine phenological patterns in the Australasian genus *Brachychiton* based primarily on summary descriptions in a published taxonomic treatise, along with relevant morphological, anatomical and ecophysiological evidence, in order to evaluate the role of leaf drop, and identify other sources of hydration that may initiate or support flowering while leafless.

**Key results** – Most of the 31 *Brachychiton* species are deciduous and many flower during the dry season following leaf drop, but some flower later in the dry season, at leaf flush, or when leafy. Many have enlarged stems, branchlets or tap roots, and the limited ecophysiological evidence suggests that these organs are associated with enhanced water storage potential. *Brachychiton* displays both considerable evidence of divergence, and a degree of phylogenetic conservatism in these traits.

**Conclusions** – Rehydration following leaf drop is not a necessary cue to initiate flowering even when leafless. Flowering time is likely to be adaptive and species-specific in a wide range of woody plants in the seasonally-dry tropics. Care is needed to disentangle phenological correlates and the proximal and ultimate factors driving flowering.

**Key words** – *Brachychiton*, deciduousness, environmental cues, kurrajong, monsoonal tropics, morphology, phenology, seasonal tropics, stem water storage, succulence.

## INTRODUCTION

To flower, plants must be sufficiently hydrated (Rathcke & Lacey 1985, Borchert 1991). This raises intriguing questions about the proximate and ultimate factors underlying flowering in trees and shrubs that flower while leafless during the tropical dry season, a phenomenon that is widespread in the seasonal tropics and sub-tropics of central America (Janzen 1967), India (Kushwaha et al. 2011), Madagascar (Baum 1995b) and northern Australia (Guymer 1988). Janzen (1967) offered an adaptionist perspective, arguing that flowering when leafless maximises visibility of flowers for pollinators and optimised growth schedules by temporal separation of leafing and reproduction. In parallel, Murphy & Lugo (1986) and van Schaik et al. (1993) argued that phenological programs in the seasonally-dry tropics are flexible, adaptive and not necessarily constrained by moisture. Others, however, have suggested that moisture availability is the proximate driver and thus the ultimate constraint on the phenological cycles of plants that flower while leafless (Rathcke & Lacey

1985, Borchert 1991, Borchert et al. 2004, Kushwaha et al. 2011). Yet another perspective on phenological schedules is that they are often phylogeny-specific (Kochmer & Handel 1986), inferring that capacity for adaptive evolution is constrained.

Plants that flower while leafless typically shed their leaves early in the dry season before substantial water stress occurs, thus maintaining some level of hydration (Wright & Cornejo 1990, Choat et al. 2006, Fallas-Cedeño et al. 2010). Further, early leaf-shed triggers an improvement in their water status and there is evidence that this improvement can be a cue to flowering (Borchert 1983, 1994b, 1994c). There are also a number of other mechanisms by which leafless plants may be or remain sufficiently hydrated to flower. While leaflessness limits transpiration and thus a plant's ability to take up moisture from soil (Worbes et al. 2013), leafless plants may transpire through taproots (Scholz et al. 2008) and this may drive uptake of moisture from soil. Some deciduous tropical plants have thickened stems or roots that permit water to be stored through the dry season (Borchert 1994b, Bullock &

Solis-Magallanes 1990, Fallas-Cedeño et al. 2010, Worbes et al. 2013). Indeed, there is considerable evidence supporting recognition of a plant functional type, water-storing light-wood trees of the seasonally-dry tropics (Borchert 1994b). These archetypically and variously have shallow roots and mesic leaves, are drought-sensitive and shed leaves early in the dry season, and flower with leaf drop (Borchert 1994b, Holbrook 1995, Holbrook et al. 1995, Kushwaha et al. 2011, Paz et al. 2015, Vico et al. 2015, Pineda-García et al. 2016).

The Australasian genus *Brachychiton* Schott & Endl. (Malvaceae: Sterculioideae; formerly Sterculiaceae; alternatively Sterculiaceae s.str.) is most speciose in the seasonal tropics (Guymer 1988). It includes a number of species that flower while leafless (e.g. Bate & Franklin 2015; fig. 1) but also considerable diversity in the extent of leaf retention, the timing of leaf drop, and the relationship between the timing of leaf drop and flowering (Guymer 1988; D.C.Franklin, pers. obs.). This diversity prompts queries about the adaptive value, evolution of, and physiological processes underlying different leaf strategies and phenologies. In this paper, I ap-



**Figure 1** – Flowering while leafless during the dry season is a notable phenomenon of the seasonally-dry tropics. The illustrated plant is *Brachychiton megaphyllus* (Red-flowered Kurrajong, subg. *Brachychiton*), photographed near Darwin, Northern Territory, Australia.

praise the genus for: (a) phenological variation among species focussing on the temporal relationship between flowering and leaf shed; (b) the occurrence and function of organs that may enable water storage; and (c) association of these traits with infrageneric structure that suggests evolutionary patterns and constraints. My aim is to identify similarities and differences among closely-related taxa that provide perspectives on the hydration underlying, and possible proximate and ultimate factors driving the phenomenon of flowering while leafless.

## STUDY GENUS AND METHODS

The genus *Brachychiton* contains 31 currently accepted named species (Guymer 1988). All species are trees or shrubs and the majority occur in tropical northern Australia where the climate is intensely seasonal. Two species (one endemic) occur in Papua New Guinea, three in semi-arid parts of Australia and four exclusively in sub-tropical areas. Guymer (1988) recognised five infrageneric sections based on “pollen morphology, wood anatomy, seedling morphology and a re-examination of floral and seed characters” (table 1). These sections are now treated as subgenera (Australian Plant Census, <https://www.anbg.gov.au/chah/apc/>, accessed 16 Jul. 2014) though four undescribed taxa are additionally recognised. As no information is available to us about these four taxa, I have not considered them further.

Guymer’s (1988) treatise is a classic, 124-page taxonomic work. Introductory sections include delineation of subgenera, and keys to species. For each species, Guymer provides a detailed morphological description and illustration, taxonomic notes, a distribution map, notes on ecology, months of flowering and fruiting, a discussion of interspecific relationships and more. I conducted frequency analyses of the species to identify relationships between the timing of leaf drop and flowering, and the presence of structures which may be associated with water storage.

## RESULTS

### Phenological patterns

Twenty-five species of *Brachychiton* are deciduous and one questionably so, three are ‘deciduous or semi-deciduous’ or ‘deciduous or semi-evergreen’, one is ‘semi-deciduous’ and one is ‘evergreen or semi-evergreen’ (Guymer 1988). Information on the time of leaf-shed is available for 28 deciduous or semi-deciduous species, of which all but two shed their leaves in the early to mid dry season (May to September, fig. 2). The exceptions (*Brachychiton acerifolius* and *Brachychiton discolor*) are leaf exchangers (brevi-deciduous) from different subgenera (*Oxystele* and *Brachychiton* respectively) that shed leaves early in the wet season, and commence flowering as they do; these occur in higher rainfall areas of sub-tropical eastern Australia where rainfall is less seasonal.

There is no clear pattern in the timing of onset of leaf shed and its relationship to the onset of flowering (fig. 2). While coincident leaf shed and flowering is the most frequent relationship (61% of species), it occurred in all months of onset of leaf shed. Alternative temporal relationships were also widely dispersed through the dry season and varied

**Table 1 – Growth form and phenological traits among subgenera of *Brachychiton*, following Guymer (1988).**  
Environments: wt = wet tropics; sdt = seasonally-dry tropics, wst = wet sub-tropics, sdst = seasonally-dry sub-tropics, a = semi-arid.

Subgenus	No. of species	Environment	Growth form	Leaf retention	Timing of flowering
<i>Oxystele</i>	2	wt, sdt, wst	trees with cylindrical trunks and thickened branchlets	deciduous or semi-evergreen	wet season
<i>Poecilodermis</i>	3	sdt, sdst, a	trees with cylindrical or slightly bulbous trunks; <i>B. populneus</i> has tuberous tap root	deciduous, semi-deciduous or evergreen	dry or wet season
<i>Delabechea</i>	2	wt, sdst	trees with strongly bulbous trunks	deciduous or semi-deciduous	late dry – early wet season
<i>Trichosiphon</i>	4	sdt, sdst, a	trees with columnar or slightly bulbous trunks; 3 spp. with thickened branchlets	deciduous	dry season
<i>Brachychiton</i>	20	sdt, wst, sdst	shrubs or trees with cylindrical trunks rarely slightly swollen at base; 4+ spp. with thickened branchlets	deciduous	mostly dry season; 1 sp. in wet season

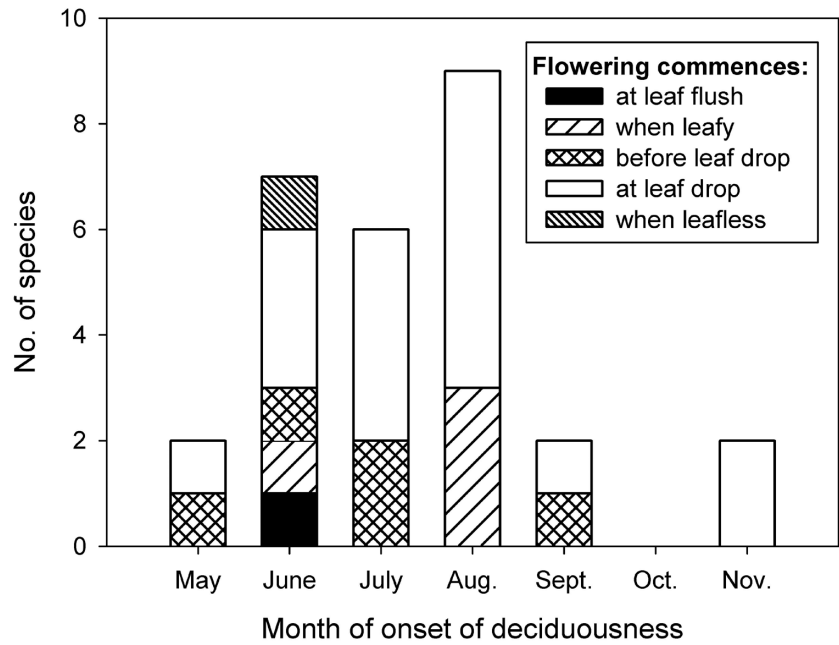
through all possible options, namely from coincident with leaf flush, when in full leaf, shortly before leaf drop (fig. 3), coincident with leaf drop and when leafless.

Stem growth in *Brachychiton diversifolius* (deciduous or semi-evergreen; seasonally-dry tropics) occurs mostly in the early wet season (Koenig & Griffiths 2012).

**Morphological, anatomical and ecophysiological evidence**

At least thirteen members of the genus have inflated growth forms – thickened trunks, branches and/or taproots (table 1).

Of these, two species have distinctly bulbous trunks (fig. 4) and four distinctly ‘columnar’ trunks (fig. 5). Seedlings of *Brachychiton populneus* and adults of *Brachychiton megaphyllus* and *Brachychiton paradoxus* have enlarged tuberous tap roots (Levitt 1981, Buist et al. 2000, Franklin & Bate 2013); the structure of the roots of other species has not been reported. The tap root of *B. megaphyllus* is cylindrical or slightly tapered (carrot-like), measuring about 10 cm diameter at the top in at least several small individuals, and has no coarse lateral roots and very few fine roots (see photos in Franklin & Bate 2013). Based on illustrations in Guymer (1988), nine species have strongly thickened termi-



**Figure 2 – The phenology of leaf drop, and of the commencement of flowering relative to canopy state, in 28 deciduous or semi-deciduous species of *Brachychiton* (based on Guymer 1988).** ‘Before leaf drop’ means up to one month before while “when leafy” means after leaf flush but more than one month before leaf drop; ‘at leaf drop’ means at or within one month after the commencement of leaf drop; and “when leafless” means more than one month after leaf drop. The tropical/sub-tropical dry season in Australia is from April–June to September–December, depending on district and year.





**Figure 3** – *Brachychiton vitifolius* (subg. *Brachychiton*) commences flowering in the early dry season prior to leaf drop. Photographed in tropical savanna in late May on Cape York Peninsula, Australia.



**Figure 4** – *Brachychiton rupestris* (Queensland Bottle Tree, subg. *Delabechea*), showing bulbous trunk. Trunks become even more bulbous with age, resembling those of baobabs (*Adansonia* spp.). Photographer: ‘djmapleferryman’. Source: [https://upload.wikimedia.org/wikipedia/commons/c/c1/Brachychiton\\_rupestris.jpg](https://upload.wikimedia.org/wikipedia/commons/c/c1/Brachychiton_rupestris.jpg), license type CC BY 2.0, modified only by cropping.

nal branchlets and a further ten species somewhat thickened (non-twiggy) branchlets. In the sparingly-branched *B. megaphyllus*, terminal branchlets are c. 1 cm diameter (pers. obs.), this having been classified as ‘strongly thickened’.

Bulbous trunks (two species) contain “extensive mucilage axial cavities ... in the vertical wood parenchyma ... , a feature not recorded for any other species of the genus nor for any other member of the Sterculiaceae” (Guymer 1988). Taproots of seedlings of *B. populneus* (subg. *Poecilodermis*) contain starch and water reserves (Buist et al. 2000). *Brachychiton australis* (subg. *Trichosiphon*) has low wood density and high water storage capacity (Choat et al. 2005). The internal structures of other species has not been reported.

One columnar-trunked species, *Brachychiton australis* (fig. 5), has been the subject of extensive ecophysiological studies (Choat et al. 2003, 2005, 2006). It has “hydraulic architecture typical of drought-sensitive plants, i.e. low wood



**Figure 5** – A c. 20-m tall specimen of the *Brachychiton australis* (Broad-leaved Bottle tree, subg. *Trichosiphon*), showing columnar trunk. Photographed in natural habitat of deciduous vine-thicket, Forty-Mile Scrub, north Queensland, Australia, whilst leafless in mid-September (mid-late dry season).

density, wider xylem vessels, higher maximal rates of sapwood specific hydraulic conductivity ( $K_s$ ) and high vulnerability to drought-induced embolism. ... shed their leaves before leaf water potentials declined below  $-2.0$  MPa" (Choat et al. 2005). "During the transition from wet season to dry season, total canopy area was reduced by 70–90% ... and stomatal conductance ( $g(s)$ ) and assimilation rate ( $A$ ) were markedly lower in the remaining leaves. ... maintained daytime leaf water potentials ( $\Psi_L$ ) at close to or above wet season values by a combination of stomatal regulation and reduction in leaf area. Thus, the timing of leaf drop ... was not associated with large negative values of daytime  $\Psi_L$  (greater than  $-1.6$  MPa) or predawn  $\Psi_L$  (greater than  $-1.0$  MPa)" (Choat et al. 2006).

### Association among traits and subgenera

To a considerable extent, variations in phenology and stem morphology within the genus correspond to variations between subgenera (table 1), traits that are largely independent of the basis upon which the infrageneric classification was derived (Guymer 1988). The four small subgenera (2–4 species each) each have a characteristic stem form (two subgenera being unusual – bulbous or columnar respectively, figs 4 & 5). Thickened branchlets are a feature of the subgenus *Oxystele* and, conversely, all species in subgenera *Poecilodermis* and *Delabechea* have slender (i.e. twiggy) terminal branchlets. However, the subgenera *Trichosiphon* and *Brachychiton* contain a diversity of branchlet forms.

Three subgenera have a characteristic flowering time; there is, however, considerable variation within subgenera in the occurrence and degree of deciduousness. The large subgenus *Brachychiton* is remarkably uniform in stem structure and in being fully deciduous, and all but one species (*B. discolor*) flower during the dry season (table 1). Within the latter subgenus, however, there is considerable variation in the relationship between the timing of leaf drop and the commencement of flowering, five species commencing flowering before leaf drop, thirteen species coincident with or soon after it, and two species two or more months after leaf drop.

Brevi-deciduousness early in the wet season occurs in two and possibly three species (*B. acerifolius*, *B. discolor* and possibly *Brachychiton compactus*), and with concurrent flowering at the same time. These three are from different subgenera (*Oxystele*, *Brachychiton* and *Delabechea* respectively) but have in common that they are the only species in the genus characteristic of sub-tropical and tropical climates with higher and relatively aseasonal rainfall, suggesting independent adaption to this environment.

'Classic' deciduousness in the dry season followed more or less immediately by flowering occurs in all subgenera except *Oxystele*, and all such species occur in the seasonal tropics or sub-tropics except for *Brachychiton obtusifolius*, which inhabits semi-arid regions.

## DISCUSSION

### Phenological theme and variation

Members of the genus *Brachychiton* at once display both a diversity of phenological patterns with respect to leaf re-

tention and its relationship to flowering, and some striking consistencies. A majority of species are deciduous during the dry season, shedding leaves in the early to mid dry season, and commencing flowering with leaf shed or soon thereafter, patterns that are clear notwithstanding the unavoidably coarse nature of the phenological data and corroborated by a number of species-specific studies (Hansman 2001, Choat et al. 2005, Bate & Franklin 2015). Variations in leaf retention include evergreenness and brevi-deciduousness early in the wet season, while flowering variously occurs before leaf shed, with or soon after it, long after it, or with leaf exchange early in the wet season. Similar variation in flowering schedules is evident in the genus *Adansonia* (baobabs), all of which have grossly enlarged trunks and are leafless during the dry season: two species flower while leafless, one with leaf flush and five while leafy (Baum 1995b). More generally, the relationship between flowering time and leafiness in deciduous species of the seasonally-dry tropics is highly variable (e.g. Singh & Kushwaha 2006).

This 'theme and variation' in phenology and morphology within *Brachychiton* is at once consistent with a degree of phylogenetic inertia (cf. Kochmer & Handel 1986) and/or commonalities in the environmental conditions encountered, and suggestive of adaptive evolution. There are no studies that directly appraise the adaptiveness of variation in the genus. However, that brevi-deciduousness early in the wet season with concurrent flowering occurs in two species from different subgenera but within a common climatic zone (less seasonal sub-tropics) strongly suggests that phenological adaption has occurred independently on multiple occasions.

Adaptiveness in flowering schedules relative to leafiness in the seasonal tropics is also suggested by the association of flowering when leafless with specialised pollinators (Janzen 1967, Bullock 1995). The pollinators of *Brachychiton* spp. are unknown, but the flowers of *B. megaphyllus* (flowers while leafless in the dry season) are visited by, and pollen carried by small 'trap-lining' honeyeaters (birds) and native bees (Franklin & Bate 2013). Within the genus *Adansonia*, the two species that flower while leafless are the only members of the section *Brevitubae* and are pollinated by nocturnal mammals. In contrast, *Adansonia* species that occur in Madagascar and elsewhere, and that flower while leafy, are pollinated by hawkmoths (Baum 1995b). Further, flowering in the dry season often yields seed drop at the beginning of the wet season, timing which may be optimal for prompt germination (minimising seed predation) and establishment of seedlings before dry conditions return (Pirani et al. 2009).

### Water storage

Direct evidence of water storage in *Brachychiton* is limited to two species, and of low wood density to one, with no contrary observations. However, the prevalence of expanded roots, stems and/or branchlets suggests that storage of water and/or carbohydrates is widespread in the genus. Such variation parallels the more dramatic variation in water storage structures within Madagascan *Euphorbia* (Evans et al. 2014). Horticulturists report that all *Brachychiton* species store water in the roots from a young age (Rathie 2014), though the basis for this claim is unclear. *Cochlospermum vitifolium*, a



member of a genus that is a close phenological and morphological analogue to *Brachychiton* – several species coexist with it – has thickened stems which store water that is used to support growth and reproduction whilst leafless in the dry season (Fallas-Cedeño et al. 2010). Madagascan baobabs (*Adansonia* spp.) store water in bulbous stems (Chapotin et al. 2006a) that are strikingly similar to those of *Brachychiton* subg. *Oxystele* (fig. 4), and use it to flush new leaves after a period of deciduousness (Chapotin et al. 2006b). Baobab seedlings store water mainly in roots and this facilitates drought survival (Randriamanana et al. 2012). Of relevance both to *Brachychiton* and *Adansonia*, co-occurrence within lineages of water storage in expanded roots and stems is near universal (Hearn et al. 2013).

Many *Brachychiton* species, therefore, can be placed in Borchert's (1994b) plant functional group of water-storing lightwood trees of the seasonally-dry tropics (Borchert 1994b); if the "seasonally-dry tropics" is loosely defined, then perhaps all species qualify. Further, many of its 31 species demonstrate a variety of associated traits including shallow root systems, drought sensitivity, early leaf shed and flowering with leaf drop, as identified in this study, and also mesic leaves (Guymer 1988, Franklin & Bate 2013). But as I have also demonstrated, there are also numerous exceptions with respect to the commencement of flowering with leaf drop. Another feature of the seasonally-dry tropics is a suite of deciduous trees which flower with leaf flush shortly *before* the first rains of the wet season (Bullock & Solis-Magallanes 1990, Bach 2002, Singh & Kushwaha 2006). These plants also require access to moisture which may come from stored reserves.

### Factors driving the timing of flowering

Plants (and animals) use cues (*proximal* factors) such as changes to day length, temperature and moisture status to trigger the physiological and molecular responses that underlie the onset of flowering (and other episodic events). The *ultimate* or ecological factors influencing these responses act by natural selection to optimise their timing, and thus fitness, by altering the nature and function of these responses (e.g. to photoperiod; Hut & Beersma 2011). It is a complication, however, that optimisation may be constrained by physiological limitations. For example, no matter how optimal dry season flowering may be for survival of seed and germinants, it is not possible if the plant is desiccated. In phenological studies, this complication appears at times to have prompted a conflation of correlation with causation, and of proximal with ultimate factors.

My evidence that the relationship between leaf drop and the onset of flowering in *Brachychiton* is far from consistent, and thus by strong implication that it is evolutionarily labile, is not consistent with proposition that plant rehydration triggered by leaf drop is a necessary cue to initiate flowering in water-storing tropical plants. Whilst there is evidence that some of water-storing plants initiate flowering in direct response to an improvement in moisture availability or status (Borchert 1994a, Díaz & Granadillo 2005), others clearly do not as shown by flowering at various times of the year. Water storage could render the purported link to leaf drop largely

irrelevant by maintaining a level of hydration throughout the dry season, though this may occur only with early leaf drop to avoid depletion of moisture reserves (Holbrook 1995).

Change to photoperiod (day length) and temperature are viable alternate cues for the initiation of flowering that should be considered for water-storing woody plants of the seasonal tropics (Holbrook et al. 1995). There is considerable evidence that plants are capable of detecting and responding to even the muted changes in photoperiod that occur in the tropics (Rivera & Borchert 2001, Rivera et al. 2002, Borchert et al. 2005, Williams et al. 2008), as there is also for other tropical organisms (e.g. Wikelski et al. 2000, Seth & Maitra 2010). Indeed, that leaf drop occurs very early in the dry season even before the cessation of rains and subsequent drop in soil moisture (in at least *B. megaphyllus*; Bate & Franklin 2015), suggests preemptive scheduling of leaf drop cued perhaps by day length. Rising temperature may induce leaf flush and the more-or-less concurrent flowering that is common in some tropical deciduous species (Vico et al. 2015). Change to day length and temperature as possible cues opens the potential for adaptive evolution unconstrained by physiology, and could explain the diversity of flowering patterns evident in *Brachychiton* and also *Adansonia*.

### CONCLUSION

I have demonstrated use of a taxonomic treatise to address biological and ecological questions by the extraction of patterns of diversification that reflect evolution within the genus. This marriage of the usually-discrete disciplines of taxonomy, natural history and ecology has considerable value and, I suggest, should be encouraged. The parallel taxonomic and ecological studies of *Adansonia* by Baum (e.g. 1995a, 1995b) provide an interesting example which have also here proved to be of value.

Deciduous water-storing tropical plants may be shallow-rooted and have mesic leaves and, as a result, be particularly prone to desiccation during an extended dry season (Holbrook 1995). As noted by Holbrook, this yields the paradox that these plants may need to drop their leaves early in the dry season in order to flower during the dry season. However, even where flowering immediately follows the improvement in plant water status that is caused by leaf drop, it does not follow that leaf drop is the cue for flowering. I have demonstrated that flowering in some species of *Brachychiton* does not follow leaf drop and thus that leaf drop is not universally the cue. Further investigation of the drivers of the phenological system of flowering while leafless in the tropical dry season would benefit from more rigorous consideration of the relationship between, and potential distinctness of phenological correlates, physiological processes and evolutionary drivers.

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