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Plants that lead: do some surface features direct enemy traffic on leaves and stems?

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Land plants exhibit a wide variety of defences that deter the consumption of leaves and stems, including trichomes (hairs), thorns, and thick cuticles. In many plants, trichomes are hooked or inclined to the leaf or stem surface, and the teeth on leaf margins point either apically or more rarely toward the base. The role of these anisotropic structures as potential defences has been largely ignored. In the present study, it is proposed that apically oriented surface features function as ratchets directing the movements of small herbivores toward the leaf ends and ultimately off the leaf, whereas basally oriented protrusions interfere with the ascent of consumers to the upper parts of the plant. These proposed defencive functions do not exclude other potential benefits of anisotropic features, such as self-cleaning of surfaces. The proposed defencive role of apically oriented trichomes and teeth may represent an unusual class of physical defences that speed up rather than slow down encounters between enemies and their plant victims. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, **116**, 288–294.

ADDITIONAL KEYWORDS: anisotropy – defence – herbivory – water repellence.

INTRODUCTION

As stationary organisms, plants offer abundant and accessible food for legions of herbivores, ranging from small arthropods to large vertebrates. Intense natural selection as a result of consumers has led to the evolution of a bewildering array of defences for vegetative organs, especially stems and leaves. The most intensively studied countermeasures to herbivory are secondary metabolites, although most plants also possess structural and sometimes animal-assisted deterrents (Sack *et al.*, 2008).

Structural properties that slow down herbivores or make tissues less accessible include spininess, abrasiveness as a result of silica, pubescence as a result of nonglandular hairs (trichomes), hidden meristems, stickiness, toughness, small leaf size, and high-angle branching with leaves inside a welter of twigs (Corner, 1964; Levin, 1973; Johnson, 1975; Brown, Lawton & Grubb, 1991; Díaz *et al.*, 2007; Hanley *et al.*, 2007). Waxes and high leaf mobility (fluttering in the wind) cause small arthropods to lose their grip and fall off (Jeffree, 1986; Bernays, 1991; Yamazaki,

2011). Network leaf venation provides a redundancy of function when damage does occur (Vermeij, 2004).

One category of potential structural defences of plants that has received very little attention comprises the trichomes, spines, scales, and marginal teeth of serrations that are either hooked or oriented at an acute angle to the leaf edge, leaf surface or stem. These anisotropic projections point either apically toward the top of the plant or the distal ends of the leaf, or downward toward the base. Their general effect is to act as a ratchet, favouring the movement of animals, fluids or the plant itself in one direction more than in other directions (Wolgemuth, 2009; Hancock, Sekeroglu & Demirel, 2012). Anisotropic structures in plants have been shown to promote the burial of seeds in soil (Kulić *et al.*, 2009), to allow climbing plants to initiate attachment and cling to neighbouring plants (Schenck, 1892; Haberlandt, 1914; Putz, 1984, 1990; Krings & Kerp, 1999; Bauer *et al.*, 2011), to trap or puncture small arthropods (McKinney, 1938; de Fluiter & Ankersmit, 1948; Johnson, 1953; Schillinger & Gallun, 1968; Gilbert, 1971; Pillemer & Tingey, 1976, 1978; Sutherst & Wilson, 1986; Quiring, Timmins & Park, 1992), to guide prey insects to their doom in the leaves of

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carnivorous plants (Haberlandt, 1914; Voigt & Gorb, 2008; Gorb & Gorb, 2011; Bauer *et al.*, 2013), and to speed the drainage of water from surfaces (Hancock *et al.*, 2012).

The studies cited above, as well as general reviews of plant-surface characteristics (Beck, 1965; Juniper & Jeffree, 1983; Southwood, 1986; Vogel, 1988; Endara & Coley, 2011), have almost universally overlooked an obvious and potentially effective way in which anisotropic surfaces and edges could limit access of herbivores to plants. Haberlandt (1914: 126, 210–211) noted the possibility that insects ascending plants would encounter resistance from downwardly pointing hairs. Kevan, Chaloner & Savile (1975) also noted that upwardly pointing spines on leafless Early Devonian vascular plants might have directed arthropods toward the sporangia so that these animals disperse the spores as they ate. The hypothesis proposed in the present study, namely that asymmetrically disposed features lead small herbivorous arthropods inexorably toward the ends of leaves, was considered *en passant* for Mesozoic cycadeophytes (Moisan *et al.*, 2011; Pott *et al.*, 2012), although the implications of this potential antiherbivore defence have not previously been considered.

The present study first describes the types, variations, and distribution of anisotropic features within and among plants. Second, a novel hypothesis for the adaptive, antiherbivorous significance of anisotropic trichomes, scales, teeth, and serrations is considered and proposed, together with possible alternatives or contributing explanations.

MATERIAL AND METHODS

The observations prompting the present study were made on numerous visits to coastal California, as well as to the University of California, Davis, Arboretum and greenhouses; Hortus Botanicus in Leiden; and tropical rain forests in Costa Rica and on Barro Colorado Island, Panama. An informal survery of plants (mainly herbaceous species but also some shrubs and small trees) was carried out on coastal meadows (excluding salt marshes) in the vicinity of Bodega Bay, California, on 17 and 18 April, 2015. The presence or absence of trichomes on stems or leaves, the orientation of trichomes or scales, and the presence and orientation of marginal serrations, were all noted.

TYPES OF ANISOTROPY

The most common anisotropic condition in plants is the adapical orientation of marginal and surface features. Apically oriented leaf teeth are extremely widespread in dicotyledonous angiosperms, and similarly oriented protrusions are almost the rule in members of the Poaceae and Cyperaceae. Similar features adorn the needles of many pines (*Pinus* spp.), the segments of horsetails (*Equisetum* spp.), and the pinnule margins of many ferns. Hooked trichomes and apically directed leaf teeth are known in fossil plants as old as the Late Carboniferous (Krings & Kerp, 1999).

Anisotropic trichomes may occur on one or both surfaces of leaf depending on the species. Asymmetric roughening occurs on both the upper (adaxial) and lower (abaxial) surfaces of the leaves of *Cucurbita* (pumpkins and squashes), *Helianthus* (sunflower), and the rosaceous genus *Geum*. In *Cecropia* (Moraceae), the adaxial surface is covered with adapically oriented trichomes, whereas the abaxial side is more densely pubescent, with the hairs oriented at right angles to the leaf surface.

In *Yucca recurvifolia* (Agavaceae), the underside of the long leaf has adapically oriented trichomes, whereas the upper surface is macroscopically smooth. The Californian asteraceous herb *Psathyretos annua* has adapically oriented trichomes on both leaf surfaces and coarser trichomes on the stem that appear to lack a preferred orientation. In the marsh-dwelling Californian mint *Stachys chamaessonis* (Menthaceae), barbs on the stem point downward, whereas the trichomes on both leaf surfaces have no obvious anisotropy. In the Californian herb *Amsinckia menziesii* (Boraginaceae), trichomes on the abaxial surface of the narrow stem leaves are apically oriented, whereas those on the upper surface are less obviously anisotropic.

A much less common condition occurs in *Galium aparine*, *Asperula aparine*, and *Rubia tinctorum* (Rubiaceae). In these plants, all leaf surfaces are strongly anisotropic, with the trichomes pointing toward the base of leaves and stems. This anisotropy is associated with the scrambling habit in *G. aparine* but not in the other species, and is therefore likely to function in ways besides clinging to neighbouring plants.

Although rarely mentioned, many plants exhibit a reversal in the direction of anisotropy on their surfaces. Downwardly directed trichomes, prickles or spines are concentrated on the stem or on the basal portions of rosette leaves; whereas apically directed or hooked features occur on the distal portions of rosette leaves or on the upper part of the plant. In many species of *Rosa*, for example, spines along the stem tend to be downwardly hooked, whereas prickles on the major veins and serrations along the leaf margins have an adaxial orientation. In *Agave marmorata* (Agavaceae) and the bromeliad *Canistrum*

lindinii, basal prickles along the leaf margins point downward, whereas prickles on the distal two-thirds to three-quarters of the leaf margin point toward the leaf apex. In many grasses such as species of *Pennisetum* and *Lolium*, the stem below the inflorescence has downwardly pointing fine trichomes, whereas the margins and surfaces of the leaves show adapical anisotropy. The twining vine *Humulus lupulus* (Urticaceae) has downwardly pointing trichomes on the stem but apically oriented ones on both surfaces of the leaves. A similar condition occurs in *Lantana* (Verbenaceae). The eastern North American mulberry *Morus alba* (Moraceae) has downwardly pointing trichomes on the leaf petioles and apically oriented trichomes on the upper side of the leaf; trichomes on the leaf's underside are not anisotropically oriented.

INCIDENCE OF ANISOTROPY

The preliminary survey of 80 plant species in the meadows and dunes in the vicinity of Bodega Bay, California, indicated 18 species with trichomes (22.5%), of which five (6.3% of the total) were anisotropic; another five species (four grasses and a species of *Equisetum*) had anisotropic surfaces imparted by silica bodies. Anisotropic surfaces therefore occurred in 10 species (12.5% of the total). Anisotropic serrations occurred in five species (6.3%), all different from those with anisotropic surfaces.

Anistropic surfaces and edges are essentially unknown among tropical rain-forest canopy trees, salt-marsh and mangrove plants, redwood-forest species in both the canopy and understory, and submerged water plants. Trichomes on sticky leaves also do not appear to exhibit anisotropy.

THE HYPOTHESIS

When a small herbivore moves on an anisotropic surface or along an edge with asymmetrically disposed serrations or teeth, it is directed by differential friction along a path of least resistance. For apically (or upwardly) directed features, this path leads to the end or ends of the leaf where, given the difficulty of return, the herbivore would fall off. Bernays (1991) has shown that insects losing their grip on leaves and falling to the ground are subject to predation that may be even more intense than it would be if the insect were still on the plant. Downwardly projecting serrations, scales or trichomes would make ascent to the upper parts of the plant more difficult for a small herbivore (Haberlandt, 1914). Plant surfaces and edges can therefore direct enemy traffic either toward the exits or restrict it to parts near the ground.

The cases of anisotropic reversal between lower and upper reaches of a plant or leaf indicate a dual economic 'strategy' of defence. The first line of defence is preventing ascent of herbivores by impeding movement. If that fails, the second line of defence is to minimise damage by directing the enemy toward the ends of leaves, which are most susceptible to desiccation and where injury least compromises the photosynthetic and hydraulic functions of the leaf. Rather than interfering with locomotion, this second phase of resistance hastens the departure of the unwanted guest not by making adhesion to the leaf surface difficult but by manipulating the locomotor behaviour of the herbivore.

The potential benefits of an anisotropic surface should be especially great for large or long leaves because of the large absolute difference in time between moving with and moving against the obstacles provided by hooked or inclined trichomes. For small leaves, this time difference will be small. Moreover, a given arthropod is more likely to consume a whole small leaf than a whole large one, and the loss to a plant of a small leaf is less costly than that of a large one.

The small-scale anisotropic defence suggested here for some land plants would be effective largely against small, flightless herbivores such as caterpillars, orthopteran nymphs, and hemipterans, especially those that must grip the surface or edge on which they are moving. Leaf-miners, stem-borers, gallers, and flying insects should be less affected insofar as they do not move along stems or leaves. Larger-scale features such as hooked spines or prickles would interfere with larger herbivores' movements, especially if the thorny stems or leaves are close together, so that the enemy becomes ensnared. This ensnaring function has been suggested for the desert bromeliad *Puya raimondii*, in which the downwardly pointing marginal spines of the leaves trap small mammals (Rees & Roe, 1980).

Consistent with the appearance of foliage-feeding during the Late Early Carboniferous (Ianuzzi & Labandeira, 2008), anisotropic trichomes are known in ferns as far back as the Late Carboniferous (Krings & Kerp, 1999; Krings *et al.*, 2003) and have also been described in some Triassic and Jurassic cycadeophytes (Moisan *et al.*, 2011; Pott *et al.*, 2012). It is not known when anisotropic marginal leaf teeth first appear in the fossil record.

OTHER HYPOTHESES

A potential alternative or complement to the hypothesis proposed here is that anisotropic leaf surfaces function in self-cleaning by shedding water. Rapid drainage limits the establishment and accumulation

of dust and epiphylls, which interfere with photosynthesis. Water repellence in many plants is enhanced by the presence of micropapillae and wax crystals, which create small-scale roughness on the leaf surface and enable droplets to roll off, often aided by wind and gravity (Neinhuis & Barthlott, 1997; Holder, 2007; Hsu, Woan & Sigmund, 2011; Bixler & Bhushan, 2013; Fritsch, Willmott & Taylor, 2013; Watson, Gellender & Watson, 2014). The crystals and other microtopographic features promoting drainage are sometimes anisotropic (Hsu *et al.*, 2011; Bixler & Bhushan, 2013; Fritsch *et al.*, 2013) and some may be situated on hinged trichomes, although the ability of leaves to shed water and contaminants is not obviously linked to the presence of adapically oriented or hooked hairs.

The tendency for water droplets to collect at and drain from leaf margins is likely enhanced by the presence of marginal teeth (Feild *et al.*, 2005). It remains unclear, however, whether the abapical orientation of teeth improves this function.

Two other possible means of quickly shedding water from leaf surfaces do not appear to be associated with anisotropic features. One of these, an adaxially convex and abaxially concave leaf profile in leaves splayed horizontally, is common in mediterranean-climate shrubs and small trees, such as many species of oak (*Quercus*) and holly (*Ilex*) and the Chilean boldo (*Peumus boldus*), as well as in tropical elfin-forest plants (Howard, 1969). The undersides of such leaves are often hairy, although the hairs are not anisotropic, and the upper surface is either smooth or isotropically roughened. To my knowledge, the possible water-shedding function of this leaf morphology has been neither suggested, nor investigated previously. The other means of draining water, which has been experimentally verified, is the long, drawn-out leaf apex or 'drip tip' characteristic of tropical rain-forest canopy trees (Lightbody, 1985; Ivey & De Silva, 2001; Farji-Brener *et al.*, 2002; Burd, 2007; Malhado *et al.*, 2012; Meng *et al.*, 2014). Leaves with a drip tip are almost always smooth and have entire margins (Malhado *et al.*, 2012).

Marginal teeth are associated in young, fast-growing and short-lived temperate leaves with higher carbon gain (Royer & Wilf, 2006; Royer *et al.*, 2012) by promoting gas exchange. It is unclear whether an anisotropic orientation of marginal teeth would affect this function.

Finally, pubescence can protect plants against excessive radiation under desert conditions (Ehleringer, Bjorkman & Mooney, 1976) and retard evaporative water loss (Woodman & Fernandes, 1991). These functions would presumably be effective whether the protruding hairs are symmetrically or asymmetrically disposed to the leaf surfaces.

None of these other hypotheses adequately accounts for the observation that anisotropic trichomes often occur on (and indeed only on) the undersides of leaves, which are not exposed directly either to rain or radiation. At the very least, therefore, anisotropic features of leaves are likely to function in ways other than or in addition to water drainage, hydraulics and thermal regulation.

DISCUSSION

An evaluation of the hypothesis proposed here will require careful observations on the locomotor and feeding behaviour of herbivores, especially small ones. Simple tests in which different species or different morphs of a plant are offered to herbivores to assess 'preference' or susceptibility to attack are inadequate for assessing the function of anisotropic features or many other plant attributes as physical defence against herbivores. The outcomes of such tests indicate effects but do not illuminate the mechanisms underlying those effects. Only behavioural observations can establish how a particular physical attribute affects the activities of an enemy and how the potential defence works. As a secondary test, damage by herbivorous insects can be compared between leaves with anisotropic trichomes and those in which the trichomes are oriented perpendicular to the surface. Anisotropy should result in less damage as long as leaf lifespan and chemical defences are similar in the leaves being compared.

Comparative studies have identified a general trade-off between leaf longevity, which is correlated with traits conferring toughness and other forms of resistance to herbivores, and photosynthetic capacity, which is often linked to low antiherbivore resistance (Southwood, Brown & Reader, 1986; Reich, Walters & Ellsworth, 1992; Wright *et al.*, 2004; Onoda *et al.*, 2011; Osnas *et al.*, 2013). This trade-off represents the main axis of variation in the so-called leaf-economics spectrum. As in animals, greater investment in defence comes at the expense of rapid growth. It is noteworthy, however, that the anisotropic defence highlighted in the present study does not fit easily into this framework. Similar to chemical defences that can be translocated from one part of the plant to another as a direct response to enemy attack (Robinson, 1990), anisotropic structures can be an effective deterrent in fast-growing leaves with high photosynthetic capacity and a short lifespan. It may prove to be the case that anisotropy is a relatively cheap constitutive defence that is more common in short-leaved plants or leaves than in plants with thick leathery foliage. The economics of defence and growth will likely prove to be more complex than is

portrayed in current models of the leaf-economics spectrum.

The category of anisotropic defences explored here is unusual among enemy-related deterrents in speeding up an encounter between an enemy and its victim. In both plants and animals, most defences that function during the subjugation/resistance phase of an attack slow down and reduce the effective power of the enemy by making the attacker work harder or longer. A toxic exterior, slippery surface, and warning signals tend to limit contact between enemy and victim or to prevent contact in the first place, although they do not as a rule speed or direct locomotor activity of an attacker as anisotropic features are proposed to do.

CONCLUSIONS

The hypothesis that some surface features of plant leaves and stems direct the locomotor activity of small herbivores by creating greater friction in some directions rather than in others remains speculative. It will be important not only to test how effective this purported defence is against arthropods and other small herbivores that exhibit various locomotor and feeding behaviours, but also to document the ecological distribution of these anisotropic features. Anisotropic surfaces are common among animals, although whether any function in ways comparable to that suggested here for some land plants is unknown

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REFERENCES

Bauer G, Klein MC, Gorb SN, Speck T, Voigt D, Gallenmüller F. 2011. Always on the bright side: the climbing mechanism of *Galium aparine*. *Proceedings of the Royal Society of London Series B, Biological Sciences* **278:** 2233–2239.

Bauer G, Scharmann M, Skepper J, Federle W. 2013. 'Insect aquaplaning' on a superhydrophobic hairy surface: how *Heliamphora nutans Benth*. pitcher plants capture prey. *Proceedings of the Royal Society of London Series B, Biological Sciences* **280:** 20122569.

Beck SD. 1965. Resistance of plants to insects. *Annual Review of Entomology* **10:** 207–232.

Bernays EA. 1991. Evolution of insect morphology in relation to plants. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* **333:** 257–264.

Bixler GD, Bhushan B. 2013. Fluid drag reduction and efficient self-cleaning with rice leaf and butterfly wing bioinspired surfaces. *Nanoscale* **5:** 7685.

Brown VK, Lawton JH, Grubb PJ. 1991. Herbivory and the evolution of leaf size and shape. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* **333:** 265–272.

Burd M. 2007. Adaptive function of drip tips: a test of the epiphyll hypothesis in *Psychotria occidentalis* (Rubiaceae). *Journal of Tropical Ecology* **23:** 449–455.

Corner EJH. 1964. *The life of plants*. New York, NY: World Publishing Company.

Díaz S, Lavorel S, McIntyre S, Falczug V, Casanoves F, Michunas DG, Skarpe C, Rusch G, Sternberg M, Noy-Meir I, Landsberg J, Zhang W, Clark H, Campbell BD. 2007. Plant trait responses to grazing – a global synthesis. *Global Change Biology* **13:** 313–341.

Ehleringer J, Bjorkman O, Mooney RA. 1976. Leaf pubescence: effects on absorptance and photosynthesis in a desert shrub. *Science* **192:** 376–377.

Endara MJ, Coley PD. 2011. The resource availability hypothesis revisited: a meta-analysis. *Functional Ecology* **25:** 389–398.

Farji-Brener AG, Valverde O, Paolini L, de los Angeles La Torre M, Quintero E, Bonaccorso E, Arnedo L, Villalobos R. 2002. Acumen function in leaves and its vertical distribution in a tropical rain forest of Costa Rica. *Revista de Biología Tropical* **50:** 561–566.

Feild TS, Sage JL, Czerniak C, Iles WJD. 2005. Hydrothodal leaf teeth of *Chloranthus japonicus* (Chloranthaceae) prevent guttation-induced flooding of the mesophyll. *Plant, Cell and Environment* **28:** 1179–1190.

de Fluiter HJ, Ankersmit GW. 1948. Gegevens betreffende de aantasting van bonen (*Phaseolus vulgaris* L.) door de zwarte bonenluis (*Aphis* (*Dralis*) *fabae* Scop.). *Tijdschrift voor Plantenziekten* **54:** 1–13.

Fritsch A, Willmott GR, Taylor M. 2013. Superhydrophobic New Zealand leaves: contact angle and drop impact experiments. *Journal of the Royal Society of New Zealand* **43:** 198–210.

Gilbert LE. 1971. Butterfly-plant coevolution: has *Passiflora adenopoda* won the selectional race with heliconiine butterflies? *Science* **172:** 585–586.

Gorb EV, Gorb SN. 2011. The effect of surface anisotropy in the slippery zone of *Nepenthes alata* pitchers on beetle attachment. *Beilstein Journal of Nanotechnology* **2:** 302–310.

Haberlandt G. 1914. *Physiological plant anatomy* (transl. Drummond M.). London: McMillan.

Hancock MJ, Sekeroglu K, Demirel MC. 2012. Bioinspired directional surfaces and adhesion, wetting, and transport. *Advanced Functional Materials* **22:** 2223–2234.

Hanley ME, Lamont BB, Fairbanks MM, Rafferty CM. 2007. Plant structural traits and their role in anti-herbivore defence. *Perspectives in Plant Ecology, Evolution and Systematics* **8:** 147–178.

Holder CD. 2007. Leaf water repellency as an adaptation to tropical montane cloud forest environments. *Biotropica* **39:** 767–770.

Howard RA. 1969. The ecology of an elfin forest in Puerto Rico, VIII. Studies of stem growth and form and of leaf structure. *Journal of the Arnold Arboretum* **50:** 225–267.

Hsu S-H, Woan K, Sigmund W. 2011. Biologically inspired hairy structures for superhydrophobicity. *Materials Science and Engineering, R: Reports* **72:** 189–201.

Ianuzzi R, Labandeira CC. 2008. The oldest record of external folivory on land. *Annals of the Entomological Society of America* **101:** 79–94.

Ivey CT, De Silva N. 2001. A test of the function of drip tips. *Biotropica* **33:** 188–191.

Jeffree CE. 1986. The cuticle, epicuticular waxes and trichomes of plants, with reference to their structure, functions and evolution. In: Juniper B, Southwood R, eds. *Insects and the plant surface*. London: Edward Arnold, 23–64.

Johnson B. 1953. The injurious effects of the hooked epidermal hairs of French beans (*Phaseolus vulgaris* L.) on *Aphis craccivora* Koch. *Bulletin of Entomological Research* **44:** 779–788.

Johnson HB. 1975. Plant pubescence: an ecological perspective. *Botanical Reviews* **41:** 233–258.

Juniper BE, Jeffree CE. 1983. *Plant surfaces*. London: Edward Arnold.

Kevan PG, Chaloner WG, Savile DBO. 1975. Interrelationships of early terrestrial arthropods and plants. *Palaeontology* **18:** 391–417.

Krings M, Kerp H. 1999. Morphology, growth habit, and ecology of *Blanzyopteris praedentata* (Gothan) nov. comb., a climbing neuropteroid seed fern from the Stephanian of central France. *International Journal of Plant Sciences* **160:** 603–619.

Krings M, Kellogg DW, Kerp H, Taylor TN. 2003. Trichomes of the seed fern *Blanzyopteris praedentata*: implications for plant-insect interactions in the Late Carboniferous. *Botanical Journal of the Linnean Society* **141:** l33–l149.

Kulić IM, Mani M, Mohrbach H, Thankar R, Mahadevan L. 2009. Botanical ratchets. *Proceedings of the Royal Society of London Series B, Biological Sciences* **276:** 2243–2247.

Levin DA. 1973. The role of trichomes in plant defense. *Quarterly Review of Biology* **48:** 3–15.

Lightbody JP. 1985. Distribution of leaf shapes of *Piper* sp. in a tropical cloud forest: evidence for the role of drip-tips. *Biotropica* **17:** 339–342.

Malhado ACM, Malhi Y, Whittaker RJ, Ladle RJ, ter Steege H, Fabré NN, Phillips O, Laurance WF, Aragao LEOC, Pitman NCA, Ramirez-Angulo H, Malhado CHM. 2012. Drip-tips are associated with intensity of precipitation in the Amazon rain forest. *Biotropica* **44:** 728–737.

McKinney KB. 1938. Physical characteristics of the foliage of beans and tomatoes that tend to control some small insects. *Journal of Economic Entomology* **31:** 630–631.

Meng F, Cao R, Yang D, Niklas KJ, Sun S. 2014. Trade-offs between light interception and leaf water shedding: a comparison of shade- and sun-adapted species in a subtropical rain forest. *Oecologia* **174:** l3–l22.

Moisan P, Voigt S, Pott C, Buchwitz M, Schneider JW, Kerp H. 2011. Cycadalean and bennettitalean foliage from the Triassic Madygen Lagerstätte (SW Kyrgyzstan, central Asia). *Review of Palaeobotany and Palynology* **164:** 93–108.

Neinhuis C, Barthlott W. 1997. Characterization and distribution of water-repellent, self-cleaning plant surfaces. *Annals of Botany* **79:** 667–677.

Onoda Y, Westoby M, Adler PB, Choong AMF, Clissold FJ, Cornelissen JHC, Diaz S, Dominy NJ, Elgart A, Enrico L, Fine PVA, Howard JJ, Jalili A, Kitajima K, Kurokawa H, McArthur C, Lucas PW, Markesteijn L, Perez-Harguindeguy N, Poorter L, Richards L, Santiago LS, Sosinski EE Jr, Van Bael SA, Warton DI, Wright IJ, Wright SJ, Yamashita N. 2011. Global patterns of leaf mechanical properties. *Ecology Letters* **14:** 301–312.

Osnas JLD, Lichstein JW, Reich PB, Pacala SW. 2013. Global leaf trait relationships: mass, area, and the leaf economics spectrum. *Science* **340:** 741–744.

Pillemer EA, Tingey WM. 1976. Hooked trichomes: a physical plant barrier to a major agricultural pest. *Science* **193:** 482–484.

Pillemer EA, Tingey WM. 1978. Hooked trichomes and resistance of *Phaseolus vulgaris* to *Empoasca fabae* (Harris). *Entomologia Experimentalis et Applicata* **24:** 83–94.

Pott C, McLoughlin S, Wu S, Friis EM. 2012. Trichomes on the leaves of *Anomozamites villosus* sp. nov. (Bennettitales) from the Daohugou beds (Middle Jurassic), Inner Mongolia, China: mechanical defence against herbivorous arthropods. *Review of Palaeobotany and Palynology* **169:** 48–60.

Putz FE. 1984. The natural history of lianas on Barro Colorado Island, Panama. *Ecology* **75:** 1713–1724.

Putz FE. 1990. Growth habits and trellis requirements of climbing palms (*Calamus* spp.) in north-eastern Queensland. *Australian Journal of Botany* **38:** 603–608.

Quiring DT, Timmins SR, Park SJ. 1992. Effects of variations in hooked trichome densities of *Phaseolus vulgaris* on longevity of *Liriomyza trifolii* (Diptera: Agromyzidae)adults. *Environmental Entomology* **21:** l357–l361.

Rees WE, Roe NA. 1980. *Puya raimondii* (Pitcairnioideae, Bromeliaceae) and birds: an hypothesis on nutrient relationships. *Canadian Journal of Botany* **58:** 1262–1268.

Reich PB, Walters MB, Ellsworth DS. 1992. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs* **62:** 365–392.

Robinson JM. 1990. The burial of organic carbon as affected by the evolution of land plants. *Historical Biology* **3:** 189–201.

Royer DL, Wilf P. 2006. Why do toothed leaves correlate with cold climates? Gas exchange at leaf margins provides new insights into a classic paleotemperature proxy. *International Journal of Plant Sciences* **167:** 11–18.

Royer DL, Peppe DJ, Wheeler DA, Niinemets U. 2012. Roles of climate and functional traits in controlling toothed vs. untoothed leaf margins. *American Journal of Botany* **99:** 915–922.

Sack L, Dietrich EM, Streeter CM, Sánchez-Gómez D, Holbrook NM. 2008. Leaf palmate venation and vascular redundancy confer tolerance of hydraulic disruption. *Proceedings of the National Academy of Sciences of the United States of America* **105:** 1567–1572.

Schenck H. 1892. Beiträge zur Biologie und Anatomie der Lianen, im Besonderen der in Brasilien einheimischen Arten. I Beiträge zur Biologie der Lianen. *Botanische Mitteilungen der Tropen* **4:** 1–248.

Schillinger JA Jr, Gallun HL. 1968. Leaf pubescence of wheat as a deterrent to the cereal leaf beetle, *Oulema melanopus*. *Annals of the Entomological Society of America* **61:** 900–903.

Southwood R. 1986. Plant surfaces and insects – an overview. In: Juniper B, Southwood R, eds. *Insects and the plant surface*. London: Edward Arnold, 1–22.

Southwood TRE, Brown VK, Reader P. 1986. Leaf palatability, life expectancy and herbivore damage. *Oecologia* **70:** 544–548.

Sutherst RW, Wilson LJ. 1986. Tropical legumes and their ability to immobilize and kill cattle ticks. In: Juniper B, Southwood R, eds. *Insects and the plant surface*. London: Edward Arnold, 185–194.

Vermeij GJ. 2004. *Nature: an economic history*. Princeton, NJ: Princeton University Press.

Vogel S. 1988. *Life's devices: the physical world of animals and plants*. Princeton, NJ: Princeton University Press.

Voigt D, Gorb S. 2008. An insect trap as habitat: cohesion-failure mechanism prevents adhesion of *Pameridea roridulae* bugs to the sticky surface of the plant *Roridula gorgonias*. *Journal of Experimental Biology* **211:** 2647–2657.

Watson GS, Gellender M, Watson JA. 2014. Self-propulsion of dew drops on lotus leaves: a potential mechanism for self cleaning. *Biofouling* **30:** 427–434.

Wolgemuth CW. 2009. Plant biomechanics: using shape to steal motion. *Current Biology* **19:** 409–410.

Woodman RL, Fernandes GW. 1991. Differential mechanical defense: herbivory, evapotranspiration, and leaf-hairs. *Oikos* **60:** 11–19.

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas M-L, Niinemets U, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R. 2004. The worldwide leaf economics spectrum. *Nature* **428:** 821–827.

Yamazaki K. 2011. Gone with the wind: trembling leaves may deter herbivory. *Biological Journal of the Linnean Society* **107:** 738–747.