Plant structural traits and their role in anti-herbivore defence

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Abstract

We consider the role that key structural traits, such as spinescence, pubescence, sclerophylly and raphides, play in protecting plants from herbivore attack. Despite the likelihood that many of these morphological characteristics may have evolved as responses to other environmental stimuli, we show that each provides an important defence against herbivore attack in both terrestrial and aquatic ecosystems. We conclude that leaf-mass–area is a robust index of sclerophylly as a surrogate for more rigorous mechanical properties used in herbivory studies. We also examine herbivore counter-adaptations to plant structural defence and illustrate how herbivore attack can induce the deployment of intensified defensive measures. Although there have been few studies detailing how plant defences vary with age, we show that allocation to structural defences is related to plant ontogeny. Age-related changes in the deployment of structural defences plus a paucity of appropriate studies are two reasons why relationships with other plant fitness characteristics may be obscured, although we describe studies where trade-offs between structural defence and plant growth, reproduction, and chemical defences have been demonstrated. We also show how resource availability influences the expression of structural defences and demonstrate how poorly our understanding of plant structural defence fits into contemporary plant defence theory. Finally, we suggest how a better understanding of plant structural defence, particularly within the context of plant defence syndromes, would not only improve our understanding of plant defence theory, but enable us to predict how plant morphological responses to climate change might influence interactions at the individual (plant growth trade-offs), species (competition), and ecosystem (pollination and herbivory) levels.
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Introduction

How plants defend themselves against attack from herbivores has been the subject of considerable interest over many decades (Grime et al., 1968; Rhoades, 1979; Coley et al., 1985; Herms and Mattson, 1992; Agrawal and Fishbein, 2006). This large body of research has shown that plants are only able to live in environments where herbivores are common because of their ability to resist or recover from intense herbivore pressure (Hartley and Jones, 1997). The tissues of virtually all terrestrial, freshwater, and marine plants have qualities

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that to some degree reduce herbivory, including low nitrogen concentration, low moisture content, toxins or digestibility-reducing compounds (Hay et al., 1994; Hartley and Jones, 1997; Cronin et al., 2002). Intuitively it seems clear that many of the benefits, trade-offs and constraints attributed to the possession of chemical deterrents (Edwards, 1989; Herms and Mattson, 1992; Karban and Baldwin, 1997) must also apply to the development of structural defences, such as spines, hairs and toughened leaves. However, while considerable interest has focused on interactions between herbivory and chemical defence, less attention has been paid to the types, development and deterrent role that plant structures play in plant–herbivore interactions (Grubb, 1992; Schoonhoven et al., 2005). For example, in a recent review of ontogenetic changes in plant resistance to herbivory, of 17 papers considered only one included a structural component (Boege and Maquis, 2005). Moreover, of the reviews examining plant structural defences, none considers more than a sub-set of potential structures (Myers and Bazely, 1991; Werker, 2000), herbivore guilds (Juniper and Southwood, 1986; Schoonhoven et al., 2005) or habitats (Borowitzka, 1982; Fernandes, 1994). Our aim was to synthesise for the first time the way in which various types of plant structural defences affect the feeding behaviour of terrestrial and aquatic herbivores, and how their deployment is influenced by herbivore attack, resource availability, plant age and the conflicting demands imposed by plant growth, reproduction and chemical defence.

The concept of structural defence

Plants have a variety of herbivore-resistance mechanisms, generally assigned to two major categories: tolerance and avoidance. Some authors (Strauss and Agrawal, 1999; Stowe et al., 2000) consider 'defence' to be an umbrella term covering both avoidance and tolerance, but others (Rosenthal and Kotanen, 1994; Boege and Maquis, 2005) make a distinction between a plant's tolerance of herbivore attack, and properties to avoid herbivory through defence. Avoidance involves some kind of *structural* (e.g. leaves surrounded by thorns – Gowda, 1996), *chemical* (e.g. the production of phenolics that deter herbivores from continued feeding following an initial bite – Hanley and Lamont, 2001), or *phenological* (e.g. the rapid turnover of vulnerable parts or avoidance of herbivores through timing of the life cycle – Saltz and Ward, 2000) defence. Structural defences are avoidance mechanisms based on structural traits, whether these are conspicuous protruances supported by the plant, or microscopic changes to cell wall thickness. A useful definition of *structural defence* (consistent with Rosenthal and Kotanen, 1994; Boege

and Maquis, 2005) might therefore be: *any morphological or anatomical trait that confers a fitness advantage to the plant by directly deterring herbivores from feeding on it.*

Types of structural defence

Given the generality of our definition of structural defence, it is not surprising that many candidates for the role of structural deterrents emerge. These include various types of spines and thorns (spinescence), hairs (trichomes), toughened or hardened leaves (sclerophylly), and the incorporation of granular minerals into plant tissues. However, other forms of defence, such as mimicry (of objects such as stones and twigs, or other plants) and leaf presentation (leptophylly, rosette growth form, etc.) are not structural deterrents in the true sense as they do not involve physical contact with herbivores as the feedback mechanism. Our definition also excludes indirect defences such as domatia and extrafloral nectar glands that support populations of mutualist invertebrate defenders like ants. We also exclude resins and mucilage (produced by ducts and glandular trichomes), latex (produced by modified sieve tubes) and epicuticular waxes on the basis that these chemicals are not structural traits even though they may have some physical properties that reduce herbivore attack. See recent reviews by Werker (2000), Muller and Riederer (2005) and Konno et al. (2006) for further discussion of these defences.

We raise an additional structural trait here, 'divaricate branching', as it does not justify extended treatment elsewhere. Shoots with wiry stems produced at wide axillary angles such that they interweave is widespread among woody species in the New Zealand flora. This morphology confers some tolerance to wind and frost (Darrow et al., 2001) and reduces water loss within the crown interior (McGlone and Webb, 1981). Evidence for improved net carbon gain is equivocal as no controls were used nor is the phenomenon restricted to harsh climates (Kelly and Ogle, 1990; Lusk, 2002; Bond et al., 2004). Instead, Greenwood and Atkinson (1977) proposed that divaricate branching is a legacy of the evolutionary influence of New Zealand's extinct moas on plant resistance to browsing. In a well-executed study, Bond et al. (2004) showed how equivalent extant birds, emus and ostriches, had great difficulty removing and ingesting such tangled branches. Divaricate juveniles suffered 30−70% less mass loss than non-divaricate adult shoots.

The above example demonstrates a particular difficulty with any issue in evolutionary ecology in that adaptations that arise in response to one selective force may also provide an advantage when the organism possessing them is faced with pressure from another.

Thus a major problem when identifying any kind of anti-herbivore defence is that these 'defences' may have evolved as a response to physiological stresses and not directly to herbivory – so-called 'neutral resistance' (Edwards, 1989). Although Strauss and Agrawal (1999) argue that "a trait can be viewed as defensive even though defence is not its primary function", it is important to identify whether a defensive trait has any other adaptive significance to the plant that possesses it. Therefore, we briefly consider alternative adaptive explanations for the structural defences considered below, while highlighting the need to consider plant defence not as a single trait, but as a group of linked characteristics that form coadapted complexes (Coley, 1983; Agrawal and Fishbein, 2006).

Spinescence

Spinescence is a collective term used to describe the plant structures spines, thorns and prickles. A spine is defined as a sharp-pointed petiole, midrib, vein or stipule; thorns are woody, sharp-pointed branches; and prickles are any sharp-pointed outgrowth, from the epidermis or cortex of an organ (Grubb, 1992; Gutschick, 1999). Despite the fact that some spines may reduce radiation flux (Nobel, 1988), or assist with climbing (Grubb, 1992), most spinescence has almost certainly evolved as a defence against herbivores. Lev-Yadun (2001) has even suggested that the bright colours of thorns and spines in some Cactaceae, Agavaceae and Euphorbiaceae serve as a warning to mammal herbivores. Spinescence is generally considered to be more effective against vertebrates than invertebrates, due to the size relations of the plant–herbivore interactions (Cooper and Owen-Smith, 1986). The geographic synchrony of spinescent plants with large herbivores supports this claim (Myers and Bazely, 1991). In xeric Africa (e.g. tropical savannah) for instance, there are many large browsers and thorny plants (Grubb, 1992). Moreover, the East African *Acacia drepanolobium* is exposed to a variety of vertebrate herbivores that feed on low or high branches depending on the herbivore's reach. Thorn length in this species seems to track herbivory rates, as lower branches experience greater herbivory and they have longer thorns than the higher branches (Young and Okello, 1998; Young et al., 2003).

The efficacy of spinescence as a herbivore deterrent has been demonstrated in a number of studies. The European holly (*Ilex aquifolium*) exhibits great variation in leaf spinescence, and Obeso (1997) showed that holly shrubs with exceptionally spiny leaves were much less likely to suffer herbivory by large ungulates than neighbouring less spiny plants. In East Africa, the large thorns of *Acacia tortilis* not only protect leaves from herbivory by goats, but also protect the axillary meristems, i.e. the ability to produce new leaves (Gowda, 1996).

Spine and thorn removal experiments also demonstrate the protective value of these structures. Removal of thorns of *Acacia drepanolobium* caused a threefold increase in mammal browsing of new foliage (Milewski et al., 1991). An ingenious study by Cooper and Ginnett (1998) showed how the removal of thorns allowed southern plain woodrats (*Neotoma micropus*) greater access to raisins impaled on the branches of the shrub, *Acacia rigidula*. The removal of thorns from a range of spinescent shrub species in the Eastern Cape region of South Africa increased rates of herbivory by bushbucks (*Tragelaphus scriptus*) and boergoats (*Capra hircus*) principally by allowing both species to increase their bite size (Wilson and Kerley, 2003a). Cash and Fulbright (2005) similarly induced increased herbivory by the white-tailed deer (*Odocoileus virginianus*) when they removed thorns from two North American *Acacia* species. Spinescence is rare in aquatic plants. The leaves and stems of the freshwater macrophyte *Najas marina* do possess spiky projections, although Elger et al. (2004) reported high consumption rates by the pond snail, *Lymnaea stagnalis*, compared with 39 other macrophyte species. However, it is unclear whether spinescence in this species plays any role in deterring attack by vertebrate herbivores such as fish or waterfowl.

Despite numerous studies showing a significant effect on herbivore feeding behaviour, the role of spinescence as an herbivore deterrent has been questioned. Potter and Kimmerer (1988) examined the response of the generalist caterpillar, *Hyphantria cunea*, to unaltered leaves of the North American holly (*Ilex opaca*), and leaves from which the marginal spines had been excised. Their results indicate that the caterpillars were deterred not by marginal spines, but by the thick cuticle and tough leaf margin. These results underscore the contention that spinescence has evolved as a deterrent against large vertebrate herbivores rather than invertebrates, and the importance of sclerophylly as a defence against invertebrate herbivores (Coley, 1983; Choong, 1996). However, in the same study, Potter and Kimmerer (1988) also examined the responses of captive rabbits and deer to spinescent foliage, and foliage from which spines had been removed. They obtained little support that these larger herbivores discriminated on the basis of leaf spinescence, but did note a lack of herbivore damage on holly trees by larger mammals in the field.

In a similar study, Rafferty (1999) presented captive kangaroos, *Macropus fuliginosus,* with a choice between Western Australian *Hakea* (Proteaceae) foliage with leaf spines intact, or with spines removed (Table 1). For mature plants of two species (*H. lissocarpha* and *H. undulata*) there was a preference for leaves from

Table 1. Mean volume of foliage (mm^3) of four Western Australian *Hakea* species consumed by western grey kangaroos (*Macropus fuliginosus*) in captive feeding trials at Perth Zoo, Western Australia

Species	Seedlings			Adults		
	Spines intact	Spines removed	P (*t*-test)	Spines intact	Spines removed	P (*t*-test)
H. erinacea[a]	182	182	0.980	1066	867	0.770
H. lissocarpha[a]	319	362	0.400	1945	2804	<0.001
H. petiolaris[b]	74	82	0.780	1185	1693	0.360
H. undulata[c]	593	537	0.420	2558	2922	<0.001

[a]Divaricate leaf segments with pungent tips.
[b]Broad leaf with blunt hard tip.
[c]Broad leaf with many marginal spines; collated from Rafferty, (1999).

which spines had been removed. In the other two species examined, spine removal had little effect, although for *H. petiolaris* this is not surprising given that it is only weakly spinescent (leaves have a single, blunt terminal spine). *Hakea erinacea* is a very spiny plant, so at first glance the results for this species seem anomalous. However, observation of feeding kangaroos suggested that they were avoiding the spines by approaching foliage from the base, a feeding method that they could not use in the wild.

Pubescence

Pubescence refers to the layer of hairs (trichomes) on stems, leaves, or even fruits. Levin (1973) defines trichomes as hair-like appendages extending from the epidermis of aerial tissues and notes that they occur in a multitude of forms, ranging from straight, spiral, stellate and hooked to glandular. Trichomes are thought to have evolved primarily as physiological barriers against water loss and excessive heat gain (Levin, 1973; Gutschick, 1999), and may also serve to protect plant tissue against UV radiation (Manetas, 2003). Rigid trichomes on seeds and fruits may also serve as a mechanism aiding propagule dispersal by animals (Werker, 2000). However, observations first made by Haberlandt (1914) indicated that leaf hairs also have a role in herbivore defence. Thus, trichomes, like most other forms of structural defence, fulfil dual roles. For example, leaf hairs on the North American species, *Verbascum thapsus*, act as a structural defence against grasshoppers, while also protecting younger leaves against water loss (Woodman and Fernandes, 1991). Nevertheless, in spite of their clear physiological benefits, it is now widely accepted that trichomes may play an important defensive role against herbivory (Werker, 2000; Dalin and Bjorkman, 2003; Handley et al., 2005).

Trichomes may fulfil several defensive roles. Most frequently their presence is associated with reduced rates of tissue ingestion by herbivores. Organisms affected in this way include molluscs (Westerbergh and Nyberg, 1995) and leaf chewing and sap-sucking insects (Eisner et al., 1998; Haddad and Hicks, 2000; Traw and Dawson, 2002; Dalin and Bjorkman, 2003). Herbivores that feed internally, such as leaf miners and leaf-gallers, and larger insects, like grasshoppers, whose size helps them avoid the effects of pubescence, are much less affected by trichomes (Andres and Connor, 2003). Trichomes may also prevent insect oviposition by affecting the security with which the eggs are attached to leaves (Haddad and Hicks, 2000; Handley et al., 2005), as well as interfering with herbivore movement: hooked trichomes entrap or even puncture some insects (Quiring et al., 1992; Eisner et al., 1998).

Their defensive role is also demonstrated by the negative relationship between trichome density and rates of herbivore damage. In *Brassica rapa*, for instance, plants with a sparse pubescence suffered greater damage by cabbage white butterfly larvae (*Pieris rapae*) than high trichome-density plants (Ågren and Schemske, 1993). Similarly, the black vine weevil (*Otiorhynchus sulcatus*) avoids *Fragaria chiloensis* plants with dense pubescence (Doss et al., 1987). The removal of leaf hairs also demonstrates their protective value. When hairs were shaved from the leaves of *Silene dioica*, they became more susceptible to attack by terrestrial snails than untreated counterparts (Westerbergh and Nyberg, 1995). However, trichomes can inadvertently protect herbivores against natural enemies (Eisner et al., 1998; Andres and Connor, 2003). Caterpillars of the Californian pipevine swallowtail butterfly (*Battus philenor*) are specialist herbivores on Dutchman's pipe (*Aristolochia californica*). Although trichomes reduce caterpillar feeding by up to 70%, they also reduce movement of the predatory lacewing, *Chrysopa carnes*, offering *Battus* larvae some protection against predation (Fordyce and Agrawal, 2001). Similarly, Eisner et al. (1998) showed that aphids (*Macrosiphium mentzeliae*) avoid entrapment on *Mentzelia pumila* trichomes by virtue of their slow walking technique and fine-tipped legs. The main

Mentzelia predator, the beetle *Hippodamia convergens*, however is often trapped by the same trichomes. The number of spider mite eggs consumed by the predatory mite, *Phytoseiulus persimilis*, is inversely related to trichome density (Stavrinides and Skirvin, 2003). However, the net effect depends on the extent to which the spider mite's life cycle and movement is also inhibited by the trichomes, and the ability of the trichomes to act as shelters for the predatory mite ('indirect defence').

Sclerophylly

Sclerophylly, a term introduced by Schimper (1903), literally means 'hard-leaved'. Scleromorphic features may have evolved for reasons of leaf support; such as resistance to wilting (Nobel et al., 1975; Chabot and Hicks, 1982), or water (Lamont et al., 2002) or nutrient (Chapin et al., 1993) conservation. Hard leaves may also enhance total (but not instantaneous) assimilation efficiency and defensive compound accumulation (Coley, 1988) via increased leaf longevity (Wright et al., 2004). Less attention has been given to increased resistance to heat (Groom et al., 2004) and cold (Mitrakos, 1980) and leaf protection against UV light (Jordan et al., 2005). Certainly, indices of sclerophylly, such as LMA (Table 2), increase in value for nutrient-poor soils, full sunlight, higher elevations and drier climates (Diemer, 1998; Wright et al., 2002; Groom et al., 2004), an effect that can be induced experimentally (Groom and Lamont, 1997a). Nevertheless it is also clear that sclerophylly can be a valuable deterrent against herbivore damage (Turner, 1994).

Scleromorphic leaves and shoots reduce both the palatability and digestibility of plant material (Grubb, 1986; Robbins, 1993), so ultimately limiting herbivore fitness (Perez-Barberia and Gordon, 1998). The digestion of cellulose in particular is a major problem for both invertebrate and vertebrate herbivores (van Soest, 1982; Hochuli, 1996). However, given that the presence of cellulose in plant tissues is characteristically associated with lignin, hemicellulose and silica (van Soest, 1982), it is difficult to disentangle effects of cellulose on digestion, and its effects on mechanical properties that directly affect palatability (Hochuli, 1996) that is the subject of our review. Nevertheless, while indigestibility of plant material *per se* may not prevent attack by vertebrate herbivores, it can act as a deterrent when more palatable plants are available (Forsyth et al., 2005), or act to deter vertebrates from consuming the tougher parts of individual leaves (Teaford et al., 2006).

A host of studies have demonstrated how non-vertebrate herbivores are deterred by scleromorphic structures. In South America, Bjorkman and Anderson (1990) showed that butterfly larvae tend to avoid feeding on toughened leaves of the blackberry (*Rubus bogotensis*). In Hong Kong, Choong (1996) described how the larvae of three Lepidopteran species avoid the structurally toughened leaf veins produced by *Castanopsis fiss*. When presented with a choice between pairs of salt-marsh plant species, the North American crab *Armases cinereum* always preferred plants with softer leaves (Pennings et al., 1998). Other authors detail the avoidance of toughened leaves by terrestrial invertebrates (Bernays, 1986; Steinbauer et al., 1998), and a similar picture emerges in aquatic ecosystems where toughened laminas deter feeding by both freshwater (Cronin et al., 2002) and marine invertebrates (Erickson et al., 2004).

There have been concerted efforts to interpret leaf structure in terms of mechanical properties that reflect palatability and digestibility better than morphological approaches (LMA) or chemical approaches (crude fibre: nitrogen ratio), both traditionally used as indices of sclerophylly (Choong et al., 1992). Table 2 describes 9 leaf properties referred to in our review. We do not

Table 2.   Mechanical properties referred to in this review

Test	Variable	Formula	Mechanical property measured
Dry leaf after taking area	Hardness (LMA)	M/A	Dry density of leaf combined with its thickness
Dry leaf after taking area and thickness	Density	M/V	Dry density of leaf
Dry leaf after taking area	Softness (SLA)	A/M	Inverse of dry density of leaf combined with its thickness
Punch (rod)	Punch strength	F_{max}/A	Pressure required by flat object to penetrate leaf
Punch (rod)	Work to punch	$(F/A) \times D$	Work required to force rod through leaf
Shear (scissors)	Work to shear	$(F \times D)/W$	Work required to cut leaf per unit leaf width
Tear	Force to tear	F_{max}/W	Force required to tear leaf per unit leaf width
Tear	Work to tear	$(F \times D)/W$	Work required to tear leaf per unit leaf width
Bend	Flexural stiffness	$(F/D) \times B^3$	Elastic resistance to bending per unit leaf strip width

M, mass of leaf (L); A, area of leaf or punch; V, volume of leaf; F, force; D, displacement of moving head of test machine; W, leaf width in plane of shear, tear or bend; B, span length between supports in bending test. 'Specific' (S) versions of these variables are derived by dividing them by leaf thickness, except LMA, density and SLA. Modified from Witkowski and Lamont (1991), Read et al. (2005).

include those standardised by leaf thickness as this is clearly a component of leaf resistance to being eaten. An alternative approach would be to use standardised properties and thickness separately. Unfortunately, the index of flexural stiffness (which we consider of great relevance to the effectiveness of spines) still corrects for leaf width partly because some leaves are too wide to be assessed. There are three issues to be considered: (1) To what extent are the indices of sclerophylly and mechanical properties correlated or provide independent information? (2) Which parameters are best correlated with levels of herbivory? (3) In multivariate studies that include these parameters what relative explanatory value do they have?

Groom and Lamont (1999) argued that conceptually LMA was a better index of sclerophylly than the crude fibre : nitrogen ratio though they are usually correlated. Edwards et al. (2000) showed a close correlation between LMA, punch strength, work to punch and the ranked assessments of seven botanists based on their impressions of leaf texture for 19 species. Because LMA is strongly influenced by leaf thickness, extremely succulent leaves can have high levels of LMA (Lamont and Lamont, 2000) making it an imprecise index of sclerophylly but not necessarily of resistance to herbivory, which is our interest here. This increases the argument for separating the density and thickness components of LMA (Witkowski and Lamont, 1991) to see if they independently affect other mechanical properties and levels of herbivory. Density then is more equivalent to mechanical properties standardised by thickness, and fibre content. This is supported by the results for 75 species in two rainfall zones in Eastern Australia (Wright and Westoby, 2002): work to shear was highly correlated with LMA (though with different slopes for each rainfall zone); this was also true for specific work to shear (work to shear divided by leaf thickness) versus density (LMA divided by thickness). In one of the few cases where density and thickness have been treated separately, the high correlation between LMA (SLA) and work to shear could be attributed to the density not thickness component (Choong et al., 1992). Accepting fibre : nitrogen as a good predictor of leaf palatability, they advocated work to shear as an alternative index because of their high correlation, but LMA (SLA) and punch strength were also highly correlated with this ratio in their study. Read and Sanson (2003) also showed a close correlation between LMA, fibre : nitrogen, and the botanists sclerophylly index in their study of 32 species in Eastern Australia.

Close correlations between LMA and leaf mechanical properties such as punch strength, work to punch, work to shear and flexural stiffness have been widely demonstrated (Diaz et al., 2001; Iddles et al., 2003; Read and Sanson, 2003; Read et al., 2005; Peeters et al., 2007). Thus, we conclude that all leaf mechanical properties are strongly correlated with LMA and rarely offer new information of their own accord. Where a simple index of mechanical resistance to herbivory is required, LMA appears to be suffice, preferably separated into its two components, dry density and thickness, for greater interpretation. Where details on how sclerophylly works to increase resistance to being bitten (punch strength, work to punch), cut (work to shear), torn (work to tear) or penetrated (flexural stiffness) are required, indices of these mechanical properties are available. Again, there may be a case for examining the specific versions of these 'material' properties separately from leaf thickness.

For a wide range of angiosperms in Argentina, work to tear was negatively correlated with leaf area consumed in cafeteria trials for snails but not LMA (SLA), while LMA was more highly negatively correlated than work to tear for grasshoppers (Perez-Harguindeguy et al., 2003). Since radulas and mandibles act more like shears than pullers (tearing) we wonder what the outcome of using work to shear might have been? There were no correlations between punch strength, work to punch, fibre content and LMA (SLA) and palatability (area eaten) when leaves of six Australian rainforest species were presented to individual snails, crickets and moth larvae, although the softest-leaved species was most palatable (Iddles et al., 2003).

For the abundance of various insect guilds on young and mature leaves of 18 Australian plant species, two of five guilds were negatively associated with LMA, one of eight with punch strength, two with work to punch, two with work to tear, and five with work to shear (Peeters et al., 2007). Only the curculionids (rostrum chewers) were negatively associated with all five indices. Overall, total suckers were associated with the last two variables (not with the punch variables as we would expect), and total chewers with all four (LMA was not included) – though they also do not tear leaves. This is a rare demonstration of the type of index being used affecting the outcome of the significance of herbivory on various insect groups (except the rostrum chewers) though in the absence of relevant hypotheses. Overall, four of the 34 comparisons reported here gave different levels of significance for the extent of herbivory between LMA and material properties, giving little support for measuring them in place of LMA in the search for better mechanistic descriptors.

For 102 rangeland species in Argentina and Israel, Diaz et al. (2001) showed that, in two-variable models for these grassland species, plant height, life history and life form were more important predictors of grazing resistance than force to tear. However, grazing response was gauged on relative abundance in lightly versus heavily grazed pastures, so that many other plant factors unrelated to grazing, such as reduced competition, could account for whether the species was categorised as

grazing-resistant or susceptible. Perez-Harguindeguy et al. (2003) observed that LMA (SLA) and work to tear were more highly correlated (negative, though there was no test whether this was significantly so) with leaf area consumed by snails and grasshoppers than leaf nitrogen and water contents (positive), and carbon : nitrogen ratio (negative), in cafetaria trials. For the two groups of herbivores combined, nitrogen content, carbon : nitrogen ratio and work to tear were equally important in field trials. They pointed out that differences in patterns between the field and cafeteria results could be attributed to specialist plant–herbivore relations, and inaccessibility of some plant species to invertebrates, in the field. Iddles et al. (2003) obtained no correlation between palatability (area eaten) and four mechanical properties, nitrogen and water contents, and leaf thickness when leaves were presented to individual snails, crickets and moth larvae. The authors noted that the level of damage in the field actually records the extent to which some herbivore species are able to overcome defences, especially highly specialised feeders not used in their tests, again leading to different patterns between palatability trials and field observations.

In a comprehensive multivariate analysis, LMA was unrelated to levels of two indices of herbivory by kangaroos and rabbits among 20-month-old juveniles of 19 species in a Western Australian woodland (Rafferty and Lamont, 2007). Grass-like species were more likely to be consumed than shrub species independent of their levels of LMA, spinescence, nitrogen, phosphorus, crude fibre or tannins. This appears to explain why the most heavily consumed species were relatively small (they were grasses) and why they were highest in potassium content (also grasses). Leaves of 4-month-old juveniles of seven needle-leaved (grass-like) Hakea species consumed by kangaroos (on a volume basis) was twice that for seven broad-leaved Hakea species (Rafferty et al., 2005). They were also larger and spinier, had three times greater LMA, one-third the content of phenolics (tannins), and no difference in nitrogen content. Overall, leaf volume consumed was best related to phenolic content with no relationship with LMA. When multivariate studies are undertaken, we conclude that leaf hardness, however measured, is rarely the overriding factor in controlling the pattern of herbivory.

Minerals

Many species of terrestrial and aquatic plants deposit minerals in leaf and stem tissues. The leaves of terrestrial grasses for instance contain silica (Grime et al., 1968), accumulated through the passive or active absorption of monosilicic acid from the soil, then transported to and deposited in epidermal cell walls to form deposits called phytoliths (Vicary and Bazely, 1993). Silicification varies with plant part, species, growth stage (mature plants tend to have a higher silica content than younger plants), and silica supply in the soil (Moore, 1984; McNaughton et al., 1985). It has been suggested that the presence of silica in grasses acts as a substitute for more energy demanding, carbon-based structural support, thus directly aiding plant growth (McNaughton et al., 1985). Nevertheless, the increased toughness and rigidity imparted by phytoliths to grass stems appears to be an important factor in increasing resistance to stem-boring insects and influencing leaf-eating invertebrates, such as molluscs and Lepidoptera (Grime et al., 1968; Vicary and Bazely, 1993; Massey and Hartley, 2007). Vertebrates may also be deterred by phytoliths. The North American prairie vole, Microtus ochrogaster, is known to avoid grasses containing silica (Galimuhtasib et al., 1992), as is the European field vole Microtus agrestis (Massey and Hartley, 2007). The presence of silica in plants is also detrimental to vertebrates by increasing tooth wear, reducing the digestibility of forage carbohydrates, and causing silica urolithiasis, a fatal condition where monosilicic acid is absorbed into the blood stream and deposited in the kidneys, leading to blockage of the urinary tract (Vicary and Bazely, 1993).

Calcium minerals also accumulate in the tissues of both terrestrial and aquatic plants. Calcium oxalate crystals have been recorded in most terrestrial plant families; the most commonly described being the star-shaped raphides that aggregate in bundles within plant cells (Franceschi and Nakata, 2005). Calcium oxalate minerals are known to protect tree bark from attack by boring insects (Hudgins et al., 2003), and to act as a foliar defence against both invertebrate (Korth et al., 2006) and vertebrate herbivores (Ward et al., 1997). Ward et al. (1997) looked at the distribution of calcium oxalate crystals in the leaves of Pancratium sickenbergeri in the Negev desert. They showed that the three species of herbivores known to feed on this lily (the gazelle Gazella dorcas, a moth larva Polytella cliens, and the snail Eremina desertorum) avoid parts of leaves containing calcium oxalate. Moreover, Pancratium populations exposed to the highest rates of gazelle herbivory also contained the highest leaf raphide concentrations.

Calcium minerals are also present in marine algae (Borowitzka, 1982), particularly in the crustose, coralline algae that are commonly associated with heavily grazed, sub-littoral rocky shores (Steneck, 1986). Nevertheless the anti-herbivore role these minerals play was long obscured by the fact that many of the algae containing them also possessed well-developed chemical defences. However, a series of experiments incorporating powdered calcium carbonate into artificial foods demonstrated that this mineral may have important deterrent qualities in its own right. The gastropod, Dolabella auricularia, and the sea urchins, Diadema setosum and Mespilia globules, avoid foods containing

powdered calcite minerals (Pennings and Paul, 1992). Some herbivorous fish have also been shown to avoid feeding on artificial foods rich in calcium minerals (Pennings et al., 1996). However, the failure of Hay et al. (1994) to demonstrate any significant deterrent effect of calcite minerals on the feeding behaviour of sea urchins, amphipods or parrot fish, led them to suggest that calcification acts to increase the potency of chemical defences by changing the gut pH of these herbivores, rather than having a direct deterrent effect. Some freshwater macrophytes, particularly members of the Nymphaeaceae, contain stellar-shaped calcium oxalate crystals associated with the aerenchyma, although their defensive function remains unclear (Kuo-Huang et al., 2000).

Herbivore foraging behaviour and adaptations

In order to continue to utilise plants as a food resource, herbivores have to develop ways of counter-acting plant defences. Indeed the evolutionary 'arms race' between plants and their herbivores is thought to be responsible for the often bewildering array of defences produced by plants (Berenbaum and Feeny, 1981; Becerra, 2003). It is clear therefore that the efficacy of any defence can be linked to the level of co-adaptation between the herbivore and its target plant (Cooper and Owen-Smith, 1986; Becerra, 2003). For every defence it is almost certain that at least one herbivore species will develop a behavioural or morphological response in order to overcome it.

As we have noted, the types of structural defence employed by a plant depend to a great extent on the size of the herbivore most likely to attack it. Differences in herbivore feeding styles and behaviour result in important differences in the character, magnitude, and long-term effects of damage inflicted on plants. Most invertebrate herbivory involves the gradual removal of small amounts of tissue over a prolonged period. As a result, plants face a continuous drain of resources at several points. The specificity of damage also means that even a relatively minor amount of tissue loss has a disproportionately large impact on the plant (Kotanen and Rosenthal, 2000). However, the specificity of attack associated with invertebrate herbivory means that plants can focus their defences upon particularly vulnerable areas. Moreover, the slower rate of damage inflicted by invertebrates allows the plant time to respond with increased (inducible) defence or re-growth. Herbivory by vertebrates is often sudden and severe, a reflection of their large size relative to that of the plants they attack (Kotanen and Rosenthal, 2000). The occurrence of damage is often spatially and temporally stochastic (Varnamkhasti et al., 1995) and so may exert a more significant impact on plant populations than attack by invertebrate herbivores (Crawley, 1989). Vertebrates, by virtue of their larger size, are much less selective in their choice of plant tissues. Therefore anti-vertebrate defences tend to be large, because it is much more difficult for the plant to defend specific parts of their anatomy against vertebrates.

Another important distinction between the ways in which structural defences work is whether they reduce consumption rates or reduce the ability of herbivores to digest material once consumed (Belovsky et al., 1991; Robbins, 1993; Laca et al., 2001). The presence of spines and thorns reduces the rate of herbivory by impeding stripping motions and forcing the herbivore to eat around the defence (Myers and Bazely, 1991; Wilson and Kerley, 2003b). Moreover, spinescent plants frequently possess small leaves, further reducing herbivore foraging efficiency as the reward received is seldom worth the time or energy needed to exploit it (Belovsky et al., 1991; Gowda, 1996). Indeed, it has been argued that one of the major factors determining which herbivores are more successful in a community is the scaling of plant traits to the herbivore's mouthparts (Palo and Robbins, 1991). Larger herbivores are poorly adapted to dealing with small amounts of plant tissue, since their feeding morphology and metabolic resource requirements mean that they require a large minimum foliage intake (Belovsky et al., 1991). It is perhaps not surprising therefore that those herbivores with smaller mouthparts are better suited to dealing with the intricate task of removing small leaves from between dense assemblages of spines and thorns (Belovsky et al., 1991; Laca et al., 2001). Even for a large vertebrate such as the giraffe, foraging on spiny acacia trees is facilitated by the possession of a long, flexible tongue. Moreover, many ungulate herbivores in the semi-arid regions where spinescence is most prevalent also tend to have tough, leathery mouthparts, and nicitating eye membranes, both thought to be adaptations for coping with foraging on spiny plants (Brown, 1960).

Pubescence works in a broadly similar way to spinescence in that herbivore intake rates are reduced because foragers attempt to avoid trichomes when feeding (Schoonhoven et al., 2005). However, since pubescence is geared towards invertebrate herbivores, adaptations are often markedly different from those developed by large vertebrates that feed on spiny vegetation. Larvae of the butterfly, *Mechanitis isthmia*, are able to exploit Venezuelan *Solanum* species by feeding communally and relying on the accumulation of silk to limit the defensive action of trichomes (Rathcke and Poole, 1975). Beetle larvae (*Gratiana spadicea*) have modified legs whose rounded tarsal apertures match that of the cylindrical pointed trichomes produced by *Solanum sisymbriifolium*. This adaptation effectively allows the larvae to move unhindered and feed on the

leaves of its food plant (Medeiros and Moreira, 2002). Other Orthopteran (Hulley, 1988) and Coleopteran (Siebert, 1975) larvae deal with trichomes by removing them before eating the exposed leaf lamina. The sphingid caterpillar (*Erinnyis ello*) has a more direct approach, eating the hairs produced by *Cnidosolus urens* prior to consuming its leaves (Hulley, 1988).

Unlike spines and trichomes, sclerophylly and mineral secretion both reduce intake rates and the digestibility of plant material. Consequently, herbivores require different adaptations to overcome them. A plant's resistance to ingestion is positively related to fibre or silica content simply because increased toughness means it takes longer for herbivores to chew and process plant material (Laca et al., 2001). The ingestion rates of both sheep (MacKinnon et al., 1988) and cattle (McLeod and Smith, 1989) are significantly reduced when fed on tougher leaves. Many insects get around the problem of toughened plant tissues by avoiding them. The larvae of several Lepidopteran species 'window feed': removing discrete areas of mesophyll and epidermis and avoiding the sclerenchymatous bundle sheaths of North American maple leaves (Hagen and Chabot, 1986). However, for most herbivores, modifications to the mouth and teeth are often important if they are to successfully exploit toughened plants.

Among marine molluscs, limpets are adapted for feeding on rocky substrates. Strong and robust silica-impregnated teeth, and a fixed radula that causes the teeth to be used in a rasping manner, reduce tooth wear and allows them to graze deeply into tough substrates. Nevertheless most limpets still feed selectively on filamentous or microalgae and avoid calcium-rich, crustose algae. The North America limpet, *Acmaea testudinalis*, actually has a preference for the crustose alga, *Clathromorphum circumscriptum* (Steneck, 1982). It is able to exploit this resource by virtue of the perpendicular alignment of its shovel-like teeth that allows it to excavate deep into the surface of *C. circumscriptum*. These unique morphological modifications make it poorly adapted to feeding on often more abundant and nutritious non-coralline alternatives (Steneck, 1982).

In terrestrial ecosystems, the robust mouthparts that characterise many insect herbivores, particularly among Orthoptera and Lepidoptera, are believed to be an adaptation to feeding on fibre- and silica-rich plant material (McNaughton et al., 1985; Hochuli, 1996; Schoonhoven et al., 2005). Bernays (1986) showed how grass-specialist Orthoptera have larger heads, mandibles, and adductor muscles than non-grass feeders. Even within a species there may be variation in mouthpart morphology depending on food plant preference. Individuals of the aquatic beetle, *Galerucella nymphaeae*, which feed on relatively tough leaves of *Nuphar lutea* have disproportionately larger mandibles than conspecifics that feed on the softer leaves of *Rumex hydrolapathum* (Pappers et al., 2002). For vertebrates, the evolution of 'hypsodonty' (hardened, high-crowned teeth) by ungulates and macropods (McNaughton et al., 1985), and the possession of continuously growing teeth by rodents (Phillips and Oxberry, 1972), are adaptations ascribed to a dietary preference for silicified grasses (Janis and Fortelius, 1988). Indeed, the rapid radiation of large ungulates during the Late Miocene has been linked to the simultaneous spread of grasses and the evolution of hypsodonty (Jernvall and Fortelius, 2002).

The dominance of ungulate herbivores across Africa, Asia and the Americas is also attributed to the evolution of a ruminant stomach and the ability to digest grasses and other toughened plant material (Perez-Barberia et al., 2004). While it is difficult to disentangle the effects of leaf toughness on intake rates and digestion, the ability to deal with tough or fibrous material once ingested is clearly an important adaptation to feeding on this kind of vegetation. Unlike monogastric animals, whose stomach's main roles are mastication and acidification, a ruminant's stomach also has an absorption function. This increased potential for nutrient uptake is facilitated by the presence of symbiotic microorganisms and their release of cellulase enzymes. These enzymes break down the cellulose-rich, cell wall fraction of plant material, releasing fatty acids that are immediately absorbed by the stomach. The ability to utilise cellulose and extract nutrients from low-quality food represents a significant advantage over other herbivores (van Soest, 1982). Few insects are able to digest cellulose or related structural components of plant cells (Hochuli, 1996). Indeed, it has been argued that the presence of cellulose in plant tissues is the main reason why the relative abundance of terrestrial plants remains high in comparison with the insects that feed on them (Abe and Higashi, 1991). Although insects do digest a far lower fraction of ingested plant material than mammals, they remain successful simply because they have relatively modest nutritional demands and can ingest a large amount of plant material quickly (Hochuli, 1996).

Induced responses to herbivory

The traditional view of plant defence was that both chemical and structural deterrents were present at fixed (constitutive) levels as a response to evolutionary interactions with herbivores. More recently it has been demonstrated that plants are able to increase (inducible) defences in the face of active tissue loss (Karban and Baldwin, 1997). Several authors have shown that, like chemical defences, the development of structural defence can be stimulated by the onset of herbivore attack, a

clear indication that these types of defence fulfil a defensive role. Indeed, structural traits such as spines or trichomes provide an ideal model system for the study of induced defences as they are easy and inexpensive to measure in the field, can be readily manipulated on the plant, and have a clear and demonstrable defensive function (Young et al., 2003).

For many years, naturalists noted the absence of spines on plants, or parts of plants, not subject to herbivore attack (O'Rourke, 1949; Abrahamson, 1975). Experimental work has highlighted a close relationship between herbivore pressure and the development of protective thorns in East African *Acacia*. Young and Okello (1998) show that 22 months after herbivore exclusion, thorn length on new shoots of *Acacia drepanolobium* was reduced by 19%. Subsequently this reduction reached 40% over 5 years (Young et al., 2003). Moreover, simulated pruning on trees previously protected from giraffe and elephants results in the rapid induction of longer spines on *A. drepanolobium*. Spine density and length were much greater in three *Berberis* species of Argentinian shrublands following pruning by fire, at a time when they are especially vulnerable to browsing by ungulates (Gowda and Raffaele, 2004). Similarly, other researchers have shown how simulated herbivory results in increased spinescence for plants as taxonomically disparate as *Hormathophylla spinosa* (Gomez and Zamora, 2002), *Opuntia stricta* (Myers and Bazely, 1991), *Rubus fruticosus* agg. (Bazely et al., 1991) and *Quercus calliprinos* (Perevolotsky and Haimov, 1992).

There are numerous examples of the induction of pubescence following leaf damage. These include increased trichome densities in willows (*Salix cinerea*) damaged by leaf beetles (*Phratora vulgatissima*; Dalin and Bjorkman, 2003) and for the tropical shrub, *Cnidoscolus aconitifolius*, following artificial defoliation (Abdala-Roberts and Parra-Table, 2005). It is clear that the induction of trichome production may be specific to the damage inflicted by a particular herbivore. Traw and Dawson (2002) show how increased trichome densities on leaves of *Brassica nigra* depend on whether plants are attacked by Lepidopteran (*Pieris rapae, Trichoplusia ni*) or Coleopteran (*Phyllotreta cruciferae*) larvae, and where on the plant the attack takes place. The seventh leaf of plants exposed to *P. rapae* had 76% more trichomes per unit area than controls, whereas equivalent leaves of plants damaged by the other two herbivores exhibited no response. The ninth leaf damaged by *T. ni* had 113% more trichomes per unit area than controls, whereas the other two herbivores elicited no response. These differences in trichome response to *P. rapae* and *T. ni* were ascribed to differences in feeding styles, and to possible variations in salivary enzymes known to stimulate the induction of defences in *Brassica* species.

The mineral content of some plant tissues also responds to changes in herbivore pressure. A study on the production of calcium oxalate in *Sida rhombifolia* showed a significant increase in raphide density in plants subjected to artificial defoliation (Molano-Flores, 2001). When tissue was removed from bulbs of the desert geophyte, *Pancratium sickenbergeri*, damaged bulbs subsequently contained more calcium oxalate than undamaged controls (Ruiz et al., 2002). Grazing pressure can induce changes in the silica content of grasses. McNaughton et al. (1985) noted that leaf silica concentrations are higher in the more intensely grazed grasslands of the Serengeti National Park. Similarly, Massey and Hartley (2007) reported increased silica content in two grass species subjected to vole and locust herbivory. Interestingly, while defoliation by both species stimulated a 400% increase, artificial defoliation had no effect on leaf silica content.

The degree of sclerophylly may also respond to herbivore attack. Perevolotsky and Haimov (1992) showed how, over a 5-year period, leaf toughness in *Quercus calliprinos* increased by 21% during grazing by goats. The marine alga, *Ascophyllum nodosum*, responded to simulated herbivory by increasing its tensile strength and lamina toughness (Lowell et al., 1991). Browsing by Sika deer on the East Asian shrub, *Viburnum dilatatum*, increases leaf hardness, with the result that the amount of leaf damage caused by insects at sites where browsing by deer is common is reduced (Shimazaki and Miyashita, 2002).

Ontogenic changes

A clear understanding of ontogenic responses to herbivory is required if we are to understand the ecological and evolutionary consequences of plant resistance to herbivory, yet few authors have addressed how patterns of herbivory relate to developmental changes in plant defence (Boege and Maquis, 2005). There are two over-arching processes associated with plant development that influence resource allocation to anti-herbivore defences. The first is an increase in plant size with age. Older plants possess larger resource-acquiring and storage organs, whereas growth rates and metabolic activity decrease. These changes bring about the second set of age-related changes: the shifting demands in the functional priorities placed upon plant growth, herbivore resistance, and reproduction (Weiner, 2004; Boege and Maquis, 2005). Ishida et al. (2005) suggest that during the transition from the seedling stage to maturity, the priority of resource use for the tropical forest tree, *Macaranga gigantea*, shifts from photosynthetic performance to herbivore defence. Hence, they reasoned that the more sclerophyllous leaves on adult trees were a response to the increased herbivore pressure

placed upon older plants. In the following section we review the development and expression of structural defences at several plant life history stages, with particular emphasis on the regeneration/reproductive phase.

Seeds and fruits

Seeds represent the most vulnerable stage of a plant's life history. Many types of animals (birds, mammals, molluscs, insects, fish, crustaceans) are known to eat seeds. Although highly variable between species, locations and years, the fractions of seeds consumed by animals often exceed 90% of all seeds dispersed (Fenner and Thompson, 2005). In many cases these losses have a major effect on subsequent rates of plant recruitment (Silman et al., 2003). It is not surprising therefore that many seeds are well protected by various types of structural defence. Structural traits that may help reduce seed losses to granivores, some of which may now be extinct (Jansen and Martin, 1982), centre on possession of a hard seed coat (van der Meij et al., 2004), the accumulation of silica raphides within the embryo (Panza et al., 2004), development of trichomes (Werker, 2000), and the protection of seeds by cones or woody fruits (Groom and Lamont, 1997b).

Although thick seed coats have been proposed as a mechanism for delaying germination (Fenner and Thompson, 2005), particularly in fire-prone environments (Whelan, 1995), it has been suggested that they also provide protection against granivory (Grubb, 1996). Van der Meij et al. (2004) showed how the time taken for five species of Javan seed-eating finches to break through a seed coat increased with seed hardness. For seeds that spend any length of time stored on the parent plant, pre-dispersal granivory can be a significant problem. This is particularly true for serotinous plants, principally the Pinaceae of Europe and America, and the Proteaceae of South Africa and Australia (Lamont et al., 1991). These species hold their seeds within protective cones for many years, only releasing seeds after the passage of fire. The woody fruits that protect the seeds inside from the high temperatures experienced during fire, may also act to reduce rates of granivory during the long periods that seeds are stored in the crown. Groom and Lamont (1997b) showed that strongly serotinous *Hakea* species had much thicker and denser follicles than weakly serotinous species.

Spines, hairs, and raphides of calcium oxalate protect the seeds held inside many non-edible fruits. Grubb et al. (1998) describe a wide array of structural defences produced by the fruits of Australian tropical trees. They also highlight a positive relationship between seed nitrogen content and the degree of structural defence present on the fruit. For plants that rely on frugivores to disperse their seeds via the consumption of their fleshy fruits, any suggestion that anti-herbivore defence plays a part in their relationship with animals would seem counterintuitive. Nevertheless, Mack (2000) proposes that fleshy fruits evolved as a means of protecting seeds from herbivores, and only subsequently did they assume their current role of a reward for promoting seed dispersal. Partial support for this hypothesis comes from West Africa, where Tutin et al. (1996) showed how *Diospyros mannii* fruits retain their irritant hairs until ripe, thereby deterring ingestion by primates until the seeds inside had fully developed.

Seedlings and young leaves

Newly emerging seedlings are often more vulnerable to herbivory than mature plants (Fenner et al., 1999; Boege and Maquis, 2005). For seedlings, size is important as even small invertebrates such as insects and molluscs can rapidly remove most biomass (Hanley, 1998; Kotanen and Rosenthal, 2000). The vulnerability of young seedlings to herbivore attack stems initially from nutritional dependency on their cotyledons (Hanley et al., 2004). Even if it fails to kill the new plant, tissue loss from the cotyledons may still exert major long-term effects on subsequent growth and reproductive potential (Hanley and May, 2006). As the cotyledons become exhausted, the seedling is faced with the need to maximise the production of aboveground biomass in order to achieve an optimal resource-foraging balance (Weiner, 2004; Boege and Maquis, 2005). During this period energy demands are high, resulting in the emergence of thin nitrogen-rich leaves with a high photosynthetic capacity (Ishida et al., 2005). It is only when the root:shoot ratio increases with plant growth that a plant can begin to invest resources in anti-herbivore defence. Based solely on these ecophysiological constraints, one might predict that structural and chemical defences would be poorly expressed in most seedlings. Indeed spines, trichomes and sclerophylly are not well developed in seedlings (Hanley et al., 1995; Groom et al., 1997; Hanley and Lamont, 2001; Iddles et al., 2003). The few studies that have examined the interaction between structural defences and herbivore selection among seedlings or juvenile plants have found no relationship between the two (Hanley and Lamont, 2001; Rafferty et al., 2005).

Table 1 underscores the point that the protective role of spinescence may vary with plant age, since the removal of spines from juvenile plants had no effect on the rates of herbivory recorded for any of the four species. Except in one case, of 14-month-old juveniles of 16 species tested in two eucalypt forest types, the four spinescent species were just as likely to be impacted by kangaroos as the non-spinescent species (Parsons et al.,

2006). Rafferty and Lamont (2007) also obtained no correlation between levels of spinescence and herbivory by kangaroos among 20-month-old juveniles of 19 banksia woodland species. It is clear that spinescence is poorly developed among immature leaves and young plants (and associated levels of sclerophylly; Groom et al., 1997) and its deterrence function only applies to mature leaves on adult plants.

Although emerging leaves on mature plants often undergo similar morphological changes to those described for seedlings, they have the advantage of the support provided by an established plant. As a result they are able to draw upon the resources required to develop an array of structural and chemical defences. The density of hairs on young leaves of the North America plant, *Verbascum thapsus*, exceeds that on older leaves and consequently they are eaten less by grasshoppers (Woodman and Fernandes, 1991). Similarly, a high initial trichome density in *Aristolochia californica* helps protect its emerging leaves from caterpillar attack (Fordyce and Agrawal, 2001). Other structural defences may decline with leaf age. Matsuki et al. (2004) showed how trichome density and toughness decreased with age in two Japanese Birch species. Choong (1996) reported a similar directional change in leaf toughness in the South-east Asian tree *Castanopsis fissa*, as did Kursar and Coley (2003) for five Panamanian rainforest tree species, while calcium oxalate concentration was inversely related to leaf age in five Central American rainforest species (Finley, 1999).

Flowers

Despite the obvious detrimental effects that damage to floral tissues might have on plant fitness, the mechanisms by which plants resist floral herbivores are poorly understood (Irwin et al., 2004). The traditional view that flowers have evolved solely to maximise pollination has only recently been contested by a number of studies that point to the strong selection pressures exerted by floral herbivores (Galen and Cuba, 2001; Irwin et al., 2004). It is apparent that many plant species possess chemically defended flowers in order to deter herbivore attack (Armbruster et al., 1997). Structural defences, particularly when flowers are held within protective arrays of spines, as is the case for some Proteaceae and Cactaceae species, may conceivably act to prevent attack by floral herbivores (B.B. Lamont, pers. observ.). Indeed the removal of spines from around the flowers of the yellow star thistle (*Centaurea solstitialis*) resulted in increased flower visitation by nectar-robbing Lepidoptera (Agrawal et al., 2000). Floral trichomes may also act to reduce herbivory but few species have been examined for floral pubescence,

and where it is known to exist, its function is poorly understood (Werker, 2000).

Tradeoffs with plant growth, reproduction, and chemical defences

The unpredictability of herbivore attack, coupled with the inherent costs that anti-herbivore defences are thought to impose on plant metabolism, means that plants may be faced with an allocation choice: 'to grow or defend' (Herms and Mattson, 1992). Costs can be categorised as allocation costs, i.e. resource-based trade-offs between herbivore resistance and growth, or as ecological costs that involve a decrease in fitness during interactions with other species (Koricheva, 2002). Variables that determine the amount and kind of investment directed towards defence include intrinsic ecophysiological/ontogenetic constraints (e.g. growth and reproduction) and extrinsic factors such as herbivore pressure and resource availability (Grubb, 1992; Herms and Mattson, 1992; Stamp, 2003). Therefore, where defences are produced it has long been thought likely that some kind of trade-off with other aspects of plant ecophysiology has occurred (Coley et al., 1985; Herms and Mattson, 1992).

Most studies that examine the fitness costs of plant defences measure the internal allocation costs arising from the diversion of resources from growth and reproduction to defence (Koricheva, 2002). Of the few studies available, most show that structural defences do impose costs on the growth and reproductive potential of the plants that possess them. Belovsky et al. (1991) noted how the development of spinescence limits the accumulation of leaf biomass in Australian shrubs, while Gomez and Zamora (2002) showed how the removal of spines from *Hormathophylla spinosa* and protected from subsequent ungulate herbivory had a positive effect on seed production. The relaxation of herbivore pressure also resulted in decreased spinescence, implying that there is a fitness cost associated with this defence (Gomez and Zamora, 2002).

However, the link between structural defence and growth is not a simple one. Like many aspects of the supposed growth-defence trade-off, the relationship depends on interactions between plants and their environment (Koricheva, 2002). Agrawal (2000) showed that the induction of trichomes did not reduce root or shoot biomass of *Lepidium virginicum* grown at low density, but did have this effect when grown at high density. In *Brassica rapa*, plants with high trichome densities produced more fruits than low trichome density plants, even in the absence of herbivory (Ågren and Schemske, 1994). There are at least two reasons why attempts to find a trade-off between plant fitness and defence have met

with inconsistency. First, any trade-off between growth or reproduction and defence is complicated by the presence of a 'third party' – tolerance (Stamp, 2003). Tolerance refers to a plant's ability to minimise the impact of herbivore damage on plant fitness. This property is reflected in plant traits such as intrinsic growth rate, storage capacity, and flexibility in nutrient uptake, photosynthetic rate and development (Rosenthal and Kotanen, 1994). The greater the allocation to tolerance, the more likely it is that any trade-off between plant fitness and defensive allocation will remain illusive (Mole, 1994). Second, 'defence' has traditionally been assessed simply by measuring the status of a single specific trait (Koricheva, 2002; Koricheva et al., 2004). Anti-herbivore resistance however often depends on the expression of several interacting mechanisms (Coley, 1983; Koricheva et al., 2004; Agrawal and Fishbein, 2006).

Since both structural and chemical defences rely on the allocation of nitrogen and carbohydrate resources by the plant, classical plant defence theory also predicts an allocation 'dilemma' with regard to which type of defence to invest in (Rhoades, 1979; Coley et al., 1985; Herms and Mattson, 1992). Although not necessarily mutually exclusive, species that adopt a chemical defence strategy might be expected to possess more limited structural defences, and vice versa. Pisani and Distel (1998) examined structural and chemical defences in two Argentinean Prosopis species, showing that spine density in P. caldenia was significantly greater than that for P. flexuosa, while leaf phenolic concentrations exhibited the opposite trend. Similarly, for Western Australian Gastrolobium (Twigg and Socha, 1996) and Hakea (Hanley and Lamont, 2002), species with high levels of spinescence tended to have relatively low concentrations of secondary metabolites. However, Iddles et al. (2003) noted for six rainforest species no correlations between phenolic content and five mechanical properties, even when mature leaves were damaged in the expectation of inducing chemical defences, thus providing no support for a trade-off.

Nevertheless while a trade-off between these two main types of plant defence does exist for some species groups, this trade-off is neither ubiquitous (Rohner and Ward, 1997; Schindler et al., 2003) nor does it imply that one defence is gained at the expense of the other (Koricheva et al., 2004). Despite the negative relationship between leaf spinescence and phenolic content reported in Hanley and Lamont's (2002) study of Western Australian Hakea seedlings, plants of all 14 species maintained a relatively high level of chemical defence irrespective of their allocation to structural defence. Moreover, as we have seen, (a) the likelihood of attack by vertebrate and invertebrate herbivores changes substantially as the plant develops, and (b) the effectiveness of some structures depends on the type of

herbivore. Fig. 1 shows the relative allocation to leaf chemical (phenolic) and mechanical defence (spinescence) in six species of juvenile and adult Hakea plants. The switch of emphasis from chemical defence in seedlings to spinescence in mature plants suggests that the shifting importance of invertebrate and vertebrate herbivory limits any trade-off between the expression of chemical and structural defence as they are temporally out of phase. Dahler et al. (1995) also showed how the levels of chemical defences are highest in seedlings of three Macadamia species before declining in older plants that develop tougher leaves.

Individual leaves may also exhibit a similar pattern of ontogenetic change. Newly produced Northofagus moorei leaves initially contain high levels of phenolics, but this defence drops substantially as the leaves become toughened (Brunt et al., 2006). Lamont (1993) and Choong (1996) reported comparable changes in the relative balance of chemical and structural defences in Grevillea spp. and Castanopsis fissa respectively. Similarly, a dense pubescence is only an option for young leaves as trichomes become abraided and lost with time. Strong spines require lignification, secondary wall production and cutinisation, time-dependent processes. It is also worth noting that leaves on adults of highly sclerophyllous species might be many years old whereas even mature leaves of seedlings and juveniles may only be a few months old, with little opportunity for deposition of tannins and structural compounds (Groom et al., 1997; Witkowski et al., 1992). Clearly the way in which different types of defence are expressed will depend greatly on leaf and plant age and the likelihood of attack by different herbivores. It is also apparent that in order to better understand relationships between defensive traits, its is vital that we consider plant defence in terms of interactions between co-adapted complexes rather than simple tradeoffs between individual traits (Stamp, 2003; Koricheva et al., 2004; Agrawal and Fishbein, 2006).

Resource availability and plant defence theory

A further consideration when dealing with the allocation costs of structural defences is the amount of resources that are available to the plant. It has been argued that the production of structural defences is much more expensive than chemical defences since they are (a) not recyclable, and (b) are constructed from the same material as plant biomass and are therefore always limited by the same resources (Skogsmyr and Fagerström, 1992). However, the contrary position, that structural defences (primary chemicals) are less resource demanding than secondary chemicals, has been presented (Choong, 1996). To some extent both viewpoints
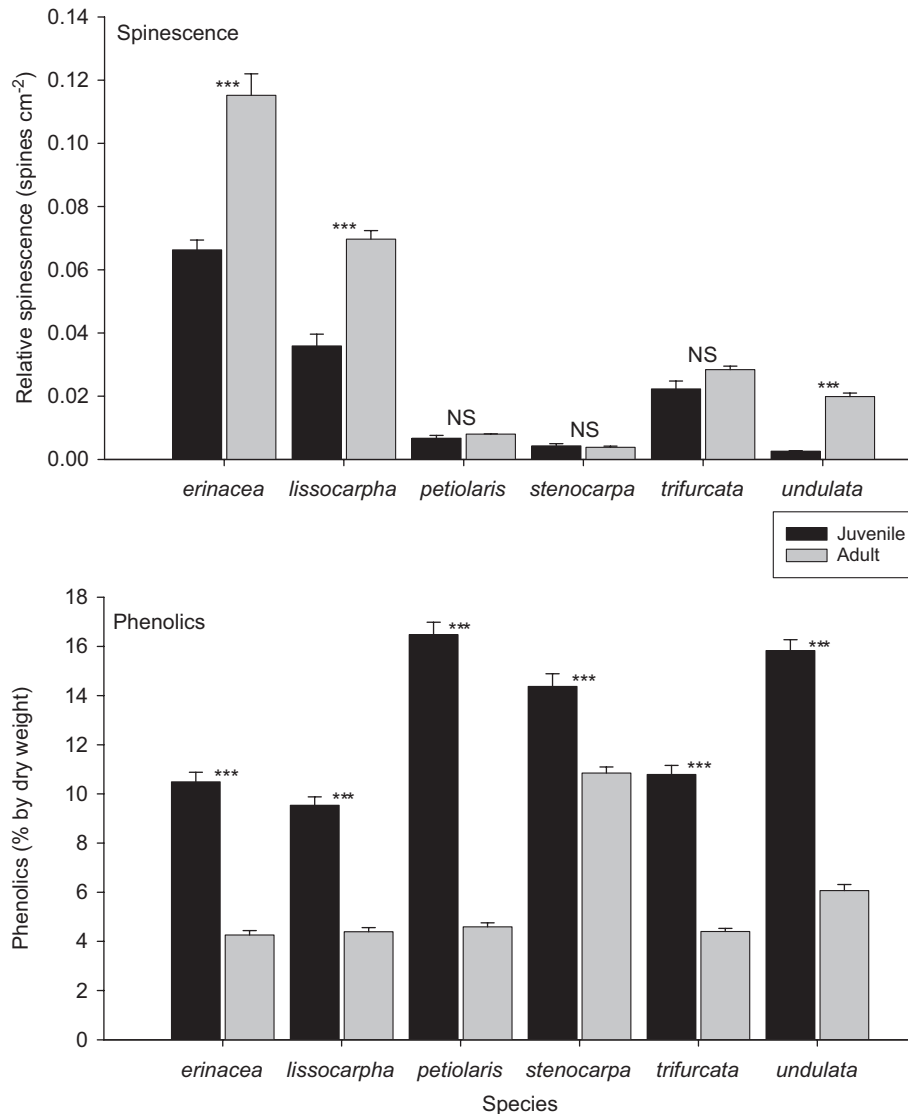
Fig. 1. Relative changes in plant structural (spinescence) and chemical defence (phenolics) in six Western Australian *Hakea* species at the juvenile (3 month old) and mature stage. Significant ($P < 0.001$) differences between mean ($\pm$SE) spinescence and phenolic content are denoted by ***; NS, Not significant ($P > 0.05$). Data collated from Rafferty (1999).

could be correct depending on the kinds of defences we are dealing with. Thickening of sclerenchyma might demand relatively fewer limiting resources than the synthesis of nitrogen-based alkaloids; but the production of low resource demanding secondary metabolites like phenolics (Gulmon and Mooney, 1986) might not exceed the costs associated with the deployment of cellulose in trichomes or spines. Variation in the resource requirements imposed by different types of chemical or structural defences may be one reason why Koricheva (2002) failed to find any consistent differences in the fitness costs of these two modes of plant defence. It is clear however that availability of mineral nutrients, light and water play a pivotal role in dictating the allocation of plant resources to growth, reproduction and the different types of plant defence.

The availability of resources in the external environment has been central to the development of plant defence hypotheses, most recently the Growth-Differentiation Balance (GDB) hypothesis (Herms and Mattson, 1992) which subsumes the earlier Growth Rate (GR) (Coley, 1983) and Carbon-Nutrient Balance (CNB) hypotheses (Bryant et al., 1983). In essence the GDB provides a framework for explaining how plants balance allocation between growth (cell production) and differentiation (cell specialisation, including for structural defences). Any environmental factor that slows growth more than it slows photosynthesis, such as shortages of mineral nutrients and water, will increase the resource pool available for allocation to differentiation. Thus, Herms and Mattson (1992) argue that resource-rich environments should favour

'growth'-dominated plants, i.e. plants that invest a high fraction of resources into processes that enhance further resource acquisition. Resource-depleted environments by contrast favour 'differentiation'-dominated plants, i.e. those that invest a high fraction of resources into processes needed to retain resources under adverse conditions and intense herbivory.

Classical plant defence theory therefore, predicts that structural defences should be most commonly encountered in resource-poor environments. Indeed, the fitness costs of plant defences do seem to be significantly greater at high nutrient levels (Koricheva, 2002), and as Grubb (1992) observes, the distribution of spinescence follows a general pattern of being more common in the drier, less fertile areas of the planet. The incidence of sclerophylly is also higher in resource-limited regions (Salleo and Nardini, 2000; Lamont et al., 2002; Wright et al., 2004). Much less is known about the biogeographical distribution of trichomes, phytoliths or raphides, although there is evidence that pubescence is favoured under resource-limited conditions (Hoffland et al., 2000). Grubb (1992) also draws attention to the fact that spinescence is not confined to resource-limited environments but is also relatively common in many resource-rich plant communities. It is also evident that sclerophylly, pubescence and mineral deposition are encountered in environments favourable to rapid plant growth. Highly pubescent plants, such as *Cerastium holosteoides, Lamium purpureum* and *Symphytum officinale*, are common in the productive habitats of temperate Europe. Clearly our understanding of the expression of structural defences must go beyond a simple link with resource availability.

Most plant defence theories extend beyond a one-dimensional association with ecosystem productivity. The GR, CNB, and GDB hypotheses incorporate caveats explaining how increased herbivore pressure and plant competition can influence the optimal investment in plant defence. Moreover, the group of hypotheses encapsulated within the Optimal Defence (OD) theory (Rhoades, 1979), consider more explicitly how plant defence is shaped by allocation costs, plant fitness, plant apparency, and herbivore behaviour. Nevertheless Grubb (1992) suggests that as many as six variables (resource availability, proportion of the landscape covered, architecture, phenology relative to neighbours, nutrient content relative to neighbours, and kinds of herbivore present) should be considered when trying to explain observed patterns of plant defence. Developing his argument about the relative importance of each of these variables, Grubb (1992) suggests that spinescence should be most conspicuous in plants from both low and high-productivity environments, and be less well developed in intermediate-productivity ecosystems: the 'scarcity-accessibility' hypothesis.

However a familiar problem emerges when we come to examine empirical support for these hypotheses. Despite a comprehensive literature documenting experimental tests of plant defence theory, there have been few attempts to determine how resource availability influences the expression of structural defences. This failure may stem from the fact that arguments presented by the proponents of particular plant defence theories are based on the synthesis of secondary metabolites, and at best only deal with structural defences as an aside. This point was made by Grubb (1992) who noted that "… the mainline theorisation in defence has been concentrated on chemical defences, and has consistently ignored physical armament." Very little has changed in the decade and a half since Grubb's observation. To compound the problem, the few studies that have examined the relationship between resource supply and structural defence have yielded contradictory results. Gowda et al. (2003) observed an increase in spine mass when *Acacia tortilis* plants were supplied with more mineral resources, while for a variety of plants, sclerophylly and pubescence respond positively to higher light intensities (Groom and Lamont, 1997a; Roberts and Paul, 2006). However, relative spinescence for two North American *Acacia* species was unaffected by the addition of fertiliser to field plots (Cash and Fulbright, 2005), while Bazely et al. (1991) showed that addition of nitrogen fertiliser reduced spine density in *Rubus fruticosus* agg. Similarly trichome density in tomatoes (*Lycopersicon esculentum*) is reduced when plants are provided with increased nitrogen (Hoffland et al., 2000) and light (Wilkens et al., 1996). There appears therefore to be little consistency in how plant structural defences respond to resource availability. To some extent this variability may be explained by the conflicting demands imposed by plant growth, reproduction and chemical defence. For example while the frequency of *Datura wrightii* plants producing non-glandular trichomes declined with increased rainfall, the fraction of plants producing water-demanding glandular trichomes increased (Hare and Elle, 2001). It is clear that in order to gain a better understanding of how structural defences respond to resource supply we must consider interactions between linked groups of plant growth and defensive traits (Koricheva et al., 2004; Agrawal and Fishbein, 2006), as well as spatial and temporal variability in herbivory (Hanley, 1998).

Our failure to understand the way in which structural defences respond to resource availability has two important consequences. Firstly, it is difficult to assess the numerous plant defence theories vying for general support without a more vigorous examination of how structural defences respond to the predictions made by these theories. Any successful model should be able to predict the deployment of raphides, sclerophylly, pubescence and spinescence as accurately as it does the

incidence of secondary metabolites. More importantly, plant communities are increasingly confronted with anthropogenic changes to resource supply. Although nitrogen addition is one obvious way in which increased resource availability can influence plant defence (Throop and Lerdau, 2004), elevated atmospheric carbon dioxide (eCO_2) is also likely to be important. Many plants subjected to eCO_2 show increased LMA (via thicker leaves) which may deter or reduce ingestion by herbivores (Knepp et al., 2005). Similarly trichome density can also be influenced by CO_2 availability as shown for *Arabidopsis thaliana* (Bidart-Bouzat et al., 2005). The influence of eCO_2 on plant defence promises to be central to the study of plant–herbivore interactions over the coming decades. The importance of structural defences in this relationship should not be underestimated.

Conclusions and future research directions

The overarching conclusion that emerges from our review is that, in spite of the wide variety of morphological structures produced by plants throughout the world, we have little information on the relative *importance* of structural defences (individually and collectively) to plant fitness in the presence of particular herbivores. This requires knowledge on the full suite of structural attributes possessed by each species as well as its chemical and growth attributes in relation to survival and fecundity. Manipulation experiments so far have been univariate and impact is gauged on immediate biomass reduction only. Multivariate studies are longer term but have yet to progress beyond the correlative approach. We also understand surprisingly little about *how* structural defences contribute to plant defence. For example, a wide array of tests on the mechanical properties of leaves is now available (Table 2). Yet there has been no attempt to predetermine the actual biting behaviour of the target herbivore, choose the most appropriate parameter from the list, and hypothesise an outcome when plant species varying widely in that parameter are exposed to that herbivore. Until this is done, the results will remain little more than informative, if not misleading, than can currently be derived from using the simple index of sclerophylly, i.e. leaf-mass–area.

It is certainly true that, while some structural defences may have originally evolved as adaptations to other environmental factors, they can markedly affect the likelihood of herbivore attack on the plants that possess them. Despite this clear defensive function, there are several reasons why a more complete understanding of the way in which structural defence fits into an overall model of plant–herbivore interactions is required. These include the important theoretical aspects of how the development of structural defences affects, and is affected by, plant ecophysiology (particularly as the plant ages). Future studies should consider the expression of anti-herbivore defence in terms of groups of mutually complementary characteristics, rather than as interactions between individual ecophysiological/structural traits (Coley, 1983; Agrawal and Fishbein, 2006). This approach may help clarify the evolutionary and ecological relationships between structural defences, plant growth and reproductive traits, and chemical defences, and develop plant defence theory beyond the simplistic view that the expression of plant defence is based on one-to-one tradeoffs between traits or a monotonic relationship with resource availability.

The recent proposal for a 'defence syndrome triangle' (Agrawal and Fishbein, 2006) offers one way of fitting plant defence into a framework that encompasses linked ecophysiological/structural traits, and how they interact with the plant environment (external resource availability, herbivore identity and density, plant competition). Tests of this model, whereby plants are grouped into one of three possible defence syndromes, must by necessity include structural defences (Agrawal and Fishbein, 2006). Such studies will improve our understanding of the evolution of plant defence, not simply because structural defences are a vital component of any successful plant defence theory, but because they offer a more tractable aspect of plant–herbivore interactions than chemical defence.

From a practical point of view, a better understanding of how and why structural defences are deployed would yield important information on how plant–herbivore interactions are likely to respond to a changing environment. Despite the bias towards the study of secondary metabolites, there can be few plants that do not possess some kind of structural defence, or interact with a competitor that does. We have outlined several important relationships between structural defence, plant ecophysiology, and herbivore and pollinator behaviour in this review. It should be apparent therefore that any factor that causes a change in the development and expression of structural defences could influence other aspects of plant growth, competitive ability, fecundity or susceptibility to herbivore attack. Recent developments in plant genomics provide a novel tool for the study of responses to a changing environment, allowing us to identify the genetic basis of trait responses to specific environmental stimuli particularly for groups of linked ecophysiological/structural traits (Howe and Brunner, 2005). Not only does this approach allow us to determine whether morphological traits are adaptations to past physiological stresses, herbivory, or both, it also provides a powerful means by which ecologists can make predictions about the way in which characteristics such as leaf toughness and pubescence

are likely to respond to the effects of climate change in the future.

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