

The functions of foliar nyctinasty: a review and hypothesis

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ABSTRACT

Foliar nyctinasty is a plant behaviour characterised by a pronounced daily oscillation in leaf orientation. During the day, the blades of nyctinastic plant leaves (or leaflets) assume a more or less horizontal position that optimises their ability to capture sunlight for photosynthesis. At night, the positions that the leaf blades assume, regardless of whether they arise by rising, falling or twisting, are essentially vertical. Among the ideas put forth to explain the *raison d'être* of foliar nyctinasty are that it: (i) improves the temperature relations of plants; (ii) helps remove surface water from foliage; (iii) prevents the disruption of photoperiodism by moonlight; and (iv) directly discourages insect herbivory. After discussing these previous hypotheses, a novel tritrophic hypothesis is introduced that proposes that foliar nyctinasty constitutes an indirect plant defence against nocturnal herbivores. It is suggested that the reduction in physical clutter that follows from nocturnal leaf closure may increase the foraging success of many types of animals that prey upon or parasitise herbivores. Predators and parasitoids generally use some combination of visual, auditory or olfactory cues to detect prey. In terrestrial environments, it is hypothesised that the vertical orientation of the blades of nyctinastic plants at night would be especially beneficial to flying nocturnal predators (e.g. bats and owls) and parasitoids whose *modus operandi* is death from above. The movements of prey beneath a plant with vertically oriented foliage would be visually more obvious to gleaning or swooping predators under nocturnal or crepuscular conditions. Such predators could also detect sounds made by prey better without baffling layers of foliage overhead to damp and disperse the signal. Moreover, any volatiles released by the prey would diffuse more directly to the awaiting olfactory apparatus of the predators or parasitoids. In addition to facilitating the demise of herbivores by carnivores and parasitoids, foliar nyctinasty, much like the enhanced illumination of the full moon, may mitigate feeding by nocturnal herbivores by altering their foraging behaviour. Foliar nyctinasty could also provide a competitive advantage by encouraging herbivores, seeking more cover, to forage on or around non-nyctinastic species. As an added advantage, foliar nyctinasty, by decreasing the temperature between plants through its effects on re-radiation, may slow certain types of ectothermic herbivores making them more vulnerable to predation. Foliar nyctinasty also may not solely be a behavioural adaptation against folivores; by discouraging foraging by granivores, the inclusive fitness of nyctinastic plants may be increased.

Key words: foliar nyctinasty, anti-herbivory, plant defence, tritrophic interactions, trophic facilitation, nocturnal carnivores, leaf movements.

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I. INTRODUCTION

Those movements that plants undergo independently of the direction of the stimulus are collectively referred to as ‘nastic movements’. Nastic movements that occur in leaves, flowers, cotyledons (Darwin, 1880) or branches (Puttonen *et al.*, 2016; Zlinszky, Molnár, & Barrfod, 2017) in response to the arrival of dusk and dawn are ‘nyctinastic’ (from Greek *nux*, *nukt-* ‘night’ + *nastos* ‘pressed’). Foliar nyctinasty (FN), the topic of this review, is a plant behaviour characterised by a pronounced daily variation in leaf (and/or leaflet) orientation.

The leaves of plants exhibiting FN assume a more or less horizontal position during the day that optimises their ability to capture sunlight for photosynthesis. At night, the positions that the leaves assume, regardless of whether they arise by rising, falling or twisting, are essentially vertical. Although FN has attracted a modicum of interest from an applied perspective with regard to the optimal times for spraying fungicides (Augusto, Brenneman, & Culbreath, 2010) and herbicides (Sellers, Smeda, & Johnson, 2003), it is best known for its prominent role in the discovery of endogenous circadian rhythms (Bünning, 1931). Indeed, it is the chronobiological aspects of FN as well as the signal transduction mechanisms underlying such movements that have engendered the most interest from researchers (Ishimaru *et al.*, 2012). In marked contrast to our progress relating to the physiological mechanisms underlying FN, the question of the function of FN, the topic of the present review, remains largely unsettled.

II. BACKGROUND INFORMATION

FN, often referred to as the ‘sleep movements of leaves’, is one of the oldest problems in botany, dating back to antiquity (Pfeffer, 1875). Some early scientists held the opinion that FN was a true manifestation of plant sleep, a sentiment suggested, for example, by *Somnus Plantarum*, the title of Linnaeus’s contribution to the subject (Linnæo & Bremer,

1759). Even in its day, however, the notion that FN was an expression of plant sleep was contentious; in a published letter to Linnaeus, Hill (1762, p. iv) respectfully chided, ‘*The word Sleep, used on this occasion, will, I am afraid, appear to the judicious British eye, an affected, as well as improper term...*’ A century later Darwin (1880, pp. 280–281) echoed this view when he wrote, ‘*Hardly any one supposes that there is any real analogy between the sleep of animals and that of plants...*’ Even now, a quarter millennium after Linnaeus, no definitive evidence exists that plants are conscious, much less that they exhibit altered states of consciousness (e.g. sleep); thus, the admittedly less friendly term ‘foliar nyctinasty’ is preferred. Even the term ‘nyctinasty’, however, has its ambiguity: in some cases, it is used to describe only the nocturnal closure of leaves, while in others, such as here, it is used as umbrella term to describe both the closure of leaves near dusk and the re-opening of leaves near dawn.

In addition to Linnaeus, a second great mind attracted to the question of FN was Charles Darwin. It is a testament to Darwin’s (1880) genius that his *Power of Movement in Plants*, which he researched with the assistance of his son, Francis, a plant physiologist, remains, more than a century after its publication, a logical starting point for a modern discussion of FN. Darwin (1880) reported the occurrence of FN in plants from 79 genera of dicotyledonous angiosperms, including 48 genera of Fabaceae, and representing seven families.

It should be noted that in compiling his list Darwin arbitrarily chose as a working definition of FN, leaf movements of more than 60° from the horizontal. Less-stringent criteria, of course, would expand the list of nyctinastic species but the extent to which they would do so is uncertain since the frequency of species in which FN is slight or fickle in nature is probably underreported. That a grey area exists between nyctinastic and non-nyctinastic is attested to by Darwin’s (1880, p. 320) statement in reference to Linnaeus’ *Somnus Plantarum*, that ‘[Linnaeus] refers to some plants as sleeping, for instance, *Lathyrus odoratus* and *Vicia faba*, in which we could observe no movement deserving to be called sleep, and as no one can doubt the accuracy of Linnaeus, we are left in doubt’.

Since more than a century has passed since Darwin's (1880) survey, an updated list of over 200 genera reported to exhibit FN has been provided (see online Supporting information, Appendix S1). These genera occur in 38 families. It should be noted that the genera listed in Appendix S1 may not necessarily adhere to Darwin's (1880) criterion that the movements be more than 60°, and that the references supplied do not imply priority of discovery. In any case, as in Darwin's day, the family with the highest number of nyctinastic species by far is the legume family (Fabaceae) but FN is by no means limited to the Fabaceae or even the eudicots: FN is also found in an aquatic fern (*Marsilea*), a gymnosperm (*Abies*) and more than a few monocots.

Although taxonomic surveys of the occurrence of FN remain of interest, more light might be shed on the question of the function of FN by considering the taxonomically disparate species in which it occurs as a behaviour-based functional group. A striking feature of this functional group is its extreme heterogeneity in terms of its members' other attributes. Examples of FN can be found in plants adapted to xeric, mesic or aquatic environments, in species indigenous to tropical or temperate zones, and in forbs, shrubs and tall trees. This heterogeneity suggests that FN has arisen in different taxa by evolutionary convergence, an idea supported by several other lines of evidence.

First, there are two broad types of FN, pulvinate and non-pulvinate (Wetherell, 1990). In some species, FN movements are achieved by motor cells located in pulvini, the enlarged bases of leaf (or leaflet) stalks that undergo marked changes in turgor, leading to movements of the leaf or leaflet. FN can also occur in plants lacking pulvini; in these cases, FN arises from the differential growth of opposite sides of elongating leaf stalks (Wetherell, 1990). Since growth variations as well as pulvinate changes are associated with changes in turgor, the distinction between pulvinate and non-pulvinate FN may be a matter of degree and intra-plant localisation rather than a fundamental difference in mechanism (Rivière, Derr, & Douady, 2017).

Second, there appears to be an enormous variety in the biochemical mechanisms underlying FN (Ueda, Shigemori, & Sata, 2000). Ueda's laboratory has isolated leaf-opening and leaf-closing chemicals from a variety of nyctinastic plants, and the general lesson to be learned is that each plant genus seems to use a completely different suite of chemicals to effect foliar nyctinastic movements.

Third, species use different types of movements to achieve the nocturnal vertical orientation, bending either towards the abaxial side or toward the adaxial side or, more rarely, by twisting to the vertical plane. For example, in Darwin's (1880) list of nyctinastic genera, the leaves of 37 genera rose at night, whereas those of 32 genera sunk.

From an evolutionary perspective, it would seem that the direction of leaf movement used to effect FN is surprisingly labile. There are interesting cases of different species within a single genus exhibiting strikingly different types of nyctinastic movements. For example, in *Desmanthus bicornutus*, FN involves both the pinnae and the petioles moving downward

at night, whereas in *D. virgatus*, the pinnae and petiole both rise at night. The FN of a third *Desmanthus* species, *D. leptophyllus* is similar to that of *D. bicornutus* except that its leaves do not employ a pulvinate at the base of its petiole to achieve a collapsed condition at night but rather a downward arching of its rachis (Luckow, 1993). Other examples exist of congeneric species showing very different types of nyctinastic movements (Darwin, 1880, 1881; Harshberger, 1922; Hughes, 1998). Different types of nyctinastic movements can even be found in ecotypes of the same species: Lavin (1988) reported that in *Coursetia heterantha*, the leaves of the squat, rosette forms found at elevations above 2000 m undergo downward movement at night, while the lankier ecotypes from the lowlands demonstrate upward movement. Thus, it seems that FN has disappeared in certain lines and arisen anew over the course of evolution. The idea that leaf movements in general are evolutionarily labile gains immense support from the molecular phylogenetic evidence that seismonasty (shaking-induced movements) may have evolved independently in eight lineages of *Mimosa* alone (Simon *et al.*, 2011).

Some authors have attached theoretical importance to the general finding that the occurrence of FN in plants is closely correlated with those species' ability to perform other types of leaf movements, particularly photo-induced leaf movements (e.g. Forseth, 1990). As Darwin (1880, p. 281) noted, however, 'The leaves of some few plants move either upwards or downwards when the sun shines intensely on them, and this movement has sometimes been called diurnal sleep; but we believe it to be of an essentially different nature from the nocturnal movement...' Although there is a strong correspondence between the respective occurrences of photo-induced leaf movements and nyctinasty in plant species, this correspondence is not perfect. *Crotalaria semperflorens*, *Desmodium parviflorum* (Pearson, 1899), *Sophora alopecuroides* (Zhu *et al.*, 2015) and *Zornia diphylla* (Pearson, 1899; Rodrigues & Machado, 2008), for example, undergo photo-induced but not nyctinastic movements. Conversely, *Pycnospora hedysaroides*, *Alylosia candollei* (Pearson, 1899) and *Talinum triangulare* (Holdsworth, 1959) demonstrate nyctinastic but not photo-induced leaf movements. Other differences between photonasty and FN have been reported as well. Pearson (1899) noted that the diurnal, light-avoiding movement of the rachis of *Biophytum proliferum* occurs in a completely opposite direction from its nocturnal nyctinastic movement. Another interesting case is *Robinia pseudoacacia*, in which the respective motor activities underlying FN and photonasty occur in different parts of its compound leaves: FN is associated with changes in the angle between the petiolule and the leaflet blade, while photonastic reorientation results from changes in the angle between the petiolule and the rachis (Liu *et al.*, 2007).

Before discussing previous proposals concerning the function of FN, it is germane to address the question of just how critical FN is to plant survival. Thoughts concerning this matter cover the full range from FN being critical for survival (Ueda *et al.*, 2002) to FN serving no purpose whatsoever (Semon, 1905, 1908). Based on their finding that the chemical

inhibition of FN caused certain leguminous plants to wither and die, Ueda *et al.* (2002) concluded that FN was critical for the survival of those species exhibiting this behaviour. Unfortunately, the pharmacology of the chemicals that these researchers used to inhibit leaf movements is poorly understood, and their lethal effects could be unrelated to their effects on FN. Semon (1905, 1908), on the other hand, working from a Lamarckian perspective, suggested that FN was a 'genetic memory' of the movements that the plant's progenitors had made in response to diurnal changes in light and temperature. Since the Lamarckian viewpoint was long ago discredited, Semon's hypothesis is a historical footnote deserving no further discussion.

Given that most plant species do not exhibit FN, these movements clearly are not critical for plant survival in general. Rather, FN is likely a useful adaptation for those plants that exhibit it but one that has some energetic cost associated with it. Movement, after all, is a form of work, and work requires energy.

Based on the physiological and pharmacological similarities of pulvinar motor cells and the guard cells that regulate stomatal aperture, Gorton (1990, p. 223) suggested that a pulvinus could be usefully compared to 'a bunch of guard cells packed together'. The first proteomic study of pulvinar motor cells seems largely to support this idea (Lee *et al.*, 2014). Since there is a bioenergetic cost associated with guard cell swelling (Assmann & Zeiger, 1987), it seems a safe assumption that there is an energetic cost associated with the iterative movements that define FN. Whichever side of the pulvinus or petiole that loses turgor in the pre-dusk hours has to regain turgor in the pre-dawn. The returgescence (swelling) of the motor cells ultimately depends upon the activity of ATP-dependent H⁺ pumps (Ishimaru *et al.*, 2012). As such, there must be some benefit accrued to the organisms that display FN, but what is it? The next section reviews previous hypotheses concerning the *raison d'être* of FN.

III. PREVIOUS HYPOTHESES CONCERNING THE FUNCTION OF FOLIAR NYCTINASTY

Previous hypotheses have sought to explain FN as a physiological adaptation to abiotic factors, such as temperature, moisture or light, or as a direct defence against herbivory. Beginning with Darwin's (1880) hypothesis that FN is a mechanism for preventing heat loss from plants, these disparate hypotheses are discussed in turn.

(1) Improving the temperature relations of plants

Darwin (1880) suggested that FN may influence a leaf's net radiation balance both by reducing the exposure of the leaf blade to the cold night sky, and by increasing the leaf blade's exposure to laterally situated objects of greater warmth. Thus, Darwin viewed FN as a mechanism for avoiding frost (or chill) damage. In support of this idea, Darwin performed experiments which showed that *Oxalis* and *Trifolium* leaves

pinned down in a horizontal orientation suffered frost damage on clear autumnal nights while leaves pinned in a vertical position on the same plant showed little damage. He concluded that on clear nights vertical leaves are warmer than horizontal leaves and that the vertical orientation protects the leaves from frost damage during light frost.

There is no doubt that the ability of a plant to stay a fraction of a thermal degree above the threshold temperature for frost (or chill) damage might mean the difference between surviving or not. There is also experimental evidence suggesting that FN influences the temperature of plants albeit to a small extent. Schwintzer (1971) determined that horizontally placed soybean (*Glycine max*) leaves radiate more heat to space than vertically placed leaves but the effect on plant temperature was exceedingly small – less than 1°C.

Schwintzer (1971) cautioned, moreover, that Darwin's results may have arisen artefactually because the corks to which he pinned the leaves may have decreased convection. Another concern with Darwin's (1880) hypothesis is its applicability to all environments. Freezing conditions, for example, are never encountered in the tropics where the Fabaceae evolved and, for the most part, still make their home (Herendeen, Crepet, & Dilcher, 1992). In nature, most plant species live their entire lives within the limits of the upper and lower limits of their individual 'cardinal temperatures'. Individuals that suffer too much from drops in temperature are soon culled by that least solicitous of forces – natural selection. Of course, there may occasionally be a 'cold front of the century' that leads to the local mass death of a given plant species but there are usually reserves of dispersed seeds present that are poised to germinate in the wake of such a calamity. Moreover, it seems unlikely that any given species would have evolved a behavioural adaptation that would permit them to escape such freak weather, and that there must be a selective advantage in practicing this energetically costly behaviour nightly throughout the long, warm growing season.

Another difficulty with Darwin's (1880) hypothesis is that plant movements become ever feebler as the threshold temperature for injury is approached. For example, in pinto bean plants (*Phaseolus vulgaris*), no significant rhythm was found in the leaf movements at 10°C, and FN ceased within 1 day at 5°C (Hoshizaki & Hamner, 1969). Similarly, Gadeceau (1926) reported that the leaves of *Oxalis tetraphylla* remained open at night when the temperature was 5°C.

Although the considerations in the preceding paragraphs would seem to trivialise frost protection *per se* as the primary function of FN, it should be borne in mind that heat conservation caused by FN may benefit in a more substantive way a few species growing in unusual circumstances. Indeed, there can be little doubt that nyctinastic closure at night does affect the temperature relations of some equatorial montane plants that are routinely subjected to extreme diurnal swings in temperature as well as freezing temperatures almost every night (Smith, 1974; Beck *et al.*, 1982). For example, the leaves of *Espeletia schultzii*, a high-altitude shrub endemic to the Andes, close upward and inward at night giving the entire plant the

appearance of a giant bud. Smith (1974) provided evidence that formation of these 'night buds' results in a damping of the diurnal temperature fluctuations. When 'night-bud' formation was prevented by means of stiff wires, the nocturnal bud core temperature fell from 2.0°C to -0.3°C.

Although Darwin's ideas about FN as an adaptation to avoid freezing stress, except in the special case of tropical alpine plants, have not gained many adherents, they did inspire others to examine the question of whether FN enhances the temperature of plants within their individual cardinal temperatures. This revised version of Darwin's (1880) hypothesis proposed that FN may simply promote the growth of plants by keeping them a fraction of a degree warmer at night and thereby enhancing growth. Enright (1982) tested this hypothesis by constraining the primary leaves of *Phaseolus coccineus* in vertical or horizontal positions from dusk to dawn for a period of several days. In seeming support of this revised version of Darwin's hypothesis, leaves that were constrained in a horizontal position for the night grew at only 71–84% of the rate of vertically clamped leaves.

Although Enright's (1982) work is currently one of the more favourably cited studies concerning the function of FN, several aspects of his methodology deserve closer scrutiny. Plants are exquisitely sensitive to touch; even measuring leaves with a ruler can inhibit their elongation (Beardsell, 1977; Klaring, 1999). Enright (1982) assumed he had circumvented the problem of plants' acute sensitivity to handling by comparing vertically and horizontally clamped leaves that presumably had been handled equally. Although the handling of the plants during their initial shackling may have been similar, the pressures of the constrained plants against their bonds over the course of the long night were undoubtedly not the same: the horizontally restrained plants spent the night straining futilely to achieve a vertical posture, whereas the vertically clamped leaves rested comfortably in their normal nocturnal position. Although no plant biologist has apparently pondered the physiology of 'bean leaves in bondage', it is reasonable to speculate that the straining of plants in such circumstances might elicit an iterative train of mechanical responses throughout the period of bondage. Indeed, nyctinastic closure is not a smooth process, and may occur in a jerky manner (Darwin, 1880; Dun & Thakurta, 1959). It is conceivable that each jerk may elicit a mechanical response. Mechanical stress is known to elicit a travelling, growth-inhibiting signal in plants (Erner, Biro, & Jaffe, 1980; Coutand & Moulia, 2000). Thus, it is conceivable that inhibition of growth in horizontally clamped leaves may have less to do with differences in temperature than with differences in mechanical stress.

Finally, all hypotheses based on the idea that the *raison d'être* of FN is related to its effects on plant temperatures fail to explain why some submerged plants, including *Myriophyllum* (Wächter, 1909), *Limnophila* (Goebel, 1908), *Cabomba*, *Hydrophila* and *Rotala* (P. V. Minorsky, unpublished observations) also display FN. Because of the high volumetric

heat capacity of water as compared to air, the amplitude of diurnal temperature changes in a body of water is essentially nil compared to diurnal temperature changes on land. Clearly, FN is not an adaptation that affects the temperature relations of aquatic plants.

(2) Facilitating the shedding of water from leaves

Another explanation pertaining to the function of FN is that it is an adaptation for facilitating the shedding from leaf surfaces of water deposited by dew (Stahl, 1897) or rain (Dean & Smith, 1978). As one might expect, the leaf angle changes effected by FN do facilitate the shedding of water from leaves (Dean & Smith, 1978; Gitari, 1986). Dean & Smith (1978), for example, measured water runoff from horizontal ($\sim 0^\circ$) and inclined ($\sim 45^\circ$) *Machaerium arborium* leaflets. After nine minutes the upper surfaces of all the inclined leaves ($N = 10$) were dry compared to only two (20%) of the horizontally placed leaves. While the matter requires more systematic study, it would appear that the leaf angles associated with the nocturnal positions of nyctinastic plants might be expected to hasten the shedding of water from leaf surfaces by tens of minutes, perhaps as much as an hour or more.

No consensus exists, however, as to why the nocturnal shedding of leaf surface moisture is beneficial to the plant. In the daily life of the plant the major effect of leaf wetness is to impede photosynthesis: this is because CO₂ diffuses about 10000 times more slowly through water than air (Smith & McClean, 1989). Although it might be assumed that the orientation of leaves at night would have no bearing on photosynthetic production, Forseth (1990) has pointed out that in the case of dew, surface wetness may cause a short-lived reduction in photosynthesis during the very early morning before the leaf surfaces dry completely (Forseth, 1990).

Because leaf surface moisture during the day inhibits photosynthesis, plants inhabiting rainy terrestrial environments have evolved a variety of adaptations, such as smooth cuticles, non-horizontal leaf angles, certain forms of pubescence, and drip-tips, for quickly shedding water from their foliage. Unlike FN, these anatomical adaptations for reducing leaf wetness are effective night and day. Of course, if nocturnal rainfall were especially problematic in certain environments such as tropical rainforests, it is possible that a strictly nocturnal ancillary mechanism, such as FN, might confer an additional selective advantage. But nocturnal rainfall is not especially common in the tropics. Most tropical regions have a fairly predictable cycle of weather dictated by temperature and humidity. Early morning mists (caused by cooling at night) evaporate as the sun rises, and by late morning these convection currents begin to rise from the forest. Clouds form and by late afternoon these have often turned to storm clouds (Park, 2002). The convective rainstorms that ensue are generally intense but of short duration. Late afternoon rain is more common than nocturnal rain in most inland parts of the tropics and sub-tropics (Yang & Smith, 2006).

Anatomical adaptations for shedding leaf moisture represent for plants a one-time investment of energy per leaf, unlike FN, which is a daily, recurring investment. Insofar as investments go, FN does not appear to be a particularly efficient water shedding mechanism. For example, it has been a general finding that the adhesion of water to leaf surfaces increases as the leaf ages (Neinhuis & Barthlott, 1998), possibly because older leaves are typically more heavily colonised by epiphytes or have suffered losses of epicuticular wax because of high precipitation totals and greater longevity (Knoll & Schreiber, 2000; Holder, 2007). Given these considerations, one might reasonably hypothesise that there would be selective pressure to ‘fine tune’ FN so that the older leaves are more strongly nyctinastic than the younger: in fact, it is generally the younger leaves of nyctinastic plants that undergo the most pronounced movements (Cunningham, 1895; Yin, 1941).

Hypotheses that propose that FN is an adaptation for shedding water from leaf surfaces raise the question of why having wet leaves at night is disadvantageous to plants. Dean & Smith (1978) provided a list of four ideas why water retention on the leaf surface at night could be maladaptive: (i) a reduction in transpiration in poorly drained leaves may slow growth rates by reducing the rates of nutrient uptake and transport (also proposed by Stahl, 1897); (ii) prolonged wetness may enhance the leaching of minerals from leaves; (iii) the weight of the water retained on leaves may necessitate more energy investment in support tissue; (iv) a lingering wet film, especially if it contains ions, may provide a more favourable habitat for pathogens and light-intercepting, foliar epiphytes. These ideas are discussed in turn below.

(a) Reducing nocturnal transpiration

The idea that FN benefits plants by reducing leaf wetness can be traced to Stahl (1897), who considered FN to be a means for preventing the accumulation of dew on leaf surfaces. He proposed that dew may be injurious to plants inasmuch as it slows transpiration so long as the leaves are wet. A low rate of transpiration, he reasoned, would lower the uptake of mineral salts by the roots, which would be disadvantageous to the plant.

One weakness inherent in Stahl’s explanation is that there is relatively little transpiration at night since the stomata of plants are typically closed. Of course, there is a growing appreciation that some plants do transpire at night albeit at a rate only 5–15% of that during the day (Caird, Richards, & Donovan, 2007; Forster, 2014). Nocturnal transpiration is a poorly understood phenomenon but it can be significant in some species. Caird *et al.* (2007) provide a list of almost 60 genera in which nocturnal transpiration occurs, but species exhibiting FN are not disproportionately represented in this list. A second problem with Stahl’s hypothesis is that there is little experimental support for the idea that transpiration benefits plants by enhancing nutrient supply (Tanner & Beevers, 2001; Christman, Donovan, & Richards, 2009; however, *cf.* Matimati, Verboom, & Cramer, 2014).

Contrary to Stahl’s idea that FN might enhance nocturnal transpiration to the benefit of the plant, it appears that a reduction of nocturnal transpiration by FN may, in fact, be useful to certain plants endemic to xeric environments (Gadeceau, 1926; Luckow, 2002). Some researchers have noted a correspondence between the stomatal distribution of leaflets and their method of nyctinastic folding (Erban, 1916; Luckow, 2002). Luckow (2002), for example, noted that in members of the dry-adapted *Dichrostachys* group of legumes, the leaflets fold in such a manner that only the abaxial surface is exposed, the stomata-rich adaxial surface thus being covered at night. Luckow (2002) further noted that many *Dichrostachys* species have stomata confined to a particular region of the leaflet, and that these regions are precisely those that are covered by a neighbouring leaflet when the leaf assumes its nocturnal position. Thus, in plant species adapted to xeric conditions, FN may actually help to reduce water loss at night (Gadeceau, 1926; Luckow, 2002).

(b) Reducing the leaching of minerals from leaves

Foliar leaching is broadly defined as the removal of substances from plant leaves by action of rain, dew, fog or leaf washing (Tukey, 1970). It is not clear, however, from a plant’s perspective whether foliar leaching is beneficial or detrimental. Some researchers have considered foliar leaching to be an excretion process by which waste products or possibly allelochemicals are eliminated. Indeed, much of the leachate apparently derives from hydathodes and glandular trichomes (Tukey, 1970).

It is also not clear that prolonged leaf wetness leads to more leaching than short-duration wetness. Mecklenburg (1964) reported that leaves need only to be wetted for leaching to occur: increasing the volume of the leaching solution had very little effect on the total amounts of cations leached. Thus, the rapidity with which leaves dry would seem to have little effect on the amount of foliar leaching. Finally, if the amelioration of foliar leaching was the *raison d’être* for FN, one would expect the older leaves, from which nearly all the leachates derive (Cholodny, 1932; Arens, 1934), would have the most dramatic nyctinastic leaf movements but in the case of the pulvinate FN of *Cassia sumatrana* (Cunningham, 1895) and *Oxalis* spp. (Gadeceau, 1926), and the non-pulvinate FN of *Carica papaya* (Yin, 1941) and *Linum usitatissimum* (Ahktar, 1974), the opposite occurs. The water-shedding hypothesis also fails to explain the occurrence of FN in aquatic plants.

(c) Reducing the need for leaf support tissue

Dean & Smith (1978) provide no evidence to support their speculation that plants exhibiting FN allocate less energy towards the production of support tissue. It is also unclear whether any energetic savings stemming from reduced support tissue would outweigh the daily energetic cost of FN. Of course, support tissues do fail in nature but they do so under extraordinary circumstances. Those who have studied

mechanical leaf failure in nature cite not mundane forces such as rain but rather falling debris (leaf fronds and branches) or extreme weather (e.g. hurricanes) as the primary cause of mechanical failure in leaves (Chazdon, 1986). Leaves have invariably been moulded by natural selection to withstand ordinary mechanical stresses, for example, the weight of a tree frog or a gecko or a perching bird, that are orders of magnitude greater than the weight of adhering rainwater. Rain simply does not cause leaves to be shed unless the leaves are damaged, sick or dying, in which case, their abscission is probably beneficial.

(d) *Preventing the growth of epiphylls and fungal pathogens*

Dean & Smith (1978) proposed that nyctinastic leaves by virtue of their quicker drying properties might suffer less from shading epiphylls than do non-nyctinastic leaves. However, if one considers another morphological adaptation that drains leaf surfaces more quickly, namely drip-tips, the evidence suggests that the quicker drying of leaves has no demonstrable effect on the colonisation of the leaf surface by epiphylls (Ivey & DeSilva, 2001; Lücking & Bernecker-Lücking, 2005; Burd, 2007). Moreover, the common assumption that epiphytes are disadvantageous to plants because they block light absorption by host leaves has not been borne out by experimentation (Roskoski, 1981; Anthony, Holtum, & Jackes, 2002).

A possibly more tenable hypothesis is that nyctinastic leaves, by virtue of their quicker drying properties, might suffer less from foliar pathogens. Some support for this idea comes from Ivey & DeSilva's (2001) observation that the removal of drip-tips from tropical understorey trees reduced the rate of water removal from leaves and led to a 1.7-fold increase in the occurrence of fungi on the surface of the leaves. Unfortunately, given the complexity of the phyllosphere community that includes, from the plant's perspective, both friend and foe, it is too simplistic to assume that the greater occurrence of fungi on the surface of the leaf is necessarily a harbinger of imminent disease and death. Not all phyllospheric fungi are harmful (Jayapal Gowdu & Balasubramanian, 1988). Phyllospheric yeasts, for example, may protect the plant against phytopathogens by successfully competing for nutrients (Fokkema *et al.*, 1979) or producing defence chemicals (McCormack, Wildman, & Jeffries, 1994).

The above considerations aside, the duration of leaf wetness is generally recognised as an important factor in the development and outbreak of plant diseases because many phytopathogens require a layer of free water for successful infection (Cook, 1980; Huber & Gillespie, 1992; Bradley, Gilbert, & Parker, 2003; Rowlandson *et al.*, 2015). The infection efficiencies of pathogens on wet leaves typically increase sigmoidally over time (Spotts, 1977; Gross *et al.*, 1998). Conceivably, if FN could reduce leaf wetness duration during the exponential phase of these curves, FN might be effective in reducing pathogen infection, especially if fungal spores are more plentiful at night (Gilbert & Reynolds, 2005). This raises the question of just how effective FN is in decreasing the duration of leaf wetness relative

to other leaf adaptations. Compared to leaf smoothness and hydrophobicity, leaf angle is of surprisingly minor significance in facilitating the shedding of agricultural sprays (Wirth, Storp, & Jacobsen, 1991) and water (Holder, 2012) from leaves.

(3) **Reducing moonlight-induced disruption of photoperiodism**

Bünning & Moser (1969) expressed the view that FN is particularly pronounced in 'short-day' plants that require uninterrupted darkness of a critical length in order to flower, and based on this premise for which they offer no evidence they proposed that FN might serve to protect the photoperiodic timekeeping system from moonlight since lunar irradiance during the night might interfere with the accurate measurement of night length in short-day plants. This hypothesis was tested by Kadman-Zahavi & Peiper (1987) and largely rejected, the authors concluding (p. 621), 'that in the natural environment moonlight may have at most only a slight delaying effect on the time of flower induction in short-day plants'. Also, contrary to Bünning & Moser's (1969) hypothesis are field observations to the effect that under brightly moonlit nights, the nyctinastic movements of some FN plants undergo anomalous reversals in the middle of the night (Ulrich, 1911; Gates, 1923).

(4) **Bitrophic interactions**

Grubb & Jackson (2007) suggested that the apposition of the leaflets during FN makes foraging more difficult for nocturnal herbivores. Of all the hypotheses discussed so far, this hypothesis is closest to the tritrophic hypothesis presented herein in that it views FN as a behaviour that deters herbivores. Unlike the tritrophic hypothesis, however, Grubb & Jackson (2007) focus on bitrophic interactions, namely how folded leaves might affect the access to and handling of leaf material by small folivores. Another difference between the two hypotheses is that the tritrophic hypothesis is not limited to folivores. For example, by facilitating the killing of granivores (e.g. rodents) by nocturnal birds of prey (e.g. owls), FN may also increase a plant's inclusive fitness.

Some other possible bitrophic interactions relating to leaf movements and herbivory are suggested by hypotheses concerning the *raison d'être* of the very rapid leaf movements executed by a few plant species such as *Mimosa pudica* in response to wounding, shaking or touch. Bose (1926), for example, proposed that the rapid closure of *Mimosa pudica* leaves in response to grazers might render the plant less obvious and, therefore, less appetizing to large herbivores. In regard to *Mimosa* he noted (p. 200), 'Nothing could be more striking than the rapid change by which a patch of vivid green becomes transformed into thin lines of dull green unnoticed against the dark ground. The plant thus saves itself by literally 'lying low' and becoming invisible'. It is possible that FN, by effecting a similar decrease in noticeability, may reduce herbivory, especially under crepuscular conditions.

Eisner (1981), on the other hand, suggested that the leaf movements of *Mimosa microphylla* (formerly *Schrankia microphylla*), including FN, may serve an aposematic function, by making the recurved prickles (not thorns as stated) lining its stem, petiole and rachis, more visible to herbivores. He envisioned that such ‘baring of claws’ might deter browsing by large mammals and also reduce trampling. In general, however, small, unidirectional, recurved prickles, such as those found on *M. microphylla*, are not major deterrents to large, browsing herbivores but rather serve as deterrents to the movements of small crawling insects which presumably would be less influenced by the more macroscopic changes in visibility effected by FN (Vermeij, 2015). Moreover, if the greater visibility of spinous processes is the overarching strategy of a given plant’s defence, would there not be a selective pressure in having such processes always visible? This would seem to be the strategy of the touch-sensitive *Mimosa pigra* leaf that has long, formidable, and obvious spines lining its rachis and jutting at right angles from the leaf’s surface.

FN may indeed serve as a deterrent to herbivores by making it more difficult to see access or handle leafy fodder. However, such bitrophic interactions between plants and herbivores do not contradict but complement the tritrophic hypothesis discussed next.

IV. THE TRITROPHIC HYPOTHESIS

To understand plant/herbivore interactions, it is necessary to consider tritrophic mechanisms in addition to bitrophic ones. To quote Price *et al.* (1980, p. 41), ‘... plants have many effects, direct and indirect, positive and negative, not only on herbivores but also on the enemies of herbivores. The third trophic level must be considered as part of a plant’s battery of defenses against herbivores’. Given that FN occurs in tropical plants and temperate plants, in small herbs and large trees, and in desert, mesic and aquatic plants, it is difficult to conceive of a major abiotic parameter such as water, temperature or light that might serve as the driving force for the convergent evolution of FN. Is it possible that FN has evolved in many cases as a plant defence against herbivory?

According to one recent analysis, on average, 5.3% of leaf biomass in vascular plants is consumed annually by herbivores (Turcotte *et al.*, 2014). The effects of folivores on plant production and fitness, however, extend beyond the quantity of biomass removed because folivory alters photosynthetic rates at a considerable distance from the damaged tissue (Zangerl *et al.*, 2002). Herbivore damage also induces some plants to divert resources from growth to defence (Coley, 1986). Additionally, the wounding of plant tissue by herbivores opens up portals for infection by pathogens. It is not surprising therefore, that the exclusion of nocturnal primary carnivores has been found to decrease plant productivity (Ward & Newman, 2006; Kalka, Smith, & Kalko, 2008; Williams-Guillen, Perfecto, & Vandermeer, 2008).

FN is not a universal behaviour shared by all plants. The Fabaceae, the third largest family of plants, is notable for the high incidence of FN amongst its members. Grubb & Jackson (2007) suggested that the unusually high incidence of FN in the Fabaceae may be related to the high nitrogen (N) titres of their leaves. Although it is often assumed that the high N titre of legume leaves is related to the symbiotic associations that nodulating legumes form with N₂-fixing rhizobial bacteria, in fact, N-rich leaves are typical of both nodulating and non-nodulating legumes (McKey, 1994). The advantage of N-rich leaves is that they have higher photosynthetic rates, assuming there are no other limitations to carbon assimilation. Thus, under favourable conditions of temperature, water and light, such as are found in the tropics where the Fabaceae are believed to have evolved, the N-rich leaves of legumes are more productive than the leaves of plant species with lower N concentrations.

There is a drawback to having leaves (and seeds and fruits) with high N titres: since the N content of fodder is often a major determinant of food quality (Mattson, 1980; Minkenberg & Fredrix, 1989; Kursar & Coley, 2003), leaves with high N titres are especially desirable to many types of herbivores. Although the legumes, in general, are well-defended against generalist herbivores by their chemical defences, they do suffer herbivore damage. There is, for example, no shortage of insects whose common name includes a legume (Mexican bean beetle, cowpea aphid, pea moth, bean leafroller, pea thrip, *etc.*). Indeed, insect pests are considered to be the main factor limiting legume production in the tropics (Singh & van Emden, 1979). In any case, as formidable as the chemical arsenals of legumes may or may not be, as Agrawal (2011, p. 420) has noted, ‘Essentially all plants employ several different lines of defence against herbivory’.

The tritrophic hypothesis of FN suggests that by facilitating hunting by nocturnal carnivores, FN constitutes an indirect plant defence against nocturnal herbivores. It is argued that FN indirectly discourages herbivory in two ways: (i) by facilitating the killing of herbivores by nocturnal predators, and (ii) by hindering the foraging behaviour of herbivores. An additional consequence of this second point is that if herbivores are spending less time foraging amidst nyctinastic species, they are presumably spending more time foraging amidst non-nyctinastic competitors.

(1) Facilitating hunting by nocturnal predators and parasitoids

Given nature’s diverse menagerie of nocturnal predators as well as the myriad ways in which they hunt, it is not feasible to consider every theoretical implication of the tritrophic hypothesis. Therefore, the following discussion focusses on four specific mechanisms by which FN might facilitate the nocturnal hunting of various herbivores; the reduction of physical clutter, the reduction of acoustical clutter, the enhancement of nocturnal light penetration, and the reduction of turbulence during the dispersion of volatile plumes.

(a) Reducing physical clutter

The nocturnal folding of leaf blades transforms the physical landscape of the canopy. Viewed from above, the pattern of vegetation is transformed from a diffuse pattern to a more punctate one: between these points are enhanced interstices that could presumably serve as effective ‘kill zones’ for many nocturnal predators. The reduction in vegetative clutter effected by FN would neither occur at every spatial scale nor in every vector but for relatively large terrestrial predators such as bats and owls whose *modus operandi* is death from above, FN could conceivably facilitate their ability to detect, identify, approach and subdue prey (Brigham *et al.*, 1997; Ciechanowski *et al.*, 2007). Depending on the size and density of the stand of nyctinastic plants, FN might also facilitate prey capture by predators operating in the horizontal plane. If the stand is not too dense, nocturnal prey that are small enough to hide behind the more columnar, nocturnal profiles of nyctinastic plants may escape detection by predators, while larger prey whose bodies protrude into the interstices may be more vulnerable.

Physical clutter is detrimental to the foraging of many predators. In some cases, clutter can lead to physical injury to less-adroit predators (Holt & Layne, 2008). Even for more dexterous predators, there is an energetic cost associated with following the circuitous paths of attack necessitated by physical clutter as well as a diminished percentage of successful strikes. Rainho, Augusto & Palmeirim (2010), for example, found that ground vegetation clutter greatly reduced the access of the greater mouse-eared bat (*Myotis myotis*) to prey, affecting both capture success and time to capture. Bats detected prey in the dense vegetation but did not attempt to capture them or did so only after a prolonged delay. The bats’ attempts often failed, because the bats landed over prey with open wings, and the dense vegetation prevented them from reaching the ground. A second example of clutter decreasing the foraging success of nocturnal predators is the finding that the average mass of the stomach quantities occurring in juvenile bluegill sunfish (*Lepomis macrochirus*) decreased as plant density increased even though more potential prey occur in dense stands of vegetation (Harrel & Dibble, 2001).

FN might also indirectly and negatively impact the speed of herbivorous ectotherms traversing the interstitial ‘kill zones’ making them easier targets for predators. This is because the larger gaps in the canopy resulting from nyctinastic leaf movements would cause more radiative heat loss from the ground to the night sky, thereby lowering the temperature between plants, and, hence the speed of ectotherms.

(b) Reducing acoustical clutter

FN would also be expected to reduce ‘acoustic clutter’ in the vertical vector. Since vegetation is known to absorb acoustic energy (Martens & Michelsen, 1981; Price, Attenborough, & Heap, 1988), nocturnal predators, such as bats and owls, should be better able to detect sounds (and echoes) made by

prey without baffling layers of foliage to damp and disperse the signal (Arlettaz, Jones, & Racey, 2001).

(c) Enhancing light penetration

FN, by increasing light penetrance through the canopy, would also effectively ‘shine light’ on the hiding places and transit paths of potential prey. Augusto *et al.* (2010), for example, studying peanut (*Arachis hypogaea*), noted that as a result of night leaf folding, the otherwise thick canopy becomes sparser to such a degree that even the soil surface is often visible. Karve *et al.* (1984), also studying peanut, found that during the daytime, when the leaves were horizontally situated, only 10% of the incident light reached the ground but at night, when the leaves assumed a vertical position, 70–90% of the incident light penetrated. Similarly, Kraatz & Anderson (1980) calculated that FN in sicklepod (*Cassia obtusifolia*) resulted in a nightly sevenfold reduction in the leaf area observed from a vantage point directly above the plant. It is reasonable to propose, therefore, that the movements of prey beneath a plant with vertically oriented foliage would be visually more obvious to a gleaner predator under crepuscular or nocturnal conditions. Even modest increases in night illumination enhance prey capture rates by many nocturnal carnivores (Dice, 1945; Gardner, 1981).

(d) Reducing turbulence within odour plumes

Under the low-light conditions of night, odours and other volatiles grow in importance as predatory cues. Parasitoid wasps, and some nocturnal predators, rely heavily on herbivore-induced plant volatiles to locate prey. The spatial matrix of volatiles within which predators locate their hosts consists of assemblages of odour plumes (volatile mosaics) scattered across space. The structural complexity of vegetation can potentially decrease the spatial information provided by such volatile mosaics by enhancing the mixing of odour plumes (Randlkofer *et al.*, 2010; Aartsma *et al.*, 2017). Odour plumes in contrasting habitats have different shapes and sizes due to differences in wind speed and turbulence (Finelli *et al.*, 2000; Murlis, Willis, & Cardé, 2000). Even modest changes in wind speed can affect insect foraging behaviour (Leonard, McArthur, & Hochuli, 2016). Thus, FN, by reducing vegetative clutter, would allow odours released by potential prey to disperse more directly to the awaiting olfactory apparatus of predators.

(2) Indirect effects of foliar nyctinasty on the lunar phobia of small predators

Another environmental influence besides FN that enhances the nocturnal light reaching the ground is the occurrence of the full moon. The phase of the moon affects animals differently depending on whether they are predators, prey or both. When high levels of light penetrate the canopy on the brightest of moonlit nights, small carnivores, such as insectivorous bats (Lang *et al.*, 2006; Ciechanowski *et al.*, 2007) or ichneumonid wasps (Short, Schmidt, & Steinbauer,

2006), that are themselves at risk of predation, are less active or avoid more open areas, a behaviour called 'lunar phobia'.

The intensity of moonlight also affects nyctinastic behaviour. Ulrich (1911, p. 226), in a field study of FN in the Oxalidaceae, noted in the case of *Oxalis stricta*, that, 'A very singular series of risings was observed on five successive nights about the middle of August. Instead of waking at 3 A.M., it started to rise at 11 P.M. The rising was gradual until about half the day angle was reached: there it remained until 7 A.M. These nights were brightly lit up by the full moon, and the regularity with which it occurred forced one to believe that it was due to the light of the moon'. Similarly, Gates (1923) reported that several tropical leguminous trees in the Philippines, most dramatically *Gliricidia sepium*, anomalously open their leaves in the middle of the night when the moon was particularly bright, and Harshberger (1922, p. 146), studying FN in *Trifolium* spp., expressed the view that, 'Some changes in the curves of the night period suggest that it might have been advisable to have data on the times and intensity of the moonlight'.

The unusual leaf movements that occur during brightly moonlit nights are antithetical to all previous hypotheses concerning the function of FN. The tritrophic hypothesis, however, offers a simple explanation for these anomalous movements: they may serve to protect primary consumers (e.g. insectivorous bats) from becoming the prey of secondary consumers (e.g. owls). Although light is known to induce leaf opening (photonasty), reorienting leaves to the diurnal position in the middle of the night serves no purpose insofar as carbon assimilation is concerned; even at its brightest, moonlight has no effect on photosynthesis (Raven & Cockell, 2006). Since these anomalous movements expend energy and have no effect on light capture for photosynthesis, they would have to be viewed, outside the context of the tritrophic hypothesis, as maladaptive. It would be interesting to determine whether species that demonstrate nyctinastic but not photonastic movements (Pearson, 1899; Holdsworth, 1959) also display these anomalous movements during brightly moonlit nights.

(3) Foliar nyctinasty and the foraging behaviour of herbivores

For many animals, foraging represents a trade-off between maximizing energy intake and avoiding predation. Numerous field studies have shown that vegetation-covered microhabitats are typically considered safer than open microhabitats for small mammals in a wide variety of ecosystems (Kotler, Brown, & Hasson, 1991; Manson & Stiles, 1998). Not only do many rodents use the cover of vegetation to move from one food patch to another but they spend more time securing food while under the cover of vegetation (Taraborelli, Dacar, & Giannoni, 2003; Orrock, Danielson, & Brinkerhoff, 2004). Rodents that feel threatened due to enhanced exposure spend more time being vigilant and consequently less time foraging (Brown *et al.*, 1988; Abramsky, Rosenzweig, & Subach, 2002). Another behavioural strategy used by nocturnal rodents exposed to too much nocturnal illumination is to carry food back to safer

locales instead of eating it in the field. This, too, limits how much they can eat (Vásquez, 1994). Finally, by encouraging small herbivorous mammals, by a reduction in safe choices, to forage and travel amidst non-nyctinastic competitors, FN also affords a competitive advantage to those plants that exhibit it.

V. FUTURE DIRECTIONS

In principle, it would seem an easy matter to tease out the function of FN if suitable controls lacking the ability to undergo FN existed. Progress would be expedited by the establishment of a 'toolbox' for tackling ecological questions related to FN. Although some progress has been made in identifying mutants (Kawaguchi, 2003; Hartati *et al.*, 2008; Chen *et al.*, 2012; Zhou *et al.*, 2012; Gao *et al.*, 2017) that lack FN, it is unclear if the mutations underlying these reductions in FN are free from pleiotropic effects. Another approach might involve more systematic comparison studies of large genera such as *Trifolium* (Harshberger, 1922), *Mimosa* (Simon *et al.*, 2011), *Cassia* (Lasseigne, 1978) and *Oxalis* (Steckbeck, 1919; Gadeceau, 1926) that are adapted to a wide range of ecological milieux, and whose members show considerable diversity in their leaf movement behaviours. A few genera, such as *Andira* (Pennington, 2003; Rodrigues & Machado, 2008) or *Coursetia* (Lavin, 1986), that have both nyctinastic and non-nyctinastic members, might also prove beneficial in studying the function and genetics of FN.

Another useful approach towards gathering data from natural experiments concerning the ecological function of FN would be to bring to bear remote sensing technologies such as light detection and ranging (LiDAR). Indeed, LiDAR has previously been used to measure many parameters relevant to testing the tritrophic hypothesis, including leaf angle inclination (Hosoi & Omasa, 2015), avian species diversity, density and occurrence (Clawges *et al.*, 2008), and the relationships between birds (Bradley *et al.*, 2005; Müller, Stadler, & Brandl, 2010) and bats (Froidevaux *et al.*, 2016) *versus* vegetation structure. It might be possible, for example, to test whether aerial predators hunt more actively at night over stands of nyctinastic *versus* non-nyctinastic plants.

VI. CONCLUSIONS

(1) FN is an evolutionarily labile plant behaviour of unequal occurrence in a wide range of taxonomically and ecologically distinct plants. It is especially pronounced and prevalent in the legume family (Fabaceae).

(2) Many hypotheses have been put forth to explain the function of FN but the most plausible of these hypotheses can only explain the benefits of FN with reference to small subsets of plants.

(3) The especially high prevalence of FN in the Fabaceae may be related to the elevated levels of nitrogen in the leaves and seeds of these plants that may make them especially desirable food sources for many herbivores.

(4) The tritrophic hypothesis proposes that FN is a plant behaviour that facilitates the hunting of nocturnal herbivores by reducing clutter (physical and acoustical), increasing light penetrance, and improving the directionality of odour plumes.

(5) A strength of the tritrophic hypothesis is its potentially broad applicability to non-marine ecosystems in all parts of the world, ranging from xeric to mesic to aquatic. It is also applicable to plants of all sizes.

(6) Modern remote-sensing technologies such as LiDAR might prove useful in testing the tritrophic hypothesis.

VII. REFERENCES

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VIII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. List of genera reported to exhibit foliar nyctinasty.

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