
Herbivory and the Evolution of Leaf Size and Shape [and Discussion]

V. K. Brown, J. H. Lawton and P. J. Grubb

Phil. Trans. R. Soc. Lond. B 1991 **333**, 265-272
doi: 10.1098/rstb.1991.0076

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

To subscribe to *Phil. Trans. R. Soc. Lond. B* go to: <http://rstb.royalsocietypublishing.org/subscriptions>

Herbivory and the evolution of leaf size and shape

V. K. BROWN AND J. H. LAWTON

Department of Biology and NERC Centre for Population Biology, Imperial College, Silwood Park, Ascot SL5 7PY, U.K.

SUMMARY

Why do leaves have such varied sizes and shapes? Part of the answer lies in physiological and biomechanical demands imposed by different habitats; selective forces that are now reasonably well understood. In contrast, the impact of herbivores on the evolution of leaf size and shape has rarely been investigated and is poorly understood. There are at least six ways in which herbivores, particularly vertebrates and insects, may have influenced the evolution of leaf size and shape, favouring leaf morphologies that differ from those dictated by physiological and biomechanical constraints acting on plants. They are mimicry, not only of leaves of other plant species but also grazed leaves and inanimate objects; crypsis; physical barriers to being eaten; interspecific differences in leaf morphology to reduce recognition by herbivores; very small or highly divided and dissected leaves that reduce feeding efficiency; and different adult and juvenile foliage. There is an urgent need for studies specifically designed to investigate the impact of herbivores on leaf size and shape.

1. INTRODUCTION

Why are there so many sizes and shapes of leaves? Within inevitable phylogenetic and developmental constraints, part of the answer lies in the physiological and biomechanical demands imposed by different habitats (i.e. light regimes, temperatures, humidities and wind speeds) interacting with nutrient and water availability (Böcher & Lewis 1962; Horn 1971; Parkhurst & Loucks 1972; Givnish 1979, 1986; Chabot & Hicks 1982). Models that assume that natural selection minimizes the costs of supporting leaves and maximizes whole-plant carbon gain predict much of the variation observed in the sizes and shapes of real leaves (Givnish 1986 and references therein).

The purpose of this paper is not to deny the importance of physiological and biomechanical constraints on the design of leaves, but rather to draw attention to the possibility that herbivory is an additional but neglected constraint. Herbivory as a selective force on the economy of leaf design is mentioned only once, and then only in passing, in the seven hundred or so pages of Givnish (1986, p. 245). Our thesis is that leaf size and shape influence the impact of herbivores, and are therefore open to selection by herbivores. It follows that some of the variation in the design of leaves seen within and between habitats may be an evolved response by plants to herbivory, rather than to light, temperature, wind and so on. How much herbivores can change the design of leaves away from purely physiological and biomechanical optima is an open question, but the answer is unlikely to be 'not at all'.

The paper is not about leaf toughness, or microscopic features (hairs, trichomes, etc.), or secondary chemistry, all of which have been implicated as plant defences against herbivory (see, for example, Southwood (1987)). It is concerned solely with the sizes and

shapes of leaves. However, size and shape may covary with other characteristics (see, for example, Givnish (1979)). Consequently, it may be difficult to attribute herbivore responses primarily, or mainly, to leaf size and shape, a caveat that must be continually borne in mind.

First, we examine how plants in New Zealand responded to a world without native, mammalian herbivores, but subject to grazing by giant extinct birds, the moas. We then consider the impact of mammalian herbivores on the evolution of leaf size and shape. The remainder of the paper focuses on insects, being the group with which we are personally most familiar. Much of the evidence assembled for the role of herbivores, both vertebrate and invertebrate, in the evolution of leaves is anecdotal and imperfect. Our intention is to stimulate more thought and more work, rather than to provide definitive answers.

There are at least six ways in which evolutionary responses by plants to herbivory may have influenced the sizes and shapes of leaves. They are: (i) mimicry, particularly of other species of plants that are unsuitable as food, but also of herbivore-damaged leaves signalling, for example, induced chemical defences; (ii) a set of leaf characteristics that range from crypsis to mimicry of inanimate objects; (iii) leaves modified to provide direct physical defences in the form of spines, or other physical barriers; (iv) divergence in leaf size and shape between species in the same habitat, a phenomenon that may reduce the risk of a particular plant species being recognized as potential food by visually searching herbivores; (v) very small or highly divided leaves that reduce the foraging efficiency of herbivores, or make effective feeding impossible; (vi) different adult and juvenile foliage in the some species, a tactic that may have evolved because the risk of herbivore attack changes with the maturity of the plant.

2. MOAS AND THE EVOLUTION OF THE NEW ZEALAND FLORA

The flora of New Zealand evolved in the absence of mammalian herbivores, but subject to grazing by moas. At least twelve species of moas, ranging in size from 20 to 200 kg and approaching 3 m tall, are known from their remains. All were exterminated by the Maoris, who first colonized New Zealand in the eleventh century. Relations between moas and plants are reconstructed and reviewed by Atkinson & Greenwood (1989).

Browsing and grazing mammals detect food by smell, touch and sight, but lack colour vision; they cut chunks of plant tissue with a rotatory action of the jaw. Moa browsing and grazing subject plants to very different selection pressures. Moas, in common with extant, diurnal birds presumably had acute colour vision, but a poor sense of smell. Birds peck, and can only bite food with a scissor action, swallowing it without chewing. Atkinson & Greenwood argue that four widespread features of the New Zealand flora evolved in response to moa grazing. They are spiny tussocks, mimicry, reduced visual apparency and divarication.

Spines are uncommon among New Zealand plants. However, the genus *Aciphylla* (Apiaceae) is exceptional, and several species form vicious, hemispherical tussocks, presenting a surface of closely spaced, rigid, sharp points borne on modified leaves. The hypothesis, first mooted by Wallace in 1889, is that the unusual leaves and growth form of aciphyllas may have reduced attack by moas, seeking to feed on the nutritious leaf bases. A bird pecking into the tussocks would risk impaling an eye, unless it was extremely careful. Consistent with this hypothesis, *Aciphylla* species growing in habitats where moas were rare or absent have reduced, or no leaf spines. For example, the Australian *A. glacialis* has short, fern-like leaves. Moreover, mature, spiny aciphyllas have seedlings with flaccid, grass-like leaves but, as plants enlarge to tussocks and become clearly visible, the juvenile foliage is quickly replaced.

By relying on acute vision for food selection, moas may have favoured the evolution of mimicry and reduced visual apparency in potential food plants. Atkinson & Greenwood recognize two sorts of models for mimetic species, namely other, unpalatable plants and dead twigs. For example, *Celmisia lyalli* and *C. petriei* (Compositae) look rather like spiny aciphyllas. Several species of woody plants mimic unpalatable species when small, but have different, non-mimetic leaves when they are larger and hence above the reach of browsing moas. Mimicry of dead twigs is illustrated by the forest vine, *Parsonia capsularis* (Apocynaceae), which has very narrow, brown leaves blotched with grey when young, and more normal, green leaves with increasing height above the ground. It is unclear from Atkinson & Greenwood's account whether mature leaves are also a different shape. Leaves of other species certainly change shape as the plant matures. *Pittosporum patulum* (Pittosporaceae), a small tree, has deep purple-bronze juvenile leaves that are long and very narrow

(2–4 mm wide) with toothed edges; adult leaves, presumably above the reach of browsers, are a completely different shape, untoothed, 10–15 mm wide and green. Juveniles of *P. patulum* do not mimic twigs, but are very difficult to see on the forest floor. It is representative of a number of New Zealand forest plants with cryptic, often brown juvenile foliage differing markedly in size or shape from the green foliage of adults; some of these species appear to be twig mimics, others are just very cryptic (J. H. Lawton, personal observation).

Divaricating shrubs are also a common feature of the New Zealand flora. The divaricating (wide branching angle) growth form has evolved several times, creating shrubs with interlacing branches, reminiscent of bundles of lightly crumpled and folded chicken wire. All have small leaves, sparse or absent on the exterior of the plant, but more dense towards the centre of the shrub. Atkinson & Greenwood suggest that the mechanical restriction presented by interlacing branches and small, inaccessible leaves would have reduced the bite size and biting rate of moas, and hence may have evolved in response to moa browsing, because they make feeding uneconomic. Other features of divaricating plants (for instance, springy, tough twigs that are difficult to pull off) may also have conferred protection by reducing moa feeding rates. *Hoheria angustifolia* (Malvaceae) is representative of a group of nine species that are divaricating when small, but which transform into normal, small trees with larger leaves above about 3 m, that is, just out of reach of the larger moas.

To the eyes of a European biologist, all these features of the New Zealand flora are peculiar, particularly the widespread prevalence of divaricating shrubs, and plants with leaves that change markedly in size, shape and colour as the plant grows. The hypothesis that moas may have driven the evolution of this suite of characteristics is simple and elegant. It may also be wrong. No other, single hypothesis satisfactorily unites these observations, but alternative hypotheses for particular features and phenomena exist, and not all the evidence adduced by Atkinson & Greenwood (1989) is beyond criticism (see, for example, McGlone & Webb (1981); McGlone (1991); M. McGlone (personal communication)). Space prevents a full discussion, but a case can be made, for instance, that the divaricating growth form is advantageous in dry, windy conditions that prevailed over large parts of New Zealand until comparatively recently. That divaricating plants now occur outside such habitats may have as much to do with phylogenetic constraints and the pool of potential colonists available to occupy more mesic habitats as it has to do with moas.

3. VERTEBRATE GRAZERS IN THE REST OF THE WORLD

(a) *Spinescent leaves and other changes in leaf morphology*

So much of the world's flora has evolved in the presence of browsing and grazing mammals that we

may fail to recognize their pervasive influence on leaf design. Spines and thorns certainly play a role in defence against browsing mammals, and sometimes, as in holly (*Ilex* spp.), they adorn the edges of leaves (where they may also serve to deter insect herbivores; see Ehrlich & Raven 1967). However, leaves with spines large enough to deter mammals are not common. In the flora of southern Africa, spinescent plants make up between 3 and 12% of species, depending upon the biome; of these, species with spiny leaf-tips and margins are a minority, constituting between 1 and 2% of the total flora and 9–52% of spinescent species (Milton 1991). In detailed line transects, Milton reported 12 species with spiny leaves, from a sample of 47 species of spinescent plants. It would be interesting to know whether leaf spines are comparatively rare because they are less efficient physical defences than tougher thorns on stems and branches; or because it is more costly to manufacture short-lived spines on leaves that will eventually be shed; or because spines compromise the physiological and biomechanical properties of leaves (see Givnish (1979) for further discussion).

Spines aside, certain leaf shapes may reduce the impact of grazing or browsing mammals, by allowing a partly eaten leaf to continue to function. For example, if leaflets are bitten off pinnate leaves, the remaining intact leaflets may be less prone to premature shedding or to the entry of pathogens through the wound than a simple leaf of the same total area, subject to the same percentage removal of tissue. Very small, pinnate leaves may also make browsing by mammals less economic (M. Coe, personal communication). We know of no tests of these possibilities.

(b) *Crypsis and mimicry*

Crypsis and mimicry could also evolve in response to mammalian herbivores, although examples that have received even cursory examination are hard to find, with the possible exception of Australian mistletoes (discussed below). There is evidence, however, that some weeds mimic the crops in which they grow, the selective pressure being hand weeding (Barrett 1983): a form of artificial selection that resembles heavy grazing by a visually searching herbivore. Furthermore, it is difficult to think of a good reason, other than escape from grazing mammals, why the paired, fused and fleshy leaves of about fifty species of South African stone plants (*Lithops* spp.) (Aizoaceae) should so beautifully mimic the stones and pebbles among which they grow, although Everard & Morley (1970) describe the idea as controversial. Barlow & Wiens (1977) briefly review mimicry in *Lithops* and in other, unrelated, succulents in several families. In Europe, the foliage and general appearance of vegetative plants of white dead-nettles (*Lamium album*) (Labiatae) bear a close resemblance to stinging nettles (*Urtica dioica*) (Urticaceae). Stinging hairs deter soft-muzzled, grazing mammals, suggesting that dead-nettles are harmless Batesian mimics. However, many other labiates that do not closely mimic nettles have ovate leaves with serrate margins, so if this is a case of true mimicry, it

may have involved rather little modification in leaf shape.

(c) *Australian mistletoes that mimic their host-plants*

Several dominant genera of Australian trees (e.g. *Eucalyptus*, *Acacia*, *Casuarina*) have mistletoes (Loranthaceae) with leaves that resemble those of the host (Barlow & Wiens 1977). From a total of 64 Australian mistletoe species, 20 are highly host-specific mimics, and a further 16 species are mimics of one or more of their several hosts. Leaves of a wide variety of sizes and shapes are involved: filiform, falcate, lanceolate, elliptical and even the rounded-oval, amplexicaul juvenile leaves of *Eucalyptus*. Only evergreen hosts serve as models; mistletoes do not mimic deciduous hosts on which they would obviously be very conspicuous after leaf fall (J. L. Harper, personal communication).

The convergence in appearance between hosts and parasites appears not to be due to selection imposed by similar physical environments. Rather, Barlow and Wiens argue, it is most easily explained as protective mimicry against grazing by arboreal, herbivorous marsupials, particularly ringtails (*Pseudocheirus*) and possums (*Trichosurus*) in the extant fauna, although it may have evolved in the face of grazing pressures from other genera, now extinct. They argue that possums eat mistletoes and have excellent vision; they also provide anecdotal evidence to suggest that possums can have a considerable impact on the plants. Moreover, mimicry is most prevalent in species of mistletoes with high levels of foliage nitrogen, perhaps because they are most sought after by mammalian herbivores (Ehleringer *et al.* 1986).

However, not all biologists with a good knowledge of Australian mistletoes are agreed about the critical facts of Barlow and Wiens's arguments, still less about their interpretation (Atsatt 1983). Despite mimetic leaves, some mistletoes, Atsatt argues, are conspicuous because they stand out as dense clumps among sparse host foliage, or because they match the shape but not the colour of host leaves, and because mistletoes bear obvious flowers and berries. More startling, in limited feeding trials with a single possum, mistletoes were always rejected in favour of host foliage, except for 'small, exploratory bites upon the first encounter'. *Ergo*, mistletoes are unpalatable, an inference confirmed by extensive field searches that revealed little evidence of possum grazing on the plants (although it is clearly impossible to rule out selection by other arboreal herbivores that are now extinct). Finally, mimetic mistletoes are not confined to Australia; cases are reported from Africa and India, as well as North, Central and South America.

We are struck by the fact that both Atsatt (1983) and Barlow & Wiens (1977) dismiss an alternative hypothesis for the evolution of foliage mimicry in mistletoes. In Australia, the most damaging mistletoe herbivores are not vertebrates, but the caterpillars of lycaenid and pierid butterflies. The interaction between butterflies and mistletoes is complicated, at least for the lycaenids, by a mutualistic association between

caterpillars and protective ants (Atsatt 1981), and Atsatt argues that there is no evidence that mistletoe leaf shape is important in host-plant recognition or selection by adult butterflies. But as far as we are aware nobody has tested adult, mistletoe-associated butterflies, under properly controlled conditions, to see if they respond to leaf shape. Females of at least one Australian lycaenid (*Jalmenus evagoras*), albeit not a mistletoe feeder, appear to use vision when searching for hosts (D. Nash, personal communication).

It is to the role of leaf shape in another butterfly-plant interaction that we now turn.

4. HELICONIUS BUTTERFLIES AND PASSIFLORA VINES

In the tropical rain forests and secondary woodlands of Central and South America, some of the most conspicuous insects are brightly coloured *Heliconius* butterflies. Their caterpillars feed on passion vines in the family Passifloraceae, particularly the genus *Passiflora*, that live scattered through the forest, and Gilbert (1975, 1982) has suggested that herbivory by *Heliconius* caterpillars has been a major selective force on the evolution of leaf shape in these vines. The butterflies are very host-specific, and adult females rely strongly on vision to locate suitable vines. Caterpillar attack can significantly reduce the growth and performance of the passion vines. Given these conditions, Gilbert suggests that three elements in the morphology of the leaves of these plants may have evolved in response to selection imposed by *Heliconius*. They are mimicry, divergence in leaf shape between species, and markedly different adult and juvenile foliage.

The case for mimicry rests on the observation that in many habitats, leaves of passion vines closely resemble, in both shape and texture, leaves of abundant, non-host plants. Models include *Philodendron* and *Rubus*. Gilbert suggests that an egg-laying female, searching visually, could easily overlook suitable, mimetic hosts. Second, in many areas where different species of passion vines coexist, they often differ markedly from one another in leaf shape, even though they are closely related and share similar physical conditions. Gilbert sees divergence in leaf shape as a means of reducing attack, because ovipositing *Heliconius* overlook potential hosts with the wrong leaf shape. (Consistent with this hypothesis, caterpillars of some species can feed and develop on the 'wrong' hosts, if introduced onto them experimentally (Smiley 1978, 1985).) Divergence in leaf shape between species can therefore be viewed as an example of selection for 'enemy-free space' (Jeffries & Lawton 1984). Finally, differences between adult and juvenile foliage within one species of vine, Gilbert argues, has also evolved in response to selection from *Heliconius*. Juvenile foliage may mimic other plants on the forest floor, and altering the appearance of the leaves as the plant matures may further reduce the chances of female butterflies recognizing vulnerable juveniles.

Gilbert himself is the first to admit the speculative nature of these arguments. As in the case of Australian

mistletoes, one could postulate, for example, that convergence in leaf size and shape is a response to shared physical environmental variables, rather than mimicry. It is also possible that different adult and juvenile foliages are adaptations to different physical environments on the shade of the forest floor and in the canopy. More work is required to distinguish between the herbivore hypothesis and the physiological and biomechanical hypotheses that have so far dominated thinking about the design of leaves.

5. INTERACTIONS BETWEEN OTHER INSECT HERBIVORES AND LEAF SIZE AND SHAPE

A necessary, although not sufficient, condition for insects to influence the design of leaves is that herbivores must respond to, and be affected by, leaf size and shape. Then, if these responses ultimately change herbivore abundances and hence damage-levels experienced by the plant, the way is open for insect herbivores to influence the evolution of leaf size and shape. Aside from the *Heliconius*-*Passiflora* system discussed above, there is sufficient evidence scattered through the literature to make a case for other insects as selective agents on the size and shape of leaves. We have gathered the arguments together under five headings, namely that leaf size and shape are involved in host-plant recognition and selection by insects; they can modify the efficiency with which herbivores exploit leaves; certain leaf shapes may act as physical barriers to insect herbivory; leaf size and shape also influence the number of species of herbivores attacking plants; and sometimes, at least, they alter herbivore abundances.

An added, but very poorly studied, possibility is that leaf size and shape have similar effects on the parasitoids and predators of herbivores, thereby changing herbivore abundances via the third trophic level. Insect herbivores may also be better camouflaged and concealed from enemies on leaves of certain sizes and shapes. There is no explicit discussion of these problems in the major review of plant-herbivore-enemy interactions undertaken by Price *et al.* (1980); we touch on some possible examples.

(a) Leaf size and shape influence selection of plants by insects

Both psilids (Diptera) and butterflies (Lepidoptera) are attracted towards plants bearing leaves of a particular shape (Prokopy & Owens 1983). Well studied examples are provided by ovipositing female butterflies searching for hosts; they include not only the *Heliconius* spp. discussed above, but also *Battus philenor* (Rauscher 1978) and two species of *Eurema* (Mackay & Jones 1989). Adults of the fly *Pegomya nigritarsis* (Diptera) can gauge leaf size because they adjust the number of eggs laid according to the sizes of the leaves of their *Rumex* hosts (Godfray 1986), although they may do this using chemical cues correlated with leaf size, rather than vision. Aphids

(Homoptera), too, may be sensitive to leaf size; adult females of *Pemphigus betae* seek out and preferentially colonize large leaves of *Populus angustifolia* (Whitham 1978), with marked effects on aphid fitness (see below). This is not to say that any of these herbivores have influenced the evolution of leaf size or shape in these particular plants; the examples simply illustrate that herbivores are sensitive to gross aspects of leaf morphology.

Evidence that some insects recognize and respond to leaf shape prompted Niemela & Tuomi (1987) to suggest that narrow, irregular hollows on the leaf blades of certain Moraceae mimic caterpillar feeding damage. These irregular 'incisions' occur on some of a plant's leaves, but not others, enhancing resemblance to feeding damage. Niemela & Tuomi speculate that false damage could protect the plant in several ways. Ovipositing females may avoid it because real damage signals the presence of competing larvae, or induced biochemical defences in leaves; false damage may also be avoided because real damage serves to attract parasitoids and predators. Niemela & Tuomi point out that if natural enemies are attracted to false damage, thereby increasing herbivore mortality rates, selection may also operate on leaf shape via the third trophic level. A wide range of plants outside the Moraceae also have leaves with herbivore-like indentations and holes (M. J. Crawley, personal communication; V. K. Brown & J. H. Lawton, personal observations). The mature, but not the juvenile, leaves of *Monstera deliciosa* are a familiar example. The hypothesis that 'pseudo-damage' is mimetic and protective against herbivores (including vertebrates), deserves more attention, along with the related suggestion that variegated colour patterns on certain leaves may serve a similar function, for example by mimicking leaf-mines (Smith 1986; but see Givnish (1990)).

(b) Leaf size and shape influence the performance of individual insects

It would be remarkable if the size and shape of leaves did not influence the lives of insects living on and in them. Movement, mating, oviposition, feeding, hiding and sheltering by both herbivores and their enemies must all be affected by the design of leaves (see, for example, Heinrich (1971)). Surprisingly, the problem has received little systematic attention. Leaf-surface properties (roughness, waxiness, pubescence, etc.) influence the ability of insects to hold on, move about and feed (see Strong *et al.* 1984), but lie outside the scope of this paper. Nevertheless, there are data showing that more macroscopic properties of leaves also impinge on many aspects of the lives of insects.

Female *Lithocolletis quercus* (Lepidoptera) preferentially oviposit in large leaves, although discrimination is not very acute (Auerbach & Simberloff 1989), and how they judge leaf size is unclear. In contrast, female *Perga affinis* (Hymenoptera: Symphyta) cannot oviposit on wide-leaved hosts, because they need to grip the leaf edges when laying (Carne 1962). Feeding efficiency in adult Christmas beetles, *Anoplognathus chloropyrus* (Coleoptera), is similarly re-

duced on narrow *Eucalyptus* leaves because they cannot manoeuvre effectively (Carne *et al.* 1974). The juvenile leaves of blue gums lack petioles, a characteristic (together with the fact that they are softer than adult foliage) that makes them particularly susceptible to attack by caterpillars of the autumn gum moth, *Mnesampela privata* (Lepidoptera); the caterpillars can more easily withdraw into protective daytime shelters on leaves without petioles (Elliot & Bashford 1978). Conversely, lepidopteran caterpillars may find the small and often sparse leaflets on the pinnate leaves of African *Acacias* difficult to manoeuvre and eat; leaflets are also very loosely attached and often fall off as caterpillars try to grasp them (M. Coe, personal communication). Exploitation of some pinnate leaves by caterpillars may also be made more difficult, and the risk of herbivore damage to the petiole reduced, because basal leaflets are less palatable than lateral or terminal leaflets (Gall 1987).

Finally, at least three measures of reproductive success in *Pemphigus* aphids are correlated with the size of the mature leaf upon which they are feeding (Whitham 1978). In comparisons between large (more than 15 cm long) and small (up to 5 cm long) leaves on the same branch, aphids survived better (0 versus 80% mortality), were 70% larger, and gave birth to 220% more progeny on large leaves.

We are surprised that more data do not exist on the behaviour and performance of individual insects exploiting different sizes and shapes of leaves. Three sorts of data would be instructive.

1. Observations on polyphagous species moving about a range of their normal host plants that differ in leaf size and shape. Heinrich (1971) provides a pioneering example.

2. Comparisons of the performance of herbivores (and natural enemies) on single species of plants with variable shaped leaves, for example the dissected and pinnatifid cultivars of some *Betula*, *Fagus* and *Acer* spp. compared with normal phenotypes.

3. Information on the performance and survival of leaf miners and gall formers on leaves of different sizes and shapes.

(c) Leaves as physical barriers to insect herbivores

Leaves may present physical barriers to insect herbivores in other ways than being tough, or by having hairs, trichomes, and marginal teeth or spines. *Blackstonia perfoliata*, a European member of the Gentianaceae, has connate stem leaves. By surrounding the stem, these leaves present a formidable barrier to any small insect trying to climb the plant, reminiscent of the discs on the ropes of ships to keep rats ashore. The juvenile foliage of some eucalypts is very similar. Do leaves that completely surround the stem function as 'rat stops' for herbivores seeking terminal buds?

(d) Effects of leaf size and shape on herbivore species richness

British umbellifers (Apiaceae) have leaf shapes ranging from finely divided, filiform leaves to the

broad, and simply pinnate. Controlling for size of host-plant geographic range (which has a large influence on herbivore species richness), umbellifers with finely divided leaves support significantly fewer species of agromyzid leaf-miners (Diptera) (Lawton & Price 1979), and significantly fewer species of insect herbivores in general (Jones & Lawton 1991) than umbellifers with large, undivided leaves. Although the mechanism is not well understood, it presumably rests on the difficulties herbivores experience in exploiting more finely divided leaves. There must, for example, be a critical width of tissue and a critical size for individual leaflets, below which leaf-mining is impossible, and external feeding becomes inefficient. Trees yield similar results, with fewer insect species exploiting species with smaller leaves (Moran & Southwood 1982; Kennedy & Southwood 1984).

Subtle effects on different guilds are revealed by comparisons of herbivore assemblages on two vetches (Leguminosae) both with pinnate leaves, *Vicia hirsuta* (with very narrow leaflets) and *V. sativa* (with broader leaflets); *hirsuta* hosts fewer species of external chewing herbivores than *sativa*, but has more sucking (sap-feeding) species (Brown *et al.* 1987).

(e) Effects on population dynamics and abundance of insects

Rates of population growth of pea aphids, *Acyrtosiphon pisum*, are significantly lower on cultivars of peas lacking leaves than on normal plants (Kareiva & Sahakian 1990). Because the leafless cultivars have tendrils, they are analogues of plants with exceptionally finely divided, filiform leaves. Aphids perform better on normal plants, because ladybird predators (Coccinellidae) fell off the normal variety about twice as often as they did from the leafless variety, reducing predation rates on normal plants; beetles can cling to stems and tendrils much better than to smooth, flat leaves.

Absolute abundances of herbivores are difficult to compare between plants with markedly different sizes and shapes of leaves, unless scaled for leaf area. In insecticide-knockdown samples collected in 1 m² sheets (which may roughly control for leaf area), narrow leaved trees supported only about one quarter the number of individual insects fogged from species with broader leaves (Moran & Southwood 1982). Brown *et al.* (1990) and Sterling *et al.* (1991) found that sheep grazing modified the sizes of leaves of *Ranunculus repens* and *Medicago lupulina*. Two species of leaf-mining flies (Diptera) were more abundant in grazing treatments, where host plants had larger leaves, even though the absolute abundance of their food plants was much reduced. Similarly, P. Niemela (personal communication) found more eriophyid (Acari) galls per unit area on large, palmate leaves than on smaller ovate leaves.

(f) Insect herbivores: an overview

Drawing these arguments together, there is scattered but growing evidence showing that insect herbivores (and their enemies) respond to and are affected by leaf

size and shape, generating differences in herbivore species richness, or herbivore abundances, on different species or genotypes of plants with different sizes and shapes of leaves. In general, small or highly divided leaves appear more difficult for insect herbivores to exploit than large, entire leaves. However, there are as yet no direct demonstrations that herbivore responses to leaf size and shape translate into effects on plant fitness, or plant performance, so that the case for insect herbivores as significant players in the evolution of leaf size and shape is circumstantial.

6. CONCLUDING REMARKS

There are at least six ways in which herbivores may have influenced the evolution of leaf size and shape, favouring leaf morphologies that differ from those dictated by physiological and biomechanical constraints acting on plants. They are mimicry, not only of leaves of other species of plants but also grazed leaves and inanimate objects; crypsis; physical barriers to being eaten; interspecific differences in leaf morphology to reduce recognition by herbivores; very small or highly divided and dissected leaves that reduce feeding efficiency; and different adult and juvenile foliage.

We do not know how common most of these responses are. Nor do we know the extent to which carbon gain by individual plants is compromised below physiological optima by changes in leaf size and shape that serve to reduce herbivory. Grazing jeopardizes the plant in several ways. As well as the initial loss of biomass, the future photosynthetic contribution of the grazed tissue is also lost (Chabot & Hicks 1982), and may be exacerbated by premature abscission of damaged leaves. Wounds are also vulnerable to invasion by pathogens. Selection may therefore favour leaf sizes and shapes that differ from physiological and biomechanical optima, providing such leaves bring compensating gains to the plant via reduced risks of attack by herbivores (Givnish 1979). It is currently unclear whether herbivory is more likely to influence the evolution of leaf size and shape in some habitats than others; or whether certain types of plants, for instance particularly palatable species high in nitrogen, are more or less likely to respond to herbivore attack by changes in leaf macro-morphology (see Givnish (1990) for a brief discussion). The problem is further complicated by the need to consider the costs and benefits of alternative means of defence open to the plant, not least allelochemicals. There are, however, no reasons to believe that changes in leaf size and shape are any more difficult to evolve than other aspects of plant morphology or biochemistry (Gottlieb 1984).

Insights into the evolutionary impact of herbivores can be gained by studying plant morphology in the absence of key players, mammals in New Zealand for instance. An alternative would be to examine leaf size and shape in early angiosperm floras, before the evolution of herbivorous mammals (Collinson & Hooker, this symposium), or significant numbers of extant insect herbivores (for examples, see Strong *et al.* (1984); Chaloner *et al.* (this symposium)). To our

untutored eyes, the fossil leaves of many early angiosperms have a very simple, rather uniform morphology (see, for example, Hickey & Wolfe (1975); Hughes (1976)), although pinnate and palmate forms appear early in some Cretaceous floras (Hallam 1977), and it may be difficult to separate the role of herbivores from the effects of palaeo-climate. Comparisons between floras, both extant and extinct, would be easier if the range and variety of leaf sizes and shapes could be quantified objectively. It would be particularly valuable to have data on leaf sizes and shapes, gathered in a standard way, for representative samples of plant communities in different biomes and biogeographic regions.

We have the impression that in some habitats plants have leaves of a rather uniform size and shape, whereas in others leaves of different species span a much greater range of morphologies. Why? Is it that certain habitats are physiologically demanding and strongly constrain leaf design, or is it because herbivore pressures are very different in different habitats? The answer is probably both. Speculating, we predict that habitats where visually searching herbivores are common will display a greater range and variety of leaf sizes and shapes than habitats where such herbivores are rare or absent. As well as selecting for mimicry in plants, visually searching herbivores may also impose strong selection for leaves of different species of plants to be different shapes, to reduce risks of being recognized as food. There may often be nothing special about particular shapes of leaves; only that they should be different from leaves of other species in the same habitat.

There are a number of ways in which an assessment of the role of herbivores in the evolution of leaf size and shape could be made more rigorous. One is to exploit genetic and phenotypic differences in leaf morphology between individual plants, or between adult and juvenile foliage or between normal and regrowth leaves, in experiments that measure the performances of both plants and herbivores. Without such experiments, an assessment of the role of herbivores in the evolution of leaves will always be difficult. Our view is that herbivores have played a significant role in determining the sizes and shapes of leaves, and that without herbivores, leaf morphology would be simpler and less interesting.

We are extremely grateful to Bill Chaloner, Malcolm Coe, Mick Crawley, Penny Edwards, John Harper, Matt McGlone, Pekka Niemela, Dave Parkhurst and John Richards for ideas and valuable discussions, and to Matt McGlone and Sue Milton for permission to quote from manuscripts prior to publication.

REFERENCES

- Atkinson, I. E. A. & Greenwood, R. M. 1989 Relationships between moas and plants. *N.Z. J. Ecol.* **12** (suppl.), 67–96.
- Atsatt, P. R. 1981 Lycaenid butterflies and ants: selection for enemy-free space. *Am. Nat.* **118**, 638–654.
- Atsatt, P. R. 1983 Mistletoe leaf shape: a host morphogen hypothesis. In *The biology of mistletoes* (ed. M. Calder & P. Bernhardt), pp. 259–275. Sydney: Academic Press.
- Auerbach, M. & Simberloff, D. 1989 Oviposition site preference and larval mortality in a leaf-mining moth. *Ecol. Ent.* **14**, 131–141.
- Barlow, B. A. & Wiens, D. 1977 Host-parasite resemblance in Australian mistletoes: the case for cryptic mimicry. *Evolution* **31**, 69–84.
- Barrett, S. C. H. 1983 Crop mimicry in weeds. *Econ. Bot.* **37**, 255–282.
- Böcher, T. W. & Lewis, M. C. 1962 Experimental and cytological studies on plant species VII. *Geranium sanguineum*. *Biol. Skr. Dan. Vid. Selsk.* **11** (5), 1–25.
- Brown, V. K., Gange, A. C., Evans, I. M. & Storr, A. L. 1987 The effect of insect herbivory on the growth and reproduction of two annual *Vicia* species at different stages in plant succession. *J. Ecol.* **75**, 1173–1189.
- Brown, V. K., Gibson, C. W. D. & Sterling, P. H. 1990 The mechanisms controlling insect diversity in calcareous grasslands. In *Calcareous grasslands – ecology and management* (ed. S. H. Hillier, D. W. H. Walton & D. A. Wells), pp. 79–87. Huntingdon: Bluntisham.
- Carne, P. B. 1962 The characteristics and behaviour of the saw-fly *Perga affinis* (Hymenoptera). *Aust. J. Zool.* **10**, 1–34.
- Carne, P. B., Greaves, R. T. G. & McInnes, R. S. 1974 Insect damage to plantation-growth eucalypts in north coastal New South Wales, with particular reference to Christmas beetles (Coleoptera: Scarabaeidae). *J. Aust. Entom. Soc.* **13**, 189–206.
- Chabot, B. F. & Hicks, D. J. 1982 The ecology of leaf life spans. *A. Rev. Ecol. Syst.* **13**, 229–259.
- Ehrlich, P. R. & Raven, P. H. 1967 Butterflies and plants. *Scient. Am.* **216** (6), 104–113.
- Ehrlinger, J. R., Ullmann, I., Lange, O. L., Farquhar, G. D., Cowan, I. R. & Schulze, E.-D. 1986 Mistletoes: a hypothesis concerning morphological and chemical avoidance of herbivory. *Oecologia* **70**, 234–237.
- Elliot, H. T. & Bashford, R. 1978 The life history of *Mnesampela privata* (Guan.) (Lepidoptera: Geometridae) a defoliator of young eucalypts. *J. Aust. Entom. Soc.* **17**, 201–204.
- Everard, B. & Morley, B. D. 1970 *Wild flowers of the world*. London: Ebury Press & Michael Joseph.
- Gall, L. F. 1987 Leaflet position influences caterpillar feeding and development. *Oikos* **49**, 172–176.
- Gilbert, L. E. 1975 Ecological consequences of a coevolved mutualism between butterflies and plants. In *Coevolution of animals and plants* (ed. L. E. Gilbert & P. R. Raven), pp. 210–240. Austin: University of Texas Press.
- Gilbert, L. E. 1982 The coevolution of a butterfly and vine. *Scient. Am.* **247** (August 1982), 102–107.
- Givnish, T. J. 1979 On the adaptive significance of leaf form. In *Topics in plant population biology* (ed. O. T. Solbrig, S. Jain, G. B. Johnson & P. H. Raven), pp. 375–407. London: Macmillan.
- Givnish, T. J. 1986 (ed.) *On the economy of plant form and function*. Cambridge University Press.
- Givnish, T. J. 1990 Leaf mottling: relation to growth form and leaf phenology and possible role as camouflage. *Funct. Ecol.* **4**, 463–474.
- Godfray, H. C. J. 1986 Clutch size in a leaf-mining fly (*Pegomya nigritarsis*: Anthomyiidae). *Ecol. Ent.* **11**, 75–81.
- Gottlieb, L. D. 1984 Genetics and morphological evolution of plants. *Am. Nat.* **123**, 681–709.
- Hallam, A. 1977 (ed.) *Patterns of evolution as illustrated by the fossil record*. Amsterdam: Elsevier Scientific.
- Heinrich, B. 1971 The effect of leaf geometry on the feeding behaviour of the caterpillar of *Manduca sexta* (Sphingidae). *Anim. Behav.* **19**, 119–124.
- Hickey, L. J. & Wolfe, J. A. 1975 The bases of angiosperm phylogeny: vegetative morphology. *Ann. Missouri Bot. Gard.* **62**, 538–589.

- Horn, H. S. 1971 *The adaptive geometry of trees*. Princeton University Press.
- Hughes, N. F. 1976 *Palaeobiology of angiosperm origins*. Cambridge University Press.
- Jeffries, M. J. & Lawton, J. H. 1984 Enemy free space and the structure of ecological communities. *Biol. J. Linn. Soc.* **23**, 269–286.
- Jones, C. G. & Lawton, J. H. 1991 Plant chemistry and insect species richness of British umbellifers. *J. Anim. Ecol.* **60**. (In the press.)
- Kareiva, P. & Sahakian, R. 1990 Tritrophic effects of a simple architectural mutation in pea plants. *Nature, Lond.* **345**, 433–434.
- Kennedy, C. E. J. & Southwood, T. R. E. 1984 The number of species of insects associated with British trees: a re-analysis. *J. Anim. Ecol.* **53**, 455–478.
- Lawton, J. H. & Price, P. W. 1979 Species richness of parasites on hosts: agromyzid flies on British Umbelliferae. *J. Anim. Ecol.* **48**, 619–637.
- Mackay, D. A. & Jones, R. E. 1989 Leaf shape and host-finding behaviour of two ovipositing monophagous butterfly species. *Ecol. Ent.* **14**, 423–431.
- McGlone, M. S. 1991 A critical examination of the moabrowsing hypothesis for the origin of the divaricating plant syndrome. (Submitted.)
- McGlone, M. S. & Webb, C. J. 1981 Selective forces influencing the evolution of divaricating plants. *N.Z. J. Ecol.* **4**, 20–28.
- Milton, S. J. 1991 Plant spinescence in arid southern Africa: does moisture mediate selection by mammals? *Oecologia*. (In the press.)
- Moran, V. C. & Southwood, T. R. E. 1982 The guild composition of arthropod communities on trees. *J. Anim. Ecol.* **51**, 289–306.
- Niemela, P. & Tuomi, J. 1987 Does the leaf morphology of some plants mimic caterpillar damage? *Oikos* **50**, 256–257.
- Parkhurst, D. F. & Loucks, O. L. 1972 Optimal leaf size in relation to environment. *J. Ecol.* **60**, 505–537.
- Price, P. W., Bouton, C. E., Gross, P., McPherson, B. A., Thompson, J. N. & Weis, A. E. 1980 Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *A. Rev. Ecol. Syst.* **11**, 41–65.
- Prokopy, R. J. & Owens, E. D. 1983 Visual detection of plants by herbivorous insects. *A. Rev. Ent.* **28**, 337–364.
- Rausher, M. D. 1978 Search image for leaf shape in a butterfly. *Science, Wash.* **200**, 1071–1073.
- Smiley, J. 1978 Plant chemistry and the evolution of host specificity: new evidence from *Heliconius* and *Passiflora*. *Science, Wash.* **201**, 745–747.
- Smiley, J. T. 1985 Are chemical barriers necessary for evolution for butterfly-plant associations? *Oecologia* **65**, 580–583.
- Smith, A. P. 1986 Ecology of leaf color polymorphism in a tropical forest species: habitat segregation and herbivory. *Oecologia* **69**, 283–287.
- Southwood, T. R. E. 1987 Plant variety and its interaction with herbivorous insects. In *Insects – plants* (ed. V. Labeyrie, G. Fabres & D. Lachaise), pp. 61–69. Dordrecht: Junk.
- Sterling, P. H., Gibson, C. W. D. & Brown, V. K. 1991 Leaf miner assemblages: effects of plant succession and management. (Submitted.)
- Strong, D. R., Lawton, J. H. & Southwood, T. R. E. 1984 *Insects on plants. Community patterns and mechanisms*. Oxford: Blackwell Scientific Publications.
- Whitham, T. G. 1978 Habitat selection by *Pemphigus* aphids in response to resource limitation and competition. *Ecology* **59**, 1164–1176.

Discussion

P. J. GRUBB (*Botany School, University of Cambridge, U.K.*). Two points. First, Givnish was not only one of the first to canvas the idea that mottling of the leaves of some herbs in cool temperate deciduous forests is a form of camouflage against grazing animals (in the dappled light of the forest floor), but also one of the first to emphasize the contrast in such forests between the striking convergence in leaf form among the many herbaceous and woody species that are summer-green and the equally remarkable variety in leaf-form that exists in the species of ‘spring ephemeral’ whose leaves die down soon after the trees leaf out. If a compendium of all the world’s plant species is to be drawn up, including codified records of physiognomy and habitat as suggested by Professor May, it will clearly be important to include records of the phenology (seasonal incidence) of leafing.

Secondly, the remarkable plants the authors have described from New Zealand, with various features apparently selected by grazing pressure from extinct moas, should be seen in perspective. The great majority of native plants in New Zealand have forms that would be expected by an ecologist experienced in the forests and alpine zones of the tropics, subtropics and warm temperate regions elsewhere. The plants ‘moulded’ by moas are almost all confined to specialized sites: for example, the edges of forest against swamps, etc. (the divaricating shrubs) where the plants were constantly accessible to moas, and tree-fall gaps (narrow-leaved *Pseudopanax*) where they were similarly accessible, and also scarce on the scale of the whole landscape.