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The ecology of plant/insect interactions: implications of digestive strategy for feeding by phytophagous insects

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A key question in insect/plant ecology asks why plants are abundant in relation to insect herbivores, and consequently, why insects are not capable of eating all plants (Hairston et al. 1960, Murdoch 1966, Bernays and Graham 1988, Abe and Higashi 1991). Many studies implicate plant chemistry as being primarily responsible for limiting host choice and use among insect herbivores. This contention is supported by a wealth of literature describing many secondary chemicals that inhibit herbivory by a wide range of insects (e.g. Feeny 1976, Strong et al. 1984, Howe and Westley 1988). Alternative explanations have not been considered thoroughly, although preliminary studies suggest that several other factors may play a prominent role in structuring insect/plant interactions. The role of natural enemies in limiting host range has been proposed as being much greater than perceived (Lawton and McNeill 1979, Bernays and Graham 1988) and new hypotheses describing the action of potential defences question accepted views of how plants respond to herbivory (Jermy 1993, Vicari and Bazeley 1993). Recent conjecture suggests a need to reappraise perspectives of insect-plant relationships, focussing on these alternatives (Bernays and Graham 1988, Abe and Higashi 1991).

Abe and Higashi (1991) contend that cellulose is a vital factor structuring terrestrial communities. Central to their argument is the fact that most phytophagous insects do not digest cellulose (Martin 1991), and that a restricted ability to digest cellulose limits the consumption of plants, so that cellulose acts as a broad-spectrum defence (Abe and Higashi 1991). As a consequence, most phytophagous insects are specialised consumers of cytoplasm and the abundance of plants is a result of the scarcity of generalist (cytoplasm and cell wall) plant consumers (Abe and Higashi 1991). The idea that the plant cell wall presents a physical barrier to herbivores is not new (Murdoch 1966), and the chemical problems associated with digesting the cell wall components are well documented (Van Soest 1982, Higashi et al. 1992). Despite this, cellulose and other cell wall components have not featured prominently in explaining the nutritional ecology of insects feeding on living plant material. Recent research describing how insect herbivores choose and utilise plants emphasises the roles that cellulose and associated plant components can play in the ecology of individual insects. Cellulose is characteristically associated with hemicellulose, lignin, cutin, silica and protein in cell walls (Van Soest 1982). In addition to posing similar digestibility problems, these components combine to form the fibrous cell wall conferring an assortment of mechanical properties on plants. In this paper I elaborate upon the basic premise of Abe and Higashi (1991) from the viewpoint that the effects on communities are driven by effects on individuals, given that small nutritional differences are capable of causing large changes in the population biology of herbivorous insects (McNeill and Southwood 1978). I identify further consequences of a high cellulose diet for herbivorous insects specialised for consuming cytoplasm, and examine the body of evidence supporting an alternative view of how plant attributes affect herbivory. I also suggest a framework suggesting future hypotheses and directions for research into plant/insect interactions and why there should be a shift in the emphasis in this research.

Nutrient acquisition by insect herbivores

How do most insect herbivores deal with the cell wall component of their diet? The term "fibre" describes the biological unit that is the cell wall, and not merely a

chemical entity (Van Soest 1982). The chemical composition of fibre is highly variable and this variability complicates generalisations about its role in invertebrate herbivory (Mattson and Scriber 1987). The variation has also been the justification for concentrating on studying the effects of individual components of the plant cell wall, especially cellulose, on insect herbivores (Peterson et al. 1988). Most conclusions regarding fibre indigestibility for insects have been inferred from studies focussing on cellulose and assays of digestive enzymes (Martin 1991). Studies investigating the digestibility of cell wall components suggest that hemicellulose and cellulose may be digestible for some herbivorous insects (Terra et al. 1987, Ferreira et al. 1992).

In most cases, phytophagous insects do not digest or utilise much fibre (Martin 1991, Hochuli et al. 1993), although the capability to produce cellulases may be more widespread than currently assumed (Slaytor 1992). Those that do digest cellulose are predominantly specialists on wood, and have formed associations with a variety of symbionts (Higashi et al. 1992), although some termites and cockroaches, wood-feeding cell wall specialists, are capable of cellulose digestion without the involvement of gut symbionts (Slaytor 1992). The inability to degrade the cell wall chemically has significant implications for the nutritional ecology of phytophagous insects with chewing mouthparts. The digestive strategy of most insect herbivores appears to be to satisfy their nutritional needs with plant cell contents, as most fibre is ignored as a source of energy and passed through the gut undigested. Most insect herbivores with chewing mouthparts (from the Coleoptera, Lepidoptera, Orthoptera, Diptera and Hymenoptera) appear to share, in general terms, a similar feeding strategy (Strong et al. 1984, Slansky and Scriber 1985), in that they simply disrupt cell walls mechanically to gain access to cell contents. I will restrict further discussion to these orders, the key premise being that the method insects adopt to acquire nutrients may increase their susceptibility to particular plant defences.

In general, herbivorous insects adopt a very simple strategy to use plant material. Mandibles are used to gather and process plant material which is then digested and absorbed in simple guts (Chapman 1985). This process seems to be very inefficient, as a considerable proportion of plant material is left unprocessed (Caswell and Reed 1976, Barbehenn 1992) and phytophagous insects seem to utilise a low proportion of the plant material they consume, passing significant amounts of digestible and indigestible material out in faeces (Hochuli et al. 1993). Digestibility of living leaves for insects is often low compared to other foods such as nectar, seeds and other insects, although the wide range of digestibilities associated with different plants and herbivores from different taxa overlaps digestibility values for other diets (Slansky and Scriber 1985). The strategy of herbivorous insects appears to be contrary to that used by mammalian herbivores where at least some cell wall digestion contributes significantly to the individual's nutritional needs (Van Soest 1982). The insect digestive strategy is ultimately successful because insects process large amounts of plant material relatively inefficiently to meet modest nutritional demands, particularly in relation to energy (Martin 1991). Soluble cytoplasmic nitrogen is the major nutritional factor influencing insects feeding on living plant material (McNeill and Southwood 1978, Slansky and Scriber 1985).

The focus on mechanical disruption of plant cells by mandibles does not mean that the process of cell wall disruption by various insect herbivores is identical; several methods of acquiring nutrients may operate. Holometabolous and hemimetabolous insects have fundamental differences in head and mandibular morphology that constrains the action of their mandibles. The mandibles of many holometabolous insects (e.g. larval Lepidoptera) are symmetrical whereas hemimetabolous insects such as Orthoptera have asymmetrical mandibles with specialised functions (Nininger 1915, Hillerton 1986). These structural constraints seemingly affect how mandibles overlap, restricting the ways they can process plant material (Hillerton 1986). The Coleoptera exhibit a wide array of morphological structures and the mandibles of phytophagous beetles are not strikingly asymmetrical but do have distinct grinding areas (Acorn and Ball 1991).

Animals with superficially similar processing apparatus can adopt different strategies to obtain nutrients. Bernays and Janzen (1988) showed that nutrient acquisition by saturniid and sphingid caterpillars is fundamentally different, with saturniid larvae snipping and ingesting large fragments of plant material and sphingid larvae generally comminuting it into small particles. The different modes of processing are reflected in mandibular morphology and host choice by the two taxa. Barbehenn (1992) described an alternative method of liberating cell content, where mechanical disruption of plant cells contributes only partially to the nutritional needs of some larval Lepidoptera. Conditions in caterpillar guts may allow cell contents to leak through plasmodesmata after cell death. Plant material need not be comminuted for considerable quantities of digestible nutrients to be made available; caterpillars must simply snip off leaf fragments small enough to ingest. This strategy does not circumvent possible mechanical defences because although leaf fragments do not need to be crushed, they must still be bitten off and ingested. Gut physiology can thus influence the nutritional ecology of phytophagous insects and affect the extent of mechanical processing of plant material that is required.

Locusts, and the phytophagous Orthoptera in general, comminute plant material and liberate cytoplasm by mechanically disrupting the cell wall (Hochuli et al. 1993). Measures of digestive efficiencies suggest that the emphasis of this strategy is on processing large amounts of plant material relatively inefficiently to satisfy nutritional demands (Hochuli et al. 1993), a strat-

egy placing great quantitative demands on the processing apparatus.

The division of herbivores into cytoplasm users and cell wall users (Abe and Higashi 1991) seems particularly appropriate for insect herbivores, with most relying on cytoplasm to satisfy nutritional needs. However, the general implications resulting from these dietary strategies (Fig. 2a in Abe and Higashi 1991) seem to be an oversimplification of currently perceived and pursued tenets of plant/animal ecology. In particular, their reference to plant chemistry as the limiting factor for cytoplasm specialists requires critical examination.

Abe and Higashi (1991) suggest that secondary chemicals are a major defence against cytoplasm-consuming insects. The role of plant chemicals influencing insect herbivory has been investigated and demonstrated in great detail, to the point where it has been suggested that there has been an over-emphasis on them in explanations of insect/plant interactions (Bernays and Graham 1988). Clearly, plant chemistry plays an important role in structuring many plant/insect relationships, as do natural enemies (McNeill and Southwood 1978, Lawton and McNeill 1979, Strong et al. 1984). There is also no doubt that cell wall digestion constitutes a chemical problem for phytophagous insects. However, little is known of how these animals overcome the physical problem of breaking plant cells open to obtain cytoplasm. I propose that a combination of mechanical and chemical properties of plants interact to reduce the ability of phytophagous insects to consume plants, as a direct result of dependence upon cytoplasm consumption.

The inability of most insect herbivores to chemically degrade plant cell walls and the consequent reliance on mechanical disruption to obtain nutrients suggests they may be more susceptible to the mechanical defences of plants than previously believed. The broader implications of their digestive strategy are that frequently overlooked mechanical properties of plants may be more important in structuring herbivory than currently accepted. A suite of possible physical defences has been postulated but understanding of these has been restricted by terminological confusion and limited research. In some cases cause and consequence have been confused, leading to misinterpretations of what insects must do to obtain nutrients. The following brief review describes some of the ways that the structural attributes of plants affect the ecology and morphology of chewing insects.

What are the mechanical "defences" of plants?

Although toughness and associated mechanical properties have been labelled as "defences" by some authors (Vicari and Bazeley 1993, Fernandes 1994), this may be a misnomer as defensive functions have primarily been implied indirectly, and not established (Owen 1990). The properties described below have the potential to inhibit herbivory in some way, although most evidence supporting this function is circumstantial.

Interpreting the significance of the mechanical properties of plants has proved perplexing to many ecologists in the past. Evaluation of the "toughness" and "hardness" of leaf material has often been a peripheral aspect of previous studies and, as a consequence, some conclusions have been based on misinterpretations of what factors were actually measured. Despite rigorous definitions of what mechanical properties are in structural science, ecologists have adopted a variety of methods to estimate the hardness and toughness of plants (Vincent 1990a, b, Lucas et al. 1991, Choong et al. 1992). Terms such as toughness and hardness have specific definitions, and structural scientists use specific methods to measure and express them (Vincent 1990a). Recent advances in the estimation of fracture toughness of leaves have led to suggestions that many previous studies claiming to examine toughness of leaves in relation to insect herbivory are seriously flawed (Lucas et al. 1991, Choong et al. 1992).

Toughness is a measure of the energy (work) required to fracture a material (Vincent 1990a, b, Lucas et al. 1991). Many authors use penetrometers ("plunger" tests) to measure leaf toughness; these do not provide measures of toughness, but a measure of the maximum force required to penetrate leaves (Lucas and Pereira 1990). Indeed, these measures do not allow the user to estimate any of fundamental mechanical properties of leaves, causing doubts about their usefulness in anything but correlational ecological studies (Lucas and Pereira 1990, Lucas et al. 1991, Choong et al. 1992). Accurate measures of toughness have been made for grasses (Vincent 1982) and broad-leaved plants (Lucas and Pereira 1990) in the laboratory but field measures are still difficult to obtain, although penetrometer measures using corrections for leaf lamina thickness may approximate true toughness (Choong et al. 1992).

The hardness of biological materials has been described as a "fiendishly difficult" property to measure (Vincent 1980). Hardness is measured using an indentation test, where a probe of known shape is pressed into the material at a constant load and the magnitude of deformation is measured (Vincent 1990a). This is a very difficult test to apply to complex viscoelastic materials such as plants, as they often recover from the initial indentation (Vincent 1990a). In addition, it is difficult to ascribe a value to the overall hardness of a large complex structure as there may be areas of localised hardness, such as in insect mandibles (Hillerton et al. 1982) and mammalian teeth (Palamara et al. 1984). The hardness of components of plant leaves such as silica can be measured and it is possible that a measure of the elemental composition of a sample would allow a correlational estimate of "hardness", as has been shown for locust mandibles (Smith et al. 1992). The mineral composition of plants, particularly grasses, is associated with signifi-

cant tooth wear in mammalian herbivores (Baker et al. 1959, McNaughton et al. 1985, Piperno 1988) and hence the proportion of the plant that is mineralised, siliceous, opaline phytoliths may be a measure of the "abrasiveness" of a diet. Grasses are considered to be extremely abrasive because of their high silica content (McNaughton et al. 1985) compared to non-grasses and are also generally more difficult to chew than non-grasses because of the parallel arrays of sclerenchyma fibres that must be bitten through (Vincent 1982).

A major problem with the investigation of plant physical characteristics is the complexity of factors that combine to give the plant its overall physical structure (Vincent 1990a), and these are not independent of one another. For instance, Lucas et al. (1991), in reviewing a study investigating mandibular wear in chrysomelid beetles as a response to the toughness of mature willow leaves (Raupp 1985), suggest that the mandibular wear ascribed to leaf "toughness" (= penetrability) was most likely caused by "abrasive" calcium-based druses, whose presence was correlated with increased toughness. The reduced fitness associated with mandibular wear is not questioned, simply the cause of that wear is disputable. The simple explanations that have been adopted in many studies to describe adaptations to the mechanical properties of plants (e.g. combining the definitions of hardness and toughness) are not wholly satisfactory. That hardness and toughness are fundamentally different mechanical properties is not the only reason to distinguish between them; they also have fundamentally different effects on insect herbivores.

In theory, consumption of a hard substance incorporated into leaf material would be associated with wear of chewing apparatus. Tough material will require more muscle, to generate the energy to propagate a crack in the material. Despite some terminological confusion, correlative evidence supports the notion that mechanical properties are important inhibitors of herbivory, and several direct studies suggest that mechanical properties are associated with reduced fitness and feeding performance by insect herbivores (Djamin and Pathak 1967, Raupp 1985, Bernays 1986).

Morphological and ecological responses to the structure of plants

The consequences of mechanical defences appear to be manifested morphologically in insects, particularly in mandible and head structure (Bernays 1991). Morphological adaptations to the structure of food plants are varied and often specific in response to a variety of physical characteristics, with convergent evolution of characters frequent (Herring 1993). Many adaptations to the mechanical properties of plants have been studied with non-insect herbivores (Howe and Westley 1988, Sanson 1989, Herring 1993) and similar patterns are observed in insect herbivores (Bernays 1991). Many descriptions of morphological and ecological responses to mechanical properties, particularly toughness, are complicated by the fact that most comparative studies rely on toughness estimates derived from plunger tests (Choong et al. 1992).

Head size and shape

Comparisons are often made between animals consuming grasses and non-grasses (forbs) because of their different physical structures, giving rise to many broad suggestions of adaptations to these categories of food plant. Morphological associations with graminivory, such as hypsodonty and molar progression in mammals (Howe and Westley 1988), and large heads in insects (Bernays 1986), are considered to be responses to the mechanical properties of grasses. Head size and shape has been associated with diet in caterpillars and grasshoppers (Bernays 1986, Bernays and Hamai 1987). Graminivorous grasshoppers were found to have relatively larger heads, with larger mandibular adductor muscles and larger mandibles, than herbaceous dicot-feeding grasshoppers. The relationship between head mass and diet is found with grass feeding larval Lepidoptera, which have larger heads than non-grass feeders of similar body sizes (Bernays 1986). Caterpillars reared from hatching on a "hard" grass (measured with a penetrometer) had head masses twice as great as caterpillars fed a "soft" artificial diet. Increase in head size was attributed to an increased work load for the muscle, and head size was positively related to feeding rate. As well as responding to the differences between plants, insects consuming leaves of different ages are also likely to be exposed to variation in toughness, as mature leaves of woody plants are generally tougher than young leaves whereas young leaves may contain higher amounts of potential chemical defences (Coley 1983, Larsson and Ohmart 1988). Morphological adaptations to temporal variation in food quality would also complement size and temporally related differences in feeding strategy by larval Lepidoptera (Gaston et al. 1991, Reavey 1993).

Mandibular morphology

The functional morphology of grasshopper mandibles has been the subject of considerable attention. Mandibular morphology is correlated with diet of orthopterans (Isely 1944, Gangwere 1961, Chapman 1964, Bennack 1981, Patterson 1984, Aguirre et al. 1987). Animals consuming predominantly grass diets have mandibles with extended, continuous cutting ridges, whereas forbivorous grasshoppers possess mandibles comprising with distinct teeth. The mandibles of some locusts are thought to be self-sharpening with use (Hillerton 1980), have a unique composition (Gardiner and Khan 1979) and have a very high indentation hardness (Hillerton et al. 1982), correlated with high mineral content (Smith et al. 1992). Caterpillars within the genus *Spodoptera* Guenée also exhibit mandibular morphology corresponding to food

plants (Brown and Dewhurst 1975). Such observations confirm the view that consumption of plant material by insects requires specialised processing apparatus (Bernays 1991), similar to that found in mammals (Maynard-Smith and Savage 1959, Stebbins 1981, Herring 1993). Although no broad comparative studies examining the independent evolution of traits (Harvey and Pagel 1991) have been performed, the body of anecdotal evidence suggests that there have been evolutionary responses to the mechanical properties of plants (Bernays 1991).

Mandibular wear as a consequence of feeding has been reported for beetles (Raupp 1985), grasshoppers (Chapman 1964, Zouhourian-Saghiri et al. 1983) and caterpillars (Dravé and Laugé 1978). In all cases, significant deformation of mandibles resulted from either mandible/mandible interaction or the consumption of abrasive material. The evidence for effects of wear on fitness are equivocal, as fitness of beetles may be reduced (Raupp 1985) whereas there are no apparent effects on locust fitness (Chapman 1964). Feeding rate was reduced for individuals with significant wear in both studies. The effects of wear may have to be considered with respect to mandibular function, as larvae simply cutting ingestible fragments of plant material have different processing strategies to those ingesting and comminuting it (Barbehenn 1992).

Avoidance of plants

Avoidance of "tough" and "hard" plants by invertebrate herbivores has been reported (Coley 1983, 1987, Howard 1988, Larsson and Ohmart 1988), although again, the evidence is weakened by the inappropriate methodology used to measure mechanical properties. The general evidence is equivocal, with avoidance and diet selection being a function of many chemical and physical properties of the plant that are often associated with each other (Howard 1988, Buendgen et al. 1990). Direct studies describing the resistance of plants with certain mechanical properties and the mechanisms by which these properties operate are rare, although Djamin and Pathak (1967) show that varieties of rice high in silica are relatively resistant to attack from the rice borer *Chilo suppressalis* (Walker), and that larvae consuming varieties high in silica suffer significant mandibular wear. The general consequences of mandibular wear may be inferred from other studies (e.g. Chapman 1964, Raupp 1985) although the diversity and complexity of mandibular morphology described (Bernays 1991) suggest that differential responses to wear and adaptations to the mechanical properties of plants are likely.

Conclusions

Morphological and associated ecological responses to mechanical defences are likely to be widespread, suggesting that the mechanical properties of plants are important limitations to insect herbivores. There are clearly technical dilemmas associated with the study of these properties, and clearer definitions of what can be measured and how the herbivore is affected by these properties are required. The evidence presented above reveals a need to examine the methodology of investigating how the mechanical properties of plants affect insect herbivory, as well as consider the general patterns that can be drawn from previous studies. Despite ambiguous evidence for the overall influence of mechanical properties inhibiting herbivory, the studies describing their possible effects imply strongly that they are important in restricting herbivory by insect herbivores, that are limited by their digestive strategy.

Compensatory responses to high fibre diets

Phytophagous insects disregard a major potential source of energy by not utilising the fibrous component of plants. However, as Martin (1991) pointed out, most phytophagous insects are not energy limited as nitrogen in plant protein is the major nutritional factor limiting herbivory (McNeill and Southwood 1978).

A consequence of fibre indigestibility is that plants high in fibre will effectively be nutritionally diluted (Howe and Westley 1988). An immediate repercussion of a low nutrient diet would be retarded growth and development (Slansky 1993), with resultant nutrient stressing possibly inducing supernumerary instars (Safranek and Williams 1984). Many insects consume more food as a compensatory response to diets high in indigestible components (Simpson and Simpson 1990, Slansky 1993). Although the indigestibility of cell wall components is commonly referred to, few studies examine how insects respond to diets relatively high in fibre (Mattson and Scriber 1987).

Experiments manipulating nutrient levels in diets examine the fundamental problem of how nutrient dilution affects insect herbivores (Slansky 1993). In most cases indigestible cellulose is incorporated into an artificial diet to reduce the overall digestibility of food. Compensatory patterns of feeding have been described for grasshoppers and caterpillars using this protocol (Simpson and Simpson 1990, Slansky 1993). A compensatory response by caterpillars was found when cellulose was used in conjunction with silicic acid to investigate how fibre and silica inhibit herbivory (Peterson et al. 1988). Silica has been assumed to be a major cause of tooth wear in mammalian herbivores (Piperno 1988) and may also act as a dietary diluent.

Costs of increased consumption include increased exposure to natural enemies when feeding (Lawton and McNeill 1979, Bernays 1986, Mueller and Dearing 1994) and toxic allelochemicals (Slansky and Wheeler 1992). Both costs are likely to play important roles in structuring relationships between insects and plants (Strong et al. 1984). Increased consumption also increases the likelihood of wear from mandible/mandible

Table 1. The impact of cell wall indigestibility on aspects of feeding on plants by insects. The effects on the different components of feeding depend on the perspective from which cell wall indigestibility is considered (i.e. the chemical, mechanical or general perspective).

Perspective	Choice	Consumption	Assimilation	Growth
Chemical	Avoidance of fibrous leaves (low nutrient value).	Indigestibility of fibre reduces nutrient availability and hence increases consumption. (see assimilation, as this may increase susceptibility to mechanical "defences").	Diluent effect – Increased cell wall component reduces proportion of sample that is available nutrients and hence the overall digestibility of plant material.	Limited energy – Energy is tied up in cell wall sugars while the cytoplasm is predominantly protein. This accommodates general insect nutritional strategy, as N (in protein) and not energy is limiting. Energy is required for extra moulting and growth.
Mechanical	Avoidance of fibrous leaves (tough and high proportion of abrasive silica.	Toughness – generating the force to fracture very tough plants may be beyond the muscular capabilities of some insects, head size may be modified to accommodate more muscle. "Hardness" – very hard, abrasive material is a likely cause of mandibular wear.	Compensatory responses may lead to increased consumption. Extra use of mouthparts will amplify effects of quantitative mechanical defences.	Size – scale reflects a possible constraint influencing herbivory, as smaller larvae may be unable to adopt some feeding strategies owing to mechanical constraints.
General	Rejection of high fibre leaves may mean acceptance of plants high in secondary chemicals and vice versa. Choice is also a dynamic process, different choices may be made at different times depending on feeding strategy adopted by larvae.	Different effects depending on feeding strategy; – "Biters". Caterpillars must snip pieces of leaf small enough to ingest. – "Chewers". Locusts must bite off *and* comminute plant material. Increased exposure to natural enemies when feeding.	Processing ability – reduced processing as a result of deformation of mouthparts and unsuitable processing apparatus (with respect to sizes and shapes of heads and mandibles).	Supernumerary instars – Nutrient deficiencies may induce changes in developmental strategy. They also offer the insect a chance to replace its (potentially worn) mouthparts. Orthoptera are more energy limited than Lepidoptera and may require greater access to energy rich foods.

interactions and the effects of quantitative defences such as silica. Compensatory responses to nutrient diluted diets are not independent of potential mechanical defences, as fibre content is likely to correlate with abrasiveness (Piperno 1988) and toughness (Choong et al. 1992). Interactions are therefore likely, particularly as increased feeding can increase the effect of quantitative defences like abrasiveness. If mandibles become less efficient at disrupting cell walls, herbivores may increase total consumption when consuming high fibre diets to compensate for reduced nutrient levels.

Future considerations and research directions

How can a reliance on cytoplasm obtained primarily via mechanical disruption affect herbivores? I contend that specialising on cytoplasm increases the susceptibility of most chewing insect herbivores to mechanical defences and that the mechanisms by which these defences operate are inadequately described by current literature.

The effects of fibre indigestibility on feeding by phytophagous insects can be considered from several perspectives (Table 1) although the consequences are not mutually exclusive and there are clear interrelations between some factors (Fig. 1). The studies described above are examples drawn from the general body of work investigating insect/plant relationships and justify the claims made in Table 1 and Fig. 1. Many of the ideas presented have not been central to the studies cited and there is clearly a need to integrate digestive strategy and consequences into broad descriptions of feeding by phytophagous insects (McNeill and Southwood 1978). There is also a need for a rigorous and detailed reappraisal of how mechanical attributes affect herbivory, as the true nature of their action against insect herbivores remains seemingly enigmatic to a majority of entomologists, as witnessed by the many methods used to measure these properties (Lucas et al. 1991).

Despite some confusion in previous research, this brief reappraisal of the role of mechanical properties in insect/plant interactions suggests they are a broad spectrum hurdle to insect herbivores. Fig. 1 and Table 1 describe some of the repercussions of increased exposure

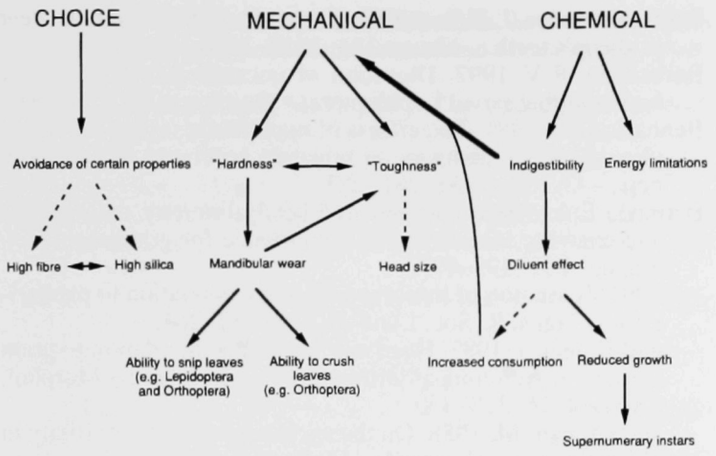

Fig. 1. Factors influencing insect herbivory, as predicted by the cellulose-centred perspective of terrestrial community structure proposed by Abe and Higashi (1991). Solid arrows describe a direct relationship where there is a likely reduction in the fitness of the herbivore while dashed arrows show possible adaptations or responses to overcome the defences. Double headed arrows indicate an interaction between two factors, where the factors act in conjunction with each other and are often associated with each other in the plant. Note the feedback loops associated with mandibular wear, where increased mandibular wear causes a reduction in processing ability and a reduction in the amount of available nutrients, necessitating increased consumption and hence exposure to the quantitative mechanical defences. The interaction between chemical indigestibility of the cell wall and mechanical defences demonstrates the quantitative nature of mechanical defences. Defences that directly reduce the fitness of insects consuming particular plants may result in the insects avoiding the plant altogether.

to mechanical defences, summarising the potential consequences of cellulose indigestibility and some of the interactions between these. The consequences summarised in Fig. 1 and Table 1 focus on overlooked questions identified in this paper as worthy of re-examination and further study.

From the basic chemical problem of cellulose/plant cell wall indigestibility and consequent reliance on mechanical disruption of plant cell walls several consequences emerge. Apart from not utilising the energy bound up in cell wall sugars (Martin 1991), the dilution of available nutrients may result in reduced growth or require compensatory feeding (Slansky 1993). The emphasis on the mechanical processing of plant material may increase the susceptibility of chewing insect herbivores to the mechanical defences of plants. There is little scope for insects to compensate for nutrient reduction with increased enzymatic activity or longer gut passage times. Using accurate functional definitions of the mechanical properties of plants, it is likely that insects utilising a tough plant will have to generate increased force and energy to fracture the plant by accommodating more adductor muscle in larger heads (Bernays 1986, 1991). Consuming plants high in hard silica is likely to result in mandibular wear so that mandibles will cut and grind less efficiently. A worn mandible is also likely to be less capable of cutting a tough plant, as pushing a blunt edge through a uniform material would require more work than pushing a sharp edge through the same material. This functional interaction between "hardness" and "toughness" in Fig. 1 is complemented by the fact that the characters conferring these properties to plants (silica and fibre respectively) are often associated (Buendgen et al. 1990). It is likely also that the effect of mandibular wear would be different for insects adopting "snipping" and "crushing" digestive strategies (Barbehenn 1992).

Avoidance of mechanical properties in broad studies of insect/plant relationships needs to be supported by descriptions of the basic biology of how mechanical properties affect phytophagous insects and direct experiments targeting these factors. Phenomena such as large-headedness (Bernays 1986), adaptive changes in mandibular morphology (Bernays 1991) and compensatory responses (Simpson and Simpson 1990, Slansky 1993) are all potential responses to mechanical properties still to be compellingly demonstrated as evolutionary responses to mechanical properties.

The complexity of responses insects may show to plant defences precludes explicit simplifications of the mechanisms involved. The distinction between chemical and mechanical defences may be blurred too, as some plants may have high levels of both (Feeny 1970) while in other systems herbivores may face a direct choice between plants with varying levels of each attribute (Larsson and Ohmart 1988). Scale may also influence herbivory significantly, as changes in feeding strategy by larval Lepidoptera as they grow are constrained by, among other factors, an inability to deal with the mechanical characteristics of the leaves they are consuming (Hagen and Chabot 1986, Gaston et al. 1991, Reavey 1993).

The lists of possible effects of cell wall indigestibility and mechanical defences presented in Table 1 and the interactions suggested in Fig. 1 are not exhaustive but predict many consequences and dynamic responses underlying the cellulose-centred view of terrestrial ecosystems proposed by Abe and Higashi (1991). Furthermore, many interactions between these responses are postulated although the mechanisms by which they operate are poorly understood. Experiments controlling abrasiveness, toughness and diluents, also examining potential interactions between these, are vital to testing the reasoning behind the predictions presented in Fig. 1. Research detailing the mechanisms (e.g. mandibular wear, toughness), ecological effects (fitness, choice) and evolutionary implications (comparative studies looking at host range and morphology) must interact to elucidate the general problem that the mechanical properties of plants pose.

There is no doubt that secondary chemicals and natural enemies inhibit herbivory and are important determinants of host range for some phytophagous insects (Lawton and McNeill 1979, Strong et al. 1984, Bernays and Graham 1988). However, insect herbivores with chewing mouthparts are also predisposed to susceptibility to mechanical defences because of their digestive strategy.

Conclusions

No dogmatic "degree of importance" can be applied to the various factors proposed as potential inhibitors of herbivory, although specific interactions may well be explained by a single factor. The complexity and sheer number of plant/insect interactions demand that a multicausative approach be used to explain the ecology of plants and insect herbivores (Abe and Higashi 1991). Rather than identify the prominent factor influencing herbivory, it is better to use a framework of potential factors restricting herbivory and identify those that are prominent in structuring specific interactions.

Understanding the nutritional needs of phytophagous insects and how these are satisfied identifies potential sources of resistance to herbivorous insects. The emphasis on mechanical and not chemical disruption of plant cells to obtain cytoplasm means that most insects adopt a totally different digestive strategy to most mammalian herbivores. This does not mean that herbivorous insects are "poor" utilisers of plant material; relatively few energy requirements have to be met by insects compared with mammals. The insect's dietary strategy is not inferior to that of animals that digest cell wall; it is a simple, successful means of utilising one of the most abundant resources in their habitat.

An animal adopting a strategy of high intake of mechanically processed plant material is likely to be susceptible to quantitative mechanical defences. Elucidating the mechanical problems associated with breaking down plant material is essential to understanding and developing the hypotheses proposed by Abe and Higashi (1991), who show that community structure can be affected by the inability of most insect herbivores to digest a large component of their diet. The mechanical properties of plants present intricate and exacting obstacles to phytophagous insects. These properties are often determined by the structure and composition of the cell wall in plants; they are therefore intrinsically associated with the chemical dilemma that cell wall indigestibility constitutes. As a consequence of the digestive strategy of most herbivorous insects, the cell wall of plants and mechanical properties associated with it establish a broad barrier to insect herbivory more elaborate and important than currently recognised.

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