The Influence of Grazing on the Evolution, Morphology and Physiology of Plants as Modular Organisms [and Discussion]

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Phil. Trans. R. Soc. Lond. B 1991 **333**, 241-247
doi: 10.1098/rstb.1991.0073

The influence of grazing on the evolution, morphology and physiology of plants as modular organisms

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SUMMARY

Plants are modular organisms, i.e. they consist of repetitive multicellular units. The integrity of the plant is arranged by active meristems that hormonally suppress activity of other meristems. This basic design makes it possible for plants to have semi-independent, or totally independent, parts even within one structural individual. Accordingly, plant parts like ramets or branches may be qualitatively different because of developmental, environmental or genetical influences. They may respond to herbivory separately from other parts in the same structural individual.

The modular structure allows easy recovery after damage by herbivores. Simultaneously it may constrain possible functions and lead to seemingly non-optimal responses. Effects of herbivory on the very basic modular design must be limited. Instead, herbivory may function as an evolutionary force modifying regulation of plant structure and function, like location of meristems, and rules determining outcomes of interactions among meristems. Indirectly, herbivory may prevent evolution of more unitary plant individuals.

1. INTRODUCTION

General theories about plant–herbivore interactions (Feeny 1975, 1976; Rhoades & Cates 1976) largely concentrated on active, exclusive, defence, and more recently, on resource availability, or on ability of plants to recovery (see, for example, Coley *et al.* (1985); Mattson *et al.* (1987). Most of the theories were developed by zoologists, who seem to have been impressed by difficulties which herbivores meet when attacking plants. This has been thought to be important for the plant. Assuming genetic basis for resistance, evolution towards more efficient defences seems inevitable; there has to be a balance settled by costs of defence and benefits of avoiding herbivory.

However, plants are modular organisms and modularity leads to some consequences that are different to those in traditional, unitary organisms (see, for example, Jackson *et al.* (1985); Jerling (1985)). These include a number of features which plant–herbivore theories have considered only superficially, or not at all. For example, the unit to which costs and benefits of defence are calculated, traditionally is an individual. But unlike in animals, functional responses may not be expressed by individuals plants, but by parts of the individual. The very basic modular structure of plants may exclude genetic variation for some responses that we would predict to evolve simply because we know they would be beneficial for unitary organisms. Induced responses of branches, instead of trees, to defoliation or pruning (Tuomi *et al.* 1988; Långström *et al.* 1990) serve as examples. Second, the modular structure of plants is accompanied by a, from a zoologist's point of view peculiar, partly sink-regulated photosynthesis (Wardlaw 1990; Marshall 1990) which may make it relatively easy for plants to increase intake of carbon. This, and an ability of plants to create new resource-catching organs (Watson 1986), makes the assumption of a fixed resource budget much less uncertain in plants than in unitary animals. Simultaneously, plants may become relatively insensitive to small losses of foliar biomass, and may recover relatively easily after herbivory. Third, the modular structure of plants allows some surprising responses, like increased plant quality due to browsing (Danell & Huss-Danell 1985), and may also lead to methodological difficulties in experimentation (Haukioja *et al.* 1990).

The other side of the problem of modularity refers to the effect of herbivory on evolution of morphological and physiological mechanisms in plants. That must be an integral part of any general plant–herbivore theory because plants are under similar evolutionary forces as animals. The problem is how the basic modular structure of plants affects the validity of evolutionary predictions (see Tuomi & Vuorisalo 1989; Eriksson & Jerling 1990). In this paper I try to elucidate some basic principles of the modular design of plants, and whether and how herbivory functions as a causative agent in moulding that design.

2. PLANTS AS MODULAR ORGANISMS

Any attempt to characterize plants generally as modular organisms falls short in front of the multitude of specific solutions. For instance, there is huge

Phil. Trans. R. Soc. Lond. B (1991) **333**, 241–247
Printed in Great Britain

variation how specific plant features (like physiological integration among ramets, or transport of nutrients) are arranged in different plant species or even populations (see, for example, van Groenendael & de Kroon (1990)). Instead of describing the multitude of solutions, I present a verbal model (modular interaction model (Haukioja 1990)) to explicitly describe such features in plant modular structure and functioning which may modify plant responses to herbivory. My views of plant responses to herbivory, as well as the treatment of modularity in this paper, have been strongly influenced by behaviours of the mountain birch, *Betula pubescens* spp. *tortuosa*, the species that I have been studying for almost two decades. A birch tree is composed of modular units but two characteristic features of the mountain birch may influence generality of the conclusions: first mountain birches usually have a huge reservoir of dormant meristems, so that, in practice, meristem limitation (see Watson 1986; Geber 1990) is unlikely to occur. Second, mountain birch is a polycormic bush and its ramets and branches are functionally, and perhaps also structurally, compartmentalized to the extent that they respond individually, for example, to defoliation treatments.

Although these features make behavioural options for the birch different to, for example, palms, they still show the degree of decentralization in structural individuals and allow some generalizations based on such features.

(*a*) *Modularity as a morphological and as a functional concept*

The concept modularity conveys two totally different views: a morphological and developmental concept, and composition of plants as conglomerates of partly independent functional units.

Modular organisms are composed of repetitive multicellular units, none of which is vital for the structural individual (Vuorisalo & Tuomi 1985). Modularity is originally a developmental and morphological concept (Hallé *et al.* 1978; White 1979; Harper 1981). A module contains, for example, a leaf, a shoot and a meristem. Depending on the size of the plant, and the phyllotactic system, all or some of the modules are directly connected by vascular systems.

The morphological definition of modularity does not necessarily emphasize those plant features that are critical for herbivory. Neither does the morphological definition help to understand how herbivory affects plant traits. From the viewpoint of survival in the presence of herbivory, an important point in modularity is that although morphologically fixed, modularity allows immense flexibility in a functional sense.

Regulation of plant integration takes place by hormones. They are produced by active meristems, and by means of hormones active meristems modify transport of nutrients. Suppressed meristems are dormant. The meristem that is responsible for causing the strongest hormonal gradient is the local centre of metabolic activity. Watson & Casper (1984) called the resulting functional unit an IPU, an integrated physiological unit. Such a unit is partially autonomous especially in carbon economy.

When the plant develops, activity of local meristems also changes. After the developmental phase of a module, its boundaries need not coincide with limits of an IPU. A particular module may belong to one IPU at one time and to another at another time. One IPU may cover one or several modules.

(*b*) *Integration of modules and IPUs: ecological and evolutionary views*

If an individual plant simultaneously is an aggregation of structural modules, and of functional IPUs, what causes the obvious integration of the individual? I propose that the very basic intermodular rules make integration very simple, almost automatic. The simplest alternative is to assume that the IPU at the best location has to get control over nearby, less optimally located, IPUs. In above-ground parts of a plant this means that (i) the meristem which has the best access to light (ii) remains or becomes metabolically active, (iii) creates high concentrations of hormones (especially auxins, see Matthysse & Scott (1984)) which (iv) both suppress nearby meristems and guide resources (water and nutrients) to that meristem. The coupling of high meristematic activity at favourable sites with production of pertinent hormones and transport of resources, incidentally creates integration among above-ground parts of the plant. Below-ground parts obviously follow analogous principles.

The genetic code for behaviour of an IPU is in genes. However, responses of an IPU cannot be directly genetically programmed. Instead, there have to be codes for alternative position-dependent behaviours for IPUs. Behaviours of an IPU have to take into account the position of the IPU within the plant (and therefore possible dominance of other, especially nearby, IPUs), and the external environment. Formation of a potential, and performance of an actual, IPU may be constrained by both. Consequently, modular, or IPU, integrations have to be programmed so that under normal conditions IPUs produce phenotypes that are locally optimal, or close to optimal, under the conditions that the IPU encounters.

This also means that there have to be genetically determined rules for achieving, maintaining and giving up dominance among competing IPUs. These rules make an aggregation of IPUs, the individual, behave in a way resembling behaviour of a true individual. Still, within the limits of these rules, there may be true competition among IPUs. The genetically constrained, but physiologically genuine competition among IPUs may be the way in which the integration and optimal, or close to optimal, functioning of the structural individual is arranged.

Although the relations among IPUs are dynamic, there exist some regularities. The most familiar is apical dominance (Hillman 1984), the phenomenon that, for example, in freely growing trees, the topmost meristem is the most active. It forms a strong sink and has access to adequate resources. Apical dominance offers an example of genetically based but environmentally modified traits. Variance in the strength of apical dominance (in addition to factors like dormancy and activity of meristems, internode length and branching angle) makes it possible to model a high number of different plant types (Sutherland & Stillman 1990). The strength of apical dominance has a hereditary basis (Kozlowski 1971) and therefore is susceptible to artificial or natural selection. Simultaneously, apical dominance is under strong influence of environmental factors, like nutrient availability (Kozlowski 1964; McIntyre 1977; Slade & Hutchings 1987). Enhanced nutrient levels increase ability of other meristems to activate their own IPUS. Therefore, in clonal herbs for instance, spread of the clone (determined by the growth rate of apical, primary branches) is relatively insensitive to environmental factors (Oinonen 1967*a*, *b*; Hutchings 1988) but growth of secondary and lower level branches is strongly modified by availability of resources.

The behaviour of a structural individual consists of behaviour of its IPUS; they are the functional units. Consequently, phenotypic selection (consequences of natural selection as a causative, instead of statistical, concept; see Endler 1986) has to concentrate on behavioural responses of functional units, IPUS. If there is genetic intra-individual variability among IPUS, produced by somatic mutations, true evolution may follow within a structural individual. Assuming no somatic mutations, phenotypic selection within or among IPUS of an individual does not lead to genetic response because of a lack of additive genetic variance.

Naturally, inter-individual selection can function as a causative evolutionary agent. It operates via the ability of individual IPUS to grow, to reproduce and to survive. The more optimal are local responses of IPUS, the higher is the fitness of the genotype. Growth and reproduction of the whole structural individual (genet in many cases) is the sum of modular values, and survival of the plant also depends on survival of the modules, although not in a straightforward fashion.

3. HOW DOES MODULARITY MODIFY CONSEQUENCES OF HERBIVORY?

Plant modularity, including functional aspects like organization of the plant to spatially and temporally dynamic IPUS, and the partially sink-regulated photosynthesis, affect some aspects of plant–herbivore interactions. Next I deal briefly with the following topics: tolerance to loss of foliage, ability of plants to recover after damage and degree of phenotypic plasticity. In addition, modularity modifies usability of some methodological practices like calculations of the value of lost tissue, and effects of simulated herbivory. In addition, it offers explanations for some seemingly non-adaptive plant responses.

(*a*) *Tolerance to loss of foliage and*
(*b*) *ability of plants to recover after damage*

Growing plants usually shed the oldest leaves. This in part depends on shelf shading; new leaves shade older ones and when the performance of old leaves becomes uneconomical, their resources are transported to younger tissues, and the old ones die. For the plant the importance of losing small amounts of foliage has to be evaluated against this background. Owing to presence of dormant meristems and sink regulation, new leaves may be easily built, and old ones can survive longer. Under moderate or good resource conditions, plants can compensate, even overcompensate, losses (Paige & Whitham 1987; Maschinski & Whitham 1989).

Accordingly, a plant may easily recover after herbivory assuming that the two preconditions for successful recovery exist: there are extra meristems and resources are available. The surprising ease of recovery largely depends on the same set of factors as above. A rearrangement of dominance hierarchies among IPUS automatically happens after disturbance caused, for example, by herbivores: IPUS at the best locations become activated and redirect resources to themselves. Sink regulation further helps the plant to recover: activated meristems create new sinks, mature source-leaves slow down the rate of senescence and may increase or prolong their photosynthetic activity.

(*c*) *Degree of phenotypic plasticity*

Alternative position-dependent behavioural rules of IPUS indicate that phenotypic plasticity in plants must be large. This has long been familiar, for example, in the ease by which plants form ecotypes. Different parts of a tree may be different for herbivores, and the same tree may, completely or locally, vary temporally in quality for herbivores due to developmental or environmental factors. For instance, juvenile trees, or parts of them, often contain spines although mature tissues do not. Furthermore, foliage quality for a herbivore in previously non-defoliated mountain birch trees may be more similar to other tree species than to mountain birches defoliated a couple of years earlier (Haukioja *et al.* 1988).

Therefore, in long-lived plants, phenotypic plasticity may reduce evolution via natural selection; temporarily perhaps also replace it. A single genotype simply may be able to create the necessary array of phenotypes. This is especially relevant for defensive functions in plant species in which the generation time is much longer than that of the herbivore. For such plants it is important to be able to phenotypically change enough to minimize risks of emergence of specialized genotypes of the main pests. As a curiosity, this seems also to be the way in which herbivores may adapt to temporal variability in host quality. The quality of mountain birches may be so variable and perhaps unpredictable within and among *Epirrita* generations that the moth manages best by corresponding phenotypic plasticity. Accordingly, although *Epirrita* broods are significantly different in most analyses concerning, e.g. growth rates, no significant brood × host-plant type interactions have been found (Ayres *et al.* 1987; K. Ruohomäki & E. Haukioja, unpublished information).

(*d*) *Calculations of the value of lost tissue*

All leaves do not have the same value for the plant. Earlier plant-defence theories assumed plant tissues to be protected in relation to their vulnerability (Feeny 1975; Rhoades & Cates 1976), or their value to the plant (McKey 1979). Leaf value presumably was equated with its photosynthetic performance. However, removing a fixed amount of foliage, of equal age, has similar consequences for the plant only if its carbon economy is totally integrated. In that case all the resources go to the general pool. Consequences of foliage removal may be modified, for example, by the role which the leaf has in feeding specific tissues. Harper (1989) has discussed the value of a leaf in relation to functions by the recipient tissue. Haukioja *et al.* (1990) showed that damage to an individual long shoot leaf of the mountain birch specifically affected growth of the potential shoot from the axillary bud of that leaf in the next year.

(*e*) *Effects of simulated herbivory*

To show the value of the approach viewing plants as populations of modules, and IPUS, I take a few examples of possible methodological problems in experiments trying to elucidate how trees respond to damage.

Damage to individual leaves leads to synthesis of compounds which spread to other parts of the plant (Green & Ryan 1972) via phyllotactic connections (see Watson & Casper 1984). Therefore rapid induced responses may not spread first to the physically nearest leaves, but to leaves that are phyllotactically closest.

Without any explicit analysis about tree organization, it has sounded totally reasonable to assume that they are individual trees which either respond or do not respond to damage. However, in the case of mountain birch, they were not trees that reacted to defoliation treatments, but ramets and branches (Haukioja & Neuvonen 1985; Tuomi *et al.* 1988).

Another confounding factor was traced when studying effects of previous defoliation to later susceptibility of the foliage to herbivores. Such experiments, or observations, were thought to test existence of induced defences. But surprisingly, previous defoliation, or browsing, in some cases caused the plants later to be better as diet for later herbivores (Niemelä *et al.* 1984; Williams & Myers 1984; Danell & Huss-Danell 1985; Roland & Myers 1987; Craig *et al.* 1988). Haukioja *et al.* (1990) offered a possible interpretation for those observations by assuming herbivores to be able to damage or to take over the regulative system of such plants. Manipulations of host plants are possible because the hormonally mediated and decentralized control of plant functions is more susceptible to external factors than centralized control by the nerve system in animals.

(*f*) *Explanations for some seemingly non-adaptive plant responses*

An example of a seemingly non-adaptive response to herbivory is the manner in which, trees like apples and birches, behave after vole or hare damage to their bark. If the bark is damaged around the stem, the tree dies because the isolated trunk and branch system can no longer feed roots with photosynthetic products. However, if the tree experiences more extensive damage, and the whole stem is cut, the tree probably recovers. The reason is that, unlike in the former case when the canopy was left intact, new meristems are activated in the stump, and the tree can continue its functions without exhausting reserves in the root system. This indicates that in the tree there is no 'programme' taking care of the benefits of an 'individual tree'; otherwise different behaviours of trees in the above cases do not seem reasonable. The tree is not a tightly integrated organism but a by-product of its parts. Still, under normal conditions, the tree function as an organized individual.

The modular design may also explain some other ostensibly problematic observations relating to defensive responses by trees. For instance, if insect-induced deterioration in foliage quality is an exclusive defence against defoliators, it is very strange that it is delimited it to some ramets or branches only; important defoliators are so mobile that they necessarily attack the whole tree. Such induced responses may not be true defences (see Haukioja & Neuvonen 1985), but at any case such trees do not respond as totally coordinated units but as largely independent subsystems.

Young tissues are often strongly avoided by vertebrate herbivores, and the reason is often chemical, as in the case of twig resins against hares (Bryant 1981). This may protect juvenile trees. However, the same difference in quality may be found between young and older parts of a ramet. In that case young parts are avoided, but still lost because the hare cuts the branch although it only eats older less resinous parts.

4. DISCUSSION

(*a*) *How does herbivory modify modularity?*

Plants contain many toxins that are detrimental for most herbivores. Demonstrations of the potency of such compounds have strongly moulded our ways of thinking how plants deter herbivory. If concentrations of these compounds have a genetic basis, herbivores can function as selective agents and guide evolution of relevant plant defences. At that level plants may defend themselves, and chemical or physical quality of the plant may be strongly modified by herbivores.

On the other hand, the deep structure of plants as modular, incompletely integrated organisms cannot change abruptly, perhaps not at all, simply because there may not be suitable additive genetic variance in relevant traits. It might be as impossible to assume that such traits can change due to herbivory as to assume rabbits can evolve wings because they would be useful for escaping from predators. Herbivory obviously has no or only a very limited role as a factor modifying structural and functional features of plants as modular organisms. Therefore, much of what plants do, and how they respond to herbivory, may have explanations that have nothing to do with herbivory.

However, herbivores may modify regulation of the deep structure. In practice this is hard to prove but there are many examples in line with this logic. For instance, unlike in trees and forbs, meristems of grasses are beneath the growing structure. Therefore, grasses are very tolerant to grazing by large herbivores (McNaughton 1985). Herbivores are known to function as an ecological force that may strongly modify plant form, apical dominance and sex expression (Whitham & Mopper 1985). Whether they can function as evolutionary forces, too, remains open. The compartmentalization of plants to semi-isolated units may be an adaptation preventing spread of diseases (Shigo 1984). It remains unclear whether herbivores can function as selective agents determining the degree of compartmentalization.

Could plants be very different and still cope with herbivory? Perhaps not. Although it is easy to find adaptive interpretations for why, for instance, plants are compartmentalized, a complete change in plant functions might be very difficult because of herbivory. For two reasons it is hard to imagine that plants could be guided by a central, localized decision-making organ: plants have hard-walled cells and it is obviously impossible for them to build complex organs at least in the same way as it happens in animals. In addition, a fixed wiring system to connect the hypothetical central processing organ with peripheral organs of a hypothetical, unitary plant, might be very sensitive to damage. Because a sedentary organism can always be caught by a mobile predator, a central processing unit should be protected extremely effectively which might be difficult. It is furthermore unclear how easily hypothetical organisms with such an organization could be able to recover after damage. Shifting dominance relations among modules, activation of previously dormant meristems and sink regulation are ways to make construction of new parts almost automatic when old parts are damaged and there are resources for recovery.

Summarizing, although the basic functions in plants cannot be easily changed by herbivory, herbivory can be an important factor preventing or making it difficult for plants to develop totally new designs: the new designs would have to be completed before they would be effective against herbivores. Still herbivores may both modify the regulative systems and therefore affect evolution of plant functions, and more directly select for features protecting the plant.

(*b*) *Implications of plant modularity for theories about plant–herbivore interactions*

The major task of general plant–herbivore theories is to explain existence of plants in spite of herbivores. The explanation why plants are able to do so does not only concern evolution of plant defences, but refers to several possible factors like: (i) herbivore numbers are low for reason unrelated to plants, (ii) most herbivores, especially insects do not recognize a specific plant as a potential host due to limitations of their host-recognition system, (iii) plants tolerate small-scale herbivory well because of features relating to their modular structure, (iv) plants may successfully recover after strong herbivory, and (v) plants defend themselves either by toxins or by low availability of nutrients.

The classic plant–herbivore theories emphasized chemical plant defences and especially the need of plants to defend themselves differently against specialized and generalized herbivores (Feeny 1975; Rhoades & Cates 1976). More recent theories have stressed importance of resources (Coley *et al.* 1985), plant ecological strategies like growth forms (Mattson *et al.* 1987), and ability to recover (van der Mejden *et al.* 1988). All these theories rest on an assumption that plants behave optimally against herbivores. I have earlier proposed that although this assumption is generally valid, the modular organization of plants may in some cases modify plant responses to an extent reversing predictions based on *a priori* logic (Haukioja 1990).

At the deepest level we may have problems relating to the fact that evolutionary theorists have only recently started to appreciate the complications produced by phenotypic selection simultaneously functioning at different hierarchical levels, from modules to genets (Tuomi & Vuorisalo 1989; Eriksson & Jerling 1990). Consequently, theories of plant defences take modularity only partially into account as a possible modifier of how evolution by natural selection takes place (see, for example, Buss (1983, 1987); Whitham & Slobodchikoff (1981)).

A further evolutionary difficulty is exemplified by sink-regulated photosynthesis. If it is possible for plants to increase the photosynthetic rate of their leaves, why do they not do so always? Whatever is the correct explanation for this question, much theorizing rests on the importance of excess carbon in relation to nutrients without understanding connections between the physiological and evolutionary mechanisms. For example, Rhoades (1979) assumed photosynthesis to be sensitive to high levels of carbon-based defences, which in turn would prevent extreme concentrations of phenols in photosynthesizing tissues. However, at least in birch well 'defended' trees (rich in phenolic compounds, poor in sugars and nitrogen) had a higher photosynthetic rate than less well 'defended' birches (Prudhomme 1982). Furthermore, the role of nutritional factors, in addition to toxins, has played a minor role in general plant herbivore theories, opposite to, for example, German forest entomological literature (for examples, see Schwenke (1968); Schopf (1981)). The partially sink-regulated photosynthesis may have repercussions at this level, too. For instance, plants recovering from defoliation are often rich in phenols, are poor resources for herbivores, and may thereby defend themselves. However, because there is a strong negative correlation between phenol and sugar levels (Jensen 1988), it is also possible that poor performance of herbivores on such diets results from low sugar levels. And their levels may be low simply because sugars are immediately conveyed from leaves to the strong sinks created by meristems in recovering tissues.

As discussed above, herbivores may be able to modify plants relatively easily, making them more suitable as food, by disturbing intermodular interactions. Understanding such relations points to the importance of basing plant–herbivore theories explicitly on structural and functional mechanisms in plants. Simultaneously it calls for caution in adaptive interpretations: successful manipulation of plants' regulative systems can lead to consequences that are opposite to defences (see, for example, Niemelä *et al.* (1984); Danell & Huss-Danell (1985); Haukioja *et al.* (1990)). If that is possible, convincing demonstrations of true defences are hard to obtain.

REFERENCES

Ayres, M. P., Suomela, J. & MacLean, S. F. Jr. 1987 Growth performance of *Epirrita autumnata* (Lepidoptera: Geometridae) on mountain birch: trees, broods, and tree-brood interactions. *Oecologia, Berl.* **74**, 450–457.

Bryant, J. P. 1981 Phytochemical deterrence of snowshoehare browsing by adventitious shoots of four Alaskan trees. *Science, Wash.* **213**, 889–890.

Buss, L. W. 1983 Evolution, development, and the units of selection. *Proc. natn. Acad. Sci. U.S.A.* **80**, 1387–1391.

Buss, L. W. 1987 *The evolution of individuality.* Princeton University Press.

Coley, P. D., Bryant, J. P. & Chapin, F. S. III 1985 Resource availability and plant antiherbivore defense. *Science, Wash.* **230**, 895–899.

Craig, T. P., Price, P. W. & Itami, J. K. 1986 Resource regulation by a stem-galling sawfly on the arroyo willow. *Ecology* **67**, 419–425.

Danell, K. & Huss-Danell, K. 1985 Feeding by insects and hares on birches earlier affected by moose browsing. *Oikos* **44**, 75–81.

Eriksson, O. & Jerling, L. 1990 Hierarchical selection and risk spreading in clonal plants. In *Clonal growth in plants: regulation and function* (ed. J. M. van Groenendael & H. de Kroon), pp. 79–94. The Hague: SPB Academic Publishing.

Endler, J. A. 1986 *Natural selection in the wild.* Princeton University Press.

Feeny, P. 1975 Biochemical coevolution between plants and their insect herbivores. In *Coevolution of animals and plants* (ed. L. E. Gilbert & P. H. Raven), pp. 3–19. Austin: University of Texas Press.

Feeny, P. 1976 Plant apparency and chemical defence. *Rec. Adv. Phytochem.* **10**, 1–40.

Geber, M. 1990 The cost of meristem limitation in *Polygonium arenastrum*: negative genetic correlations between fecundity and growth. *Evolution* **44**, 799–819.

Green, T. R. & Ryan, C. A. 1972 Wound-induced proteinase inhibitor in plant leaves: A possible defence mechanism against insects. *Science, Wash.* **175**, 776–777.

Groenendael, J. M. van & de Kroon, H. (eds) 1990 *Clonal growth in plants: regulation and function.* The Hague: SPB Academic Publishing.

Hallé, F., Oldeman, R. A. A. & Tomlinson, P. B. 1978 *Tropical trees and forests; an architectural analysis.* Berlin: Springer Verlag.

Harper, J. L. 1981 The concept of population in modular organisms. In *Theoretical ecology* (ed. R. M. May), pp. 53–77. Sunderland, Massachusetts: Sinauer Associates.

Harper, J. L. 1989 The value of a leaf. *Oecologia, Berl.* **80**, 53–58.

Haukioja, E. 1990 Toxic and nutritive substances as plant defence mechanisms against invertebrate herbivores. In *Pest, pathogens and plant communities* (ed. J. Burdon & S. Leather), pp. 219–231. Oxford: Blackwell Scientific Publications.

Haukioja, E. & Neuvonen, S. 1985 Induced long-term resistance of birch foliage against defoliators, defensive or incidental? *Ecology* **66**, 1303–1308.

Haukioja, E., Neuvonen, S., Hanhimäki, S. & Niemelä, P. 1988 The autumnal moth *Epirrita autumnata* in Fennoscandia. In *Dynamics of forest insect populations* (ed. A. A. Berryman), pp. 163–178. New York: Plenum.

Haukioja, E., Ruohomäki, K., Senn, J., Suomela, J. & Walls, M. 1990 Consequences of herbivory in the mountain birch (*Betula pubescens* ssp *tortuosa*): importance of the functional organization of the tree. *Oecologia, Berl.* **82**, 238–247.

Hillman, J. R. 1984 Apical dominance. In *Advanced plant physiology* (ed. M. B. Wilkins), pp. 127–148. London: Pitman.

Hutchings, M. J. 1988 Differential foraging for resources and structural plasticity in plants. *Trends Ecol. Evol.* **3**, 200–204.

Jackson, J. B. C., Buss, L. W. & Cook, R. E. (ed.) 1985 *Population biology and evolution of clonal organisms.* Yale University Press.

Jensen, T. S. 1988 Variability of Norway spruce (*Picea abies* L.) needles; performance of spruce sawflies (*Gilpinia hercyniae* Htg.). *Oecologia, Berl.* **77**, 313–320.

Jerling, L. 1985 Are plants and animals alike? A note on evolutionary plant population ecology. *Oikos* **45**, 150–153.

Kozlowski, T. T. 1964 Shoot growth in woody plants. *Bot. Rev.* **30**, 335–392.

Kozlowski, T. T. 1971 *Growth and development of trees*, vol. 1. New York: Academic Press.

Långström, B., Tenow, O., Ericsson, A., Hellqvist, C. & Larsson, S. 1990 Effects of shoot pruning on stem growth, needle biomass, and dynamics of carbohydrates and nitrogen in Scots pine as related to season and tree age. *Can. J. For. Res.* **20**, 514–523.

Marshall, C. 1990 Source-sink relations of interconnected ramets. In *Clonal growth in plants: regulation and function* (ed. J. M. van Groenendael & H. de Kroon), pp. 23–41. The Hague: SPB Academic Publishing.

Maschinski, J. & Whitham, T. G. 1989 The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. *Am. Nat.* **134**, 1–19.

Matthysse, A. G. & Scott, T. K. 1984 Functions of hormones at the whole plant level of organization. In *Encyclopedia of plant physiology* (ed. T. K. Scott), new series **10**, 219–243. Berlin: Springer Verlag.

Mattson, W. J., Lawrence, R. K., Haack, R. A., Herms, D. A. & Charles, P.-J. 1987 Defensive strategies of woody plants against different insect feeding guilds in relation to plant ecological strategies and intimacy of association with insects. In *Mechanisms of woody plant defenses against insects; search for pattern* (ed. W. J. Mattson, J. Levieux & C. Bernard-Dagan), pp. 3–38. New York: Springer Verlag.

McIntyre, G. I. 1977 The role of nutrition in apical dominance. *Symp. Soc. Exp. Biol.* **31**, 251–273.

McKey, D. 1979 The distribution of secondary compounds within plants. In *Herbivores. Their interaction with secondary plant metabolites* (ed. G. A. Rosenthal & D. H. Janzen), pp. 55–133. New York: Academic Press.

McNaughton, S. J. 1985 Grazing lawns: animals in herds, plant form, and coevolution. *Am. Nat.* **124**, 863–886.

Meijden, E. van der, Wijn, M. & Verkaar, H. J. 1988 Defence and regrowth alternative plant strategies in the struggle against herbivores. *Oikos* **51**, 355–363.

Niemelä, P., Tuomi, J., Mannila, R. & Ojala, P. 1984 The effect of previous damage on the quality of Scots pine foliage as food for Diprionid sawflies. *Z. angew. Entomol.* **98**, 33–43.

Oinonen, E. 1967*a* Sporal regeneration of bracken in Finland in the light of the dimensions and age of its clones. *Acta for. fenn.* **83** (1), 3–96.

Oinonen, E. 1967*b* The correlation between the size of Finnish bracken (*Pteridium aquilinum* (L.) Kuhn) clones and certain periods of site history. *Acta for. fenn.* **83** (2), 1–51.

Paige, K. N. & Whitham, T. G. 1987 Overcompensation in response to mammalian herbivory; the advantage of being eaten. *Am. Nat.* **129**, 407–416.

Prudhomme, T. 1982 The effect of defoliation history on photosynthetic rates in mountain birch. *Rep. Kevo Subarctic Res. Stat.* **18**, 5–9.

Rhoades, D. F. 1979 Evolution of plant chemical defense against herbivores. In *Herbivores. Their interaction with secondary plant metabolites* (ed. G. A. Rosenthal & D. H. Janzen), pp. 3–54. New York: Academic Press.

Rhoades, D. F. & Cates, R. G. 1976 Toward a general theory of plant antiherbivore chemistry. *Rec. Adv. Phytochem.* **10**, 168–213.

Roland, J. & Myers, J. H. 1987 Improved insect performance from host-plant defoliation: winter moth on oak and apple. *Ecol. Entomol.* **12**, 409–414.

Shigo, A. L. 1984 Compartmentalization: a conceptual framework for understanding how trees grow and defend themselves. *A. Rev. Phytopath.* **22**, 189–214.

Schopf, R. 1981 Quantitative Untersuchungen zur Nahrungsaufnahme und -ausnutzung der Blattwespe *Gilpinia hercyniae*. *Z. angew. Entomol.* **92**, 137–149.

Schwenke, W. 1968 Neue Hinweise auf eine Abhängigkeit der Vermehrung blatt- und nadelfressender Forstinsekten vom Zuckergehalt ihrer Nahrung. *Z. angew. Entomol.* **61**, 365–369.

Slade, A. J. & Hutchings, M. J. 1987 The effects of nutrient availability on foraging in the clonal herb *Glechoma hederacea*. *J. Ecol.* **75**, 95–112.

Sutherland, W. J. & Stillman, R. A. 1990 Clonal growth: insights from models. In *Clonal growth in plants: regulation and function* (ed. J. M. van Groenendael & H. de Kroon), pp. 95–111. The Hague: SPB Academic Publishing.

Tuomi, J., Niemelä, P., Rousi, M., Sirén, S. & Vuorisalo, T. 1988 Induced accumulation of foliage phenols in mountain birch: branch response to defoliation? *Am. Nat.* **132**, 602–608.

Tuomi, J. & Vuorisalo, T. 1989 Hierarchial selection in modular organisms. *Trends Ecol. Evol.* **4**, 209–213.

Vuorisalo, T. & Tuomi, J. 1986 Unitary and modular organisms: criteria for ecological division. *Oikos* **47**, 382–385.

Wardlaw, I. F. 1990 The control of carbon partitioning in plants. *New Phytol.* **116**, 341–381.

Watson, M. A. 1986 Integrated physiological units in plants. *Trends Ecol. Evol.* **1**, 119–123.

Watson, M. A. & Casper, B. B. 1984 Morphogenetic constraints on patterns of carbon distribution in plants. *A. Rev. Ecol. Syst.* **15**, 233–258.

White, J. 1979 The plant as a metapopulation. *A. Rev. Ecol. Syst.* **10**, 109–145.

Whitham, T. G. & Mopper, S. 1985 Chronic herbivory: Impacts on architecture and sex expression of Pinyon pine. *Science, Wash.* **228**, 1089–1091.

Whitham, T. G. & Slobodchikoff, C. N. 1981 Evolution by individuals, plant-herbivore interactions, and mosaics of genetic variability: the adaptive significance of somatic mutations in plants. *Oecologia, Berl.* **49**, 287–292.

Williams, K. S. & Myers, J. H. 1984 Previous herbivore attack of red alder may improve food quality for fall webworm larvae. *Oecologia, Berl.* **63**, 166–170.

Discussion

P. J. Grubb (*Botany School, University of Cambridge, U.K.*). It seems to me that the ability of plants to produce regrowth shoots from dormant buds, which is so important in their response to grazing, would have evolved in a world without animals as a result of selection for vegetative survival of drought, fire, frost and wind damage. Similarly the production of many secondary chemicals in greater concentrations in regrowth shoots would probably have evolved in a world without animals as a result of selection for survival of attack by pathogenic microorganisms. In contrast the production of spines on regrowth shoots and not on 'normal' shoots of many species does suggest that specific selection by animals has been important. Does Dr Haukioja agree?

E. Haukioja. I agree. However, animals obviously have also selected higher concentration of some secondary compounds, and presumably synthesis of some new compounds.

V. Brown (*Imperial College, Silwood Park, Berkshire, U.K.*). Does Dr Haukioja have any idea what effect the various types and levels of foliar damage have on the root system?

E. Haukioja. I do not have any real information.

W. J. Bond (*Botany Department, University of Cape Town, South Africa*). I would like to question the validity of the modular 'rules'. With the first rule 'meristems with the best ability to grow gain control over other meristems', one would predict trees shaped like solar collectors with no modules developing on the shady north-facing side of the canopy. But trees have symmetrical canopies. Is this not inconsistent with the modular argument?

E. Haukioja. I assume that that would happen if 'gaining control of other meristems' would mean total inability of all subdued meristems to develop. That is not what normally happens: the growth of some meristems is totally inhibited, whereas only lessened in some others.