

Defoliation: do physiological and morphological responses lead to (over)compensation?

A.H. Prins and H.J. Verkaar

2.1 Introduction

To a plant, defoliation is the most striking aspect of herbivory. It has immediate, negative effects on plant performance and, as a consequence, it probably affects growth, reproduction and fitness in the long term. However, one of the most puzzling discoveries made by plant ecologists and evolutionary biologists in the last decade is that an increase in plant growth and fitness sometimes results from herbivory. The consumption of vital plant organs sometimes actually seems to increase plant fitness! What constraints are released by herbivory, why do unattacked plants seem to grow or reproduce suboptimally? In this chapter, we try to answer these questions by looking in more detail at various responses to herbivory.

Plants exhibit a range of mechanisms in their responses to herbivory, the effects of which can be conveniently divided into physiological and morphological (Table 2.1). Physiological mechanisms include a stimulation of photosynthetic rate, a changed hormonal status, a redistribution of carbohydrates and mineral nutrients, and delayed plant senescence. The morphological mechanisms include changes in leaf area ratio, in plant architecture and in root development. We discuss here whether these mechanisms, either individually or collectively, can compensate partly, or even fully for tissue damage.

Plant compensation must be seen in the context of the biotic and abiotic environment: it is also affected by the plant growth stage during which damage takes place, the time available for recovery, grazing intensity and frequency. Competition and abiotic conditions affect the potential for compensation. Plants with different life strategies may show specific reactions to herbivory. These modifying factors will be discussed after we have described the possible reactions to herbivory.

Table 2.1. Plant responses to defoliation/herbivory

	Comments	Species	Lab (L)/field (F)	References
PHYSIOLOGICAL MECHANISMS				
Increased NAR	-	<i>Pinus radiata</i>	L	Sweet and Wareing (1966)
	-	<i>Nicotiana tabacum</i>	L	Kolodny-Hirsch <i>et al.</i> (1986)
Depends on N-availability		<i>Cynoglossum officinale</i>	L	Verkaar <i>et al.</i> (1986)
		<i>Verbascum thapsus</i>	L	
Limited duration		<i>Cynoglossum officinale</i>	L	Prins <i>et al.</i> (1989)
		<i>Senecio jacobaea</i>	L	
Limited duration		<i>Briza subaristata</i>	L	Oestreich and McNaughton (1991)
		<i>Bouteloua curtipendula</i>	L	Ingham and Detling (1986)
Reduced NAR		Several species	L	Ayres (1991)
Increased carbohydrate investment in above-ground plant parts		<i>Brassica</i> spp.	L	Van Emden (1990)
		<i>Lycopersicon</i>	L	Royalty and Perring (1989)
Increased nitrogen investment in above-ground plant parts		<i>Agropyron smithii</i>	L	Polley and Detling (1989)
		<i>Bouteloua gracilis</i>	L	Jaramillo and Detling (1988)
Remobilization proportional to initial contents and intensity of herbivory		<i>Euphorbia esula</i>	F	Cyr and Bewley (1990)
		<i>Trifolium repens</i>	L	Baur-Hösch <i>et al.</i> (1990)
Mobilized as soluble protein to newly formed leaves		<i>Trifolium subterraneum</i>	L	Culvenor <i>et al.</i> (1989)
		<i>Trifolium repens</i>	L	Culvenor and Simpson (1991)
				Marrion and Haystead (1990)

Delayed plant senescence	Inhibition of protein, chlorophyll and enzyme degradation, reduced starch accumulation, increased retention of mature leaves	<i>Nicotiana tabacum</i>	F	Kolodny-Hirsch <i>et al.</i> (1986)
	Regulated by hormonal activity	Several plant species	L	Thimann (1980, 1987) Nooden (1980)
	Only for two oldest, fully expanded leaves, senescence not affected in all other foliage elements	<i>Agropyron desertorum</i> <i>Agropyron spicatum</i>	F	Nowak and Caldwell (1984)
MORPHOLOGICAL MECHANISMS				
Increase in LAR	Increase higher in severely defoliated plants	<i>Cynoglossum officinale</i> <i>Senecio jacobaea</i> <i>Senecio vulgaris</i>	L	Prins <i>et al.</i> (1989)
Decrease in LAR	More inflorescences	<i>Vicia faba</i>	L	Paul and Ayres (1986)
Stimulated growth from axillary buds	More inflorescences Positive effect on seed production	<i>Jurinea mollis</i> <i>Senecio jacobaea</i> <i>Ipomopsis aggregata</i>	L F F	Paul and Ayres (1986) Inouye (1982) Islam and Crawley (1983) Paige and Whitham (1987)
	Positive effect on seed production under some circumstances	<i>Ipomopsis arizonica</i>	F	Maschinsky and Whitham (1989)
Changed leaf demography	Negative effect on seed production Decreased leaf initiation and leaf survival	<i>Epilobium latifolium</i> <i>Cardamine cordifolia</i>	F F	Doak (1991) Louda (1984)
Pseudogall formation	Induced by aphids	<i>Prunus padus</i>	F	Leather (1988)

Table 2.1. (Continued)

Comments	Species	Lab (L)/field (F)	References
Changed root development			
Decreased root length growth and root weight	<i>Agropyron desertorum</i>	F	Richards (1984)
Decrease in root:shoot ratio	<i>Rumex crispus</i>	L	Bentley and Whittaker (1979)
Decrease in root:shoot ratio	<i>Eucalyptus blakebyi</i>	L	Vranjic and Gullen (1990)
Increase in root:shoot ratio	<i>Rumex obtusifolius</i>	L	Bentley and Whittaker (1979)
Compensation for loss of above-ground tissue, at the expense of root growth	<i>Plantago lanceolata</i>	L	Fajter <i>et al.</i> (1991)
Decrease in root:shoot ratio	Several species infected by pathogens	L	Ayres (1991)

2.2 Physiological reactions to herbivory

2.2.1 Changes in efficiency of dry matter assimilation

Defoliation imparts a severe physiological stress on plants by suddenly restricting the availability of photosynthate needed for growth. Young plants, and plants that have not yet developed a storage reserve system, suffer most from this sudden stress (Cyr and Bewley, 1990). Plants may be stimulated to compensate physiologically for the removal of tissue.

In a classical experiment with *Pinus radiata*, Sweet and Wareing (1966) showed that, 6 days after removing one-third or all the fully expanded leaves, defoliated plants had a higher net photosynthetic rate per unit of remaining leaf than undefoliated plants. The severely defoliated plants even had a higher photosynthetic rate than moderately defoliated plants. Periods of increased efficiency in assimilating dry matter were found after artificial damage in *Nicotiana tabacum* (Kolodny-Hirsch *et al.*, 1986). These correlated with increases in chlorophyll, soluble proteins, and ribulose-1,5-bisphosphate carboxylase oxygenase content. Such physiological responses are found fairly often in plants affected by defoliation (Alcock, 1964; Wallace *et al.*, 1984; Danell *et al.*, 1985) and have been noted, also, in upper healthy leaves of plants infected on lower leaves by biotrophic pathogens (Walters and Ayres, 1983). Pathogens, such as rust or powdery mildew fungi, were found to reduce the rate of net photosynthesis at the site of infection in groundsel, pea and barley, but in the younger leaves net photosynthesis was temporarily increased (Ayres, 1991).

An enhanced net assimilation rate (NAR) may lead to the successful replacement of leaf tissue. However, this response depends on nitrogen availability, e.g. in situations with a high nitrogen availability NAR was significantly higher in defoliated *Cynoglossum officinale* and *Verbascum thapsus* than in undefoliated plants, but this increase did not occur when nitrogen was not available (Verkaar *et al.*, 1986).

In *Senecio jacobaea* and *C. officinale*, the increase in NAR as a result of damage was only temporary (Figure 2.1). The higher NAR was found for a short period after defoliation and only at the higher level of defoliation. After moderate defoliation in *C. officinale* no increase in NAR was found in the first few weeks, but during the second part of the experiment NAR temporarily decreased less quickly than in the undefoliated plants (Figure 2.1) (Prins *et al.*, 1989). A significantly higher NAR may be found only for a short period after defoliation, the rate soon decreasing to equal that found in non-defoliated plants. This was also found after defoliation of the grass, *Briza subaristata*, a native perennial grass from the flooding pampas of Argentina (Oesterheld and McNaughton, 1991a).

Repeated clipping may prolong increased net photosynthesis: in *Bouteloua curtipendula*, defoliated at weekly intervals, rates of photosynthesis and transpiration per unit of leaf area at final harvest (7–95 days after planting) were two to three times higher in defoliated plants than in undefoliated plants (Ingham and Detling, 1986).

Defoliation causes a sudden change in carbon status and therefore in source/sink relationships, even within the shoot. The increase in NAR in the remaining leaves suggests that photosynthesis can be temporarily increased to meet an increased

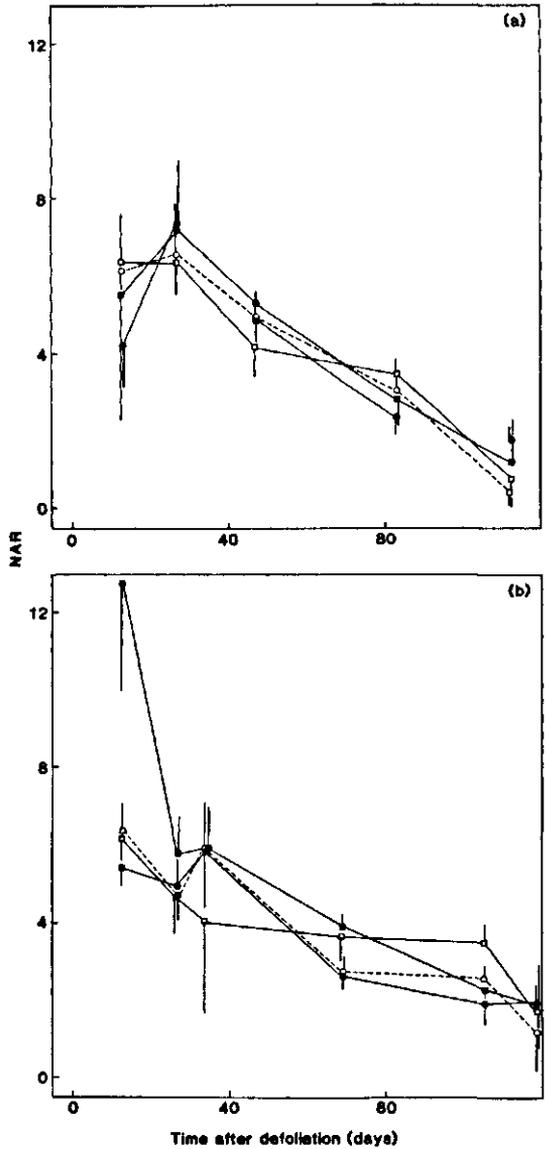


Figure 2.1. Net assimilation rate (NAR) ($g\ g^{-1}\ day^{-1} \times 10^{-4}$) in (a) *Cynoglossum officinale* and (b) *Senecio jacobaea* after defoliation. (○) Control, (●) 10-12% defoliation, (□) 30% defoliation, (■) 94.5-98% defoliation. Standard errors are indicated to one side of the mean. From Prins et al. (1989).

demand for photosynthates in the remaining root and the newly formed shoots (Neales and Incoll, 1968; Wareing and Patrick, 1975). However, no net increase and even decreasing levels of assimilation were found in some studies. The aphid, *Brevicoryne brassicae*, feeding on Brussels sprout, not only induced a decrease in the number of leaves and the leaf area, but the remaining leaves on the infested plants were less efficient assimilators. Aphid feeding results in leaf curling and a decreased density of stomata in new leaves, factors which might contribute to the difficulties the plant has in compensating for tissue damage (van Emden, 1990). Feeding of mites, *Aculops*

lycopersici, caused a reduction in net photosynthesis of affected tomato leaflets. Net photosynthesis and mite-days per cm² of leaflet were significantly negatively correlated. Moreover, healthy tomato leaflets did not show an increase in photosynthesis to compensate for the reduction in the damaged leaflets (Royalty and Perring, 1989).

2.2.2 *Redistribution of carbohydrates and mineral nutrients*

Regrowth following herbivory can be increased by changes in the translocation pattern of newly formed carbon or by the redistribution of previously accumulated carbon. Translocation of carbohydrates and nitrogen compounds from the roots to the leaves can occur at rates higher than in ungrazed conditions. Changes in the steady-state processes of carbon fixation and translocation have been extensively studied, but, at this moment, the exact mechanism governing the changes following herbivory is unknown (Dyer *et al.*, 1991). Note that Farrar (in Chapter 8) proposes that no new mechanisms need to be involved to explain carbon partitioning in the potentially more complex situation where plants are infected by a microbe; the principles of turgor-driven bulk flow apply equally well to both healthy and infected plants.

In the grasses, *Agropyron smithii* and *Bouteloua gracilis*, an increased investment in above-ground relative to below-ground biomass and nitrogen was found after defoliation (Jaramillo and Detling, 1988; Polley and Detling, 1989). However, total biomass yield was significantly reduced. Following defoliation, certain herbaceous perennials redistribute carbon primarily from leaf and stem base to active meristems, thus rapidly forming new leaves (Cyr and Bewley, 1990). In stolons of *Trifolium repens*, carbohydrate reserves, mostly starch, were remobilized in proportion to their initial contents, and when plants were more severely damaged, remobilization was greater (Baur-Hösch *et al.*, 1990).

Remobilization of nitrogen following herbivore attack has received much less attention than carbohydrate remobilization (Culvenor and Simpson, 1991), probably because net changes are smaller (Smith and Silva, 1969; Caldwell *et al.*, 1981). In *Trifolium subterraneum*, 17% of the nitrogen present in storage organs (branch, taproot, fine roots, nodules) was mobilized as soluble protein to the newly formed leaves after defoliation (Culvenor *et al.*, 1989; Culvenor and Simpson, 1991). Comparable results were found for *T. repens* (Marriot and Haystead, 1990).

2.2.3 *Delayed plant senescence*

Following herbivory, the enhanced demand for assimilates from the remaining plant tissue may delay the normal decline of photosynthetic rate with age in the unattacked or partly defoliated leaves. Arrested senescence in response to leaf loss has been reported for a wide range of plants (Woolhouse, 1967; Wareing *et al.*, 1968). Regreening of yellow senescent leaves on vegetative plants of *Nicotiana tabacum* could be induced by removal of the younger leaves of the plant (Woolhouse, 1967). Not only leaf herbivory, but also the removal of reproductive organs, such as developing fruits or seeds, can delay the onset of senescence.

A delay in leaf senescence is characterized by the inhibition of protein, chlorophyll and enzyme degradation, reduced starch accumulation, and increased retention of mature leaves (Kolodny-Hirsch *et al.*, 1986). The control of senescence processes is regulated by hormonal activity (e.g. Nooden, 1980; Thimann, 1980, 1987).

A delay in senescence is not always documented for all leaves following herbivory: in *Agropyron desertorum* and *A. spicatum* the onset of senescence was found only for the two oldest, fully expanded leaves that were present when the plants were initially clipped; the initiation and senescence of all other foliage elements were not affected by the clipping treatments (Nowak and Caldwell, 1984).

2.3 Morphological reactions to herbivory

2.3.1 Changes in leaf area ratio

The morphological mechanism behind regrowth may involve an increase in leaf area ratio (LAR, $\text{cm}^2 \text{g}^{-1}$). In the biennials, *S. jacobaea* and *C. officinale*, LAR increased at moderate (30%) and even more at high (94–100%) degrees of defoliation (Figure 2.2) (Prins *et al.*, 1989).

In plants infected by pathogens, the inhibition of net photosynthesis in the infected leaves, as mentioned in Section 2.2.1, may be compensated by an increase in leaf area ratio (Paul and Ayres, 1986; Ayres, 1991). In nutrient-rich as well as nutrient-poor situations, an increase in LAR was found in groundsel, *Senecio vulgaris*. However, the opposite reaction has also been reported: *Vicia faba* infected by rust exhibited a decreased leaf area ratio (Williams, 1978).

2.3.2 Changes in plant architecture

Damage to the shoot apex by herbivory affects apical dominance and stimulates growth of branches from axillary buds, previously inhibited by auxins produced in the shoot apex (Salisbury and Ross, 1985). The release of competition for nutrients and carbohydrates between the axillary buds and the shoot apex may also contribute to the cessation of the inhibition of axillary buds (Benner, 1988).

An alteration in branching pattern following apex removal is frequently found (e.g. Taylor and Bardner, 1968; Inouye, 1982; Islam and Crawley, 1983; Paige and Whitham, 1987; Maschinsky and Whitham, 1989). Apex removal may induce plants that normally form a terminal inflorescence to produce a greater number of inflorescences. Notwithstanding this greater number of inflorescences, a negative effect of herbivory on seed production is often found (e.g. Doak, 1991). This may be caused by the direct loss of tissue or by the loss of the future photosynthetic capacity of that tissue. Moreover, apex removal causes a delay in plant growth because the axillary branches first have to form leaves before the photosynthetic rate can reach the same level as before defoliation.

Various morphological reactions to herbivory are found when plant parts other than the apex are affected. In the birches, *Betula pendula* and *Betula pubescens*, a decrease in the number of long shoots was found, but the frequency of branched shoots

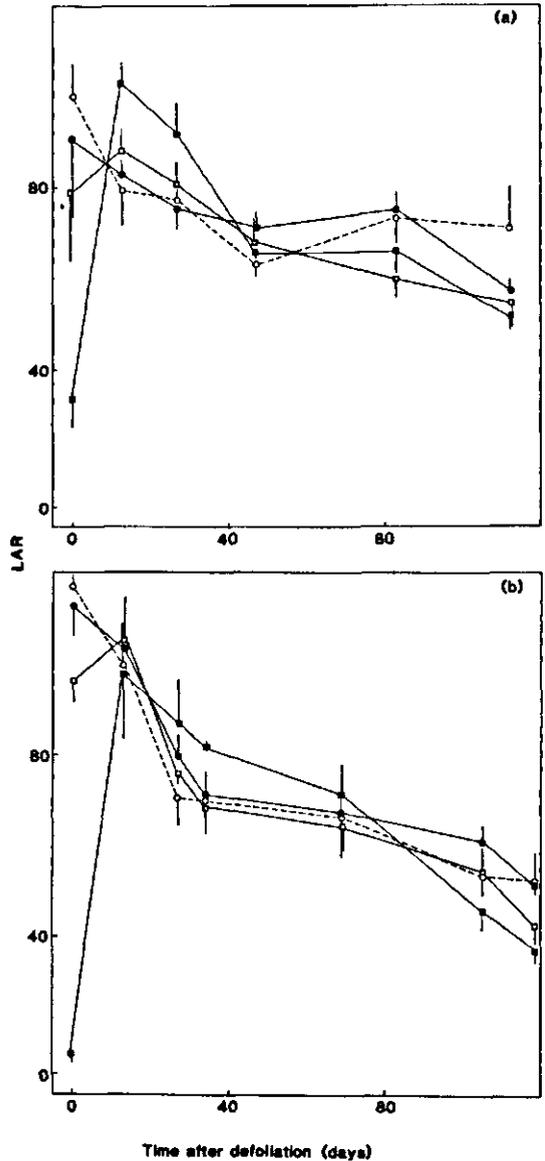


Figure 2.2. Leaf area ratio ($\text{LAR}, \text{cm}^2 \text{g}^{-1}$) after defoliation in (a) *Cynoglossum officinale* and (b) *Senecio jacobaea*. (○) Control, (●) 10-12% defoliation, (□) 30% defoliation, (■) 94.5-98% defoliation. Standard errors are indicated to one side of the mean. From Prins et al. (1989).

increased, as well as the length and dry weight of individual shoots (Danell *et al.*, 1985; Bergström and Dannell, 1987). Feeding by the weevil, *Unapsis euonymi*, increased leaf abscission in *Euonymus fortunei*. This may not have been detrimental to the plant because photosynthetic output of the leaves had already been impaired as a result of chlorosis in the insect-damaged leaves (Cockfield and Potter, 1986).

In the herbaceous crucifer, bittercress, *Cardamine cordifolia*, leaf herbivory well below complete defoliation (25% of the leaf area) changed leaf demography (leaf

initiation and leaf survival) and reduced plant performance (a decrease in plant stature, leaf area and fruit production)(Louda, 1984).

Different herbivores may attack the same plant in different ways and, therefore, cause different morphological responses. Marked changes in plant architecture are found as a result of aphid infestation (*Rhopalosiphum padi*) on bird cherry (*Prunus padus*). Aphids induce the formation of a pseudogall at high infestation levels and the shoot tip is killed, preventing terminal bud formation. Attacked leaves are likely to reduce the photosynthetic capacity of the plant during the rest of the year, because attacked leaves are discoloured and malformed. In contrast, a moth, *Yponomeuta evonymellus*, defoliates the tree after bud formation is completed. The tree can form regrowth leaves after defoliation has ended (Leather, 1986; 1988).

2.3.3 Leaf damage and root development

The allocation of more resources to above-ground regrowth is a common and widespread reaction of plants to herbivory, as well as to infection by fungi (Ayres, 1991). Sometimes this is attended by a decrease in root-length growth and weight. In *Agropyron desertorum*, a grazing-tolerant bunchgrass, root-length growth of clipped plants was 50% less than that of intact plants. Relatively more resources were allocated to above-ground plant parts, so re-establishing the root:shoot balance. In a grazing-sensitive bunchgrass, *Agropyron spicatum*, root elongation was not affected by clipping. In this species, foliage replacement was prevented, and thereby the re-establishment of the root:shoot ratio. Herbivory may, thus, weaken the competitive position of *A. spicatum*, whereas the grazing-tolerant *A. desertorum* may maintain its competitive position (Richards, 1984). In the grazing-tolerant grass, *Sporobolus kentrophyllus*, a similar decrease in biomass allocation to the roots was found. Tillering rate increased in this species (Ruess, 1988).

Rumex obtusifolius responded to heavy grazing by an increase in the root:shoot ratio. *Rumex crispus*, on the other hand, responded to defoliation by a decrease of root:shoot ratio (Bentley and Whittaker, 1979).

Patterns of dry matter allocation were altered by infestation of *Eucalyptus blakelyi* by the sap-sucking herbivore, *Eriococcus coriaceus*. Proportionally more dry matter was allocated to the leaves at the expense of root growth. This led to a significantly lower root:shoot ratio in infested than in control plants (0.50 ± 0.25 vs. 0.79 ± 0.22 ; $P < 0.001$) (Vranjic and Gullan, 1990). In response to simulated herbivory, both in ambient and enriched CO₂ environments, compensation for the loss of above-ground tissue was found in the perennial herb, *Plantago lanceolata* (Fajer *et al.*, 1991), but at the expense of root growth. Although levels of reproductive output were maintained, negative effects of defoliation on growth, or increased mortality, could be found in later years.

These studies indicate that plants tend to re-establish their root:shoot balance after defoliation, as was proposed by Brouwer (1962a, b, 1963, 1983) in his theory on the functional equilibrium between overground and underground parts. As soon as this species-specific balance is reached, investment in above-ground plant parts may stop,

and other mechanisms may contribute to compensate for the consequences of leaf losses.

The root:shoot ratio may also be altered as a result of a disease: for example, oat and barley infected with powdery mildew exhibited a decreased root:shoot ratio (Ayres, 1991). The causes of these changes may differ between species and are discussed in more detail by Farrar, in Chapter 8.

2.4 Compensation

2.4.1 Timing of damage and time for recovery

The mechanisms described above may partly or fully compensate for the negative effects of defoliation. Compensation is concluded when the cumulative dry weight of the treated plants equals that of the controls, whereas partial compensation occurs when the cumulative dry weight of the treated plants is less than that of the controls (Belsky, 1986). In terms of (over)compensation strategies, the effectiveness of the individual plant's reactions to defoliation strongly depends on growth stage, season, and environmental factors. Grazing systems are characterized by some pattern of independence from these factors, which may be quite persistent.

The possibilities for compensation are highly influenced by the developmental stage of the plant at the time of defoliation. Moreover, the moment during the season when a plant is affected by herbivores also influences possible compensation. These two factors may often be associated, especially in natural situations.

Simulated herbivory by Colorado beetle on potato cultivars resulted in greatest yield reductions when defoliation took place during the main flowering period. When herbivory was simulated through earlier or later defoliation, yield reductions were less, demonstrating that compensation is affected by the time of defoliation (Shields and Wyman, 1984). Artificial damage to *Salix smithiana* growing in central Sweden showed that the most severe growth reductions were when defoliation took place in early-mid summer. At that time, the most productive cohort of leaves was affected (Larsson, 1983). In *Agropyron desertorum*, tiller replacement was not affected by heavy grazing when this took place before the elongation of the internode. Defoliation after the elongation of the internodes (which elevates apical meristems) reduced the number and heights of replacement tillers and, moreover, increased the winter mortality of those tillers produced in autumn (Olson and Richards, 1988a). Turtlehead plants, *Chelone* spp., herbaceous perennials from wet meadows and fens, reacted to herbivory prior to flower bud development by a reduction in the number of reproductive stalks, flower buds, flowers and seed capsules. When plants were severely defoliated after flower buds appeared, only the final number of seed capsules and seeds per capsule were affected (Stamp, 1984). In the herbaceous crop, 'spring cabbage', *Brassica oleracea*, sensitivity to defoliation increased during the period from planting to head-formation. Sensitivity was maximal when plant leaf area reached approximately 2000 cm², and did not increase afterwards (Wit, 1985). All these studies indicate the importance of the timing of herbivory. Plants defoliated during flowering, or during the most produc-

tive period in the growing season, are more affected than those defoliated at other times.

Ability to recover from defoliation decreases during the growing season because progressively less time is available to overcome the delay in phenology (Inouye, 1982; Solomon, 1983; Maschinsky and Whitham, 1989). The physiological constraints on a plant may limit compensation of late damage even when environmental conditions are favourable. Therefore, damage later in the season may have an immediate effect on monocarpic species, for example resulting in a delay of flowering (Harris *et al.*, 1978). Theoretically, perennial plants may compensate in a later year for earlier damage.

Plants that flower later than normal may risk less than normal pollination. Thus, self-incompatible species may suffer most, but even in self-compatible species, e.g. *C. officinale*, individuals that flower later in the year produce significantly less seed (de Jong and Klinkhamer, 1991). This last effect emphasizes the importance of male fitness. Not only growth and seed production, but also possible effects on pollination, must be considered when studying a plant's reaction to herbivory.

2.4.2 Grazing intensity

Our knowledge of the effect of herbivory was, until the last decade, based on agricultural and forestry management practices. Establishing relationships between leaf area loss and yield loss gave an indication of the economic injury level. Correlating the consumption of a single herbivore with the maximum leaf area loss that could be sustained without any significant loss of final yield established the number of herbivores that could be safely allowed per unit leaf area. Growth and seed production were therefore the most important parameters studied. In ecological studies, however, implications for plant fitness are much more important.

In many species, low levels of herbivory do not lead to any reduction in final yield (Seastedt *et al.*, 1983; Olson and Richards, 1988b; Reichman and Smith, 1991). In many situations, growth is limited by environmental factors, and a little herbivory has no additional effect. In laboratory experiments, on the other hand, optimal conditions may quickly result in compensation for the negative effects of herbivory. Thus, when *S. jacobaea* and *C. officinale* suffered low (10%) or medium (30%) defoliation in the laboratory, plants took only 2 weeks to attain the same total plant biomass as undefoliated (control) plants. Complete defoliation affected plant dry weight for a longer period (Prins *et al.*, 1989). Plants with higher levels of defoliation require longer periods to recover than plants defoliated to a lesser extent. As long as the environmental conditions are favourable, however, even severely defoliated plants may recover, if given sufficient time.

2.4.3 The plant's environment

Most studies on compensation have been under controlled conditions. They are likely to overestimate greatly the ability of plants to compensate for herbivory. While under controlled conditions a shift from root to shoot allocation in defoliated plants may have little effect on nutrient or water uptake, the effects under changing natural

conditions may be much larger. There is good evidence that the effects of herbivory are strongest under conditions of water stress, nutrient stress or competition.

Drought can interact negatively with plant compensation characteristics. For the biennial, *S. jacobaea*, decreasing moisture availability limited plant compensation. One irrigation after defoliation was sufficient to increase significantly the mean number of nodes per plant when compared with defoliated plants that were not supplied with water. Incidentally, these results are important for the study of biocontrol agents for *S. jacobaea* in areas where the plant has become a range weed; the full potential of herbivorous agents might be found in years with low moisture conditions (Cox and McEvoy, 1983). Water stress significantly reduced regrowth after clipping in the grass, *Hyparrhenia filipendula*. Frequent watering stimulated leaf elongation but had no impact on tillering. Nitrogen addition, on the other hand, had a strong impact on tiller number but not on leaf elongation, indicating that each form of stress can act differently on growth (Coughenor *et al.*, 1985).

Differences in nitrogen availability strongly influenced the regrowth capacity of *Verbascum thapsus* and *C. officinale* in the laboratory. Without nitrogen, *V. thapsus* died after defoliation. However, if given nitrogen, growth of defoliated and unclipped plants was similar. In *C. officinale*, defoliated plants that were not supplied with nitrogen did not die, but showed only very little regrowth (Verkaar *et al.*, 1986).

Simultaneous grazing by herbivores and other forms of stress, like competition, may have additive effects on plant performance (Harris, 1973; Whittaker, 1979; Cottam *et al.*, 1986). Pathogens, in combination with other forms of stress, were also found to have additive negative effects on plants (Ayres, 1991). In a situation of combined stress, opposed allocation responses may be found in individual plants. The other stress may impair those morphological and physiological responses to grazing that normally minimize the effects of herbivory on growth rate. Oesterheld and McNaughton (1991b) describe such a situation for the combined effect of grazing and flooding on Serengeti grasses. Grazing may induce plants to allocate resources to leaf production, whereas flooding may increase the allocation of resources to the roots, because the maintenance of roots in an anoxic environment may be costly. A synergism between invertebrate herbivory and another form of stress, i.e. competition, was found in *R. obtusifolius*. Only in competing plants did herbivory cause a significant reduction in plant growth (Cottam *et al.*, 1986).

Particular situations are conceivable, however, in which some forms of stress may interact positively with grazing. The removal of self-shading by grazing is an example. Under conditions of high atmospheric humidity and ample water supply, grazing may be beneficial by removing transpiring leaf area. Grazed plants may survive a drought period, whereas ungrazed plants may desiccate (Verkaar, 1988). Thus, in the grasses, *Hyparrhenia rufa* and *Trachypogon plumosus*, grazing and water stress interacted strongly; the effects of defoliation were reduced under water stress, probably because there was a more gradual depletion of soil water when the transpiring surface was reduced by grazing (Simoes and Baruch, 1991).

An unexpected interaction between herbivory and field conditions was found by Michaud (1989); herbivory led to reduced nectar production in flowers of fireweed, *Epilobium angustifolium*. Plants were thus less attractive to pollinators, resulting in

reduced female and male fitness. As already mentioned, for a better understanding of the effects of herbivory on plant fitness, field studies are preferable, and both male and female fitness must be examined, a point made again by Parker in Chapter 12. Few studies have looked at effects on female fitness, and not a single study has examined male fitness. To understand compensation in an evolutionary context, the latter is by far the most important issue that should be addressed in herbivory experiments.

2.5 Overcompensation

During the last two decades, debate about the beneficial effects of herbivores has engaged plant ecologists. Although compensatory productivity, enabling plants to replace tissue lost to herbivores, was discussed by Eaton in 1931, the possibility of overcompensation was not considered until the much cited paper of Owen and Wiegert (1976). In this theoretical study, they proposed that an extension of the period of leaf fall, through the effects of primary consumers, might increase decomposition and, therefore, nutrient conservation and utilization efficiency, thus resulting in an overall increase in plant fitness. However, there has been little evidence until recently that plants subjected to herbivory actually increase their production.

Increased fitness can only be demonstrated if grazed plants are larger or form more numerous offspring at the end of the season than ungrazed plants (Westoby, 1989). (Again, we stress that not only female fitness, i.e. seed production, but also male fitness has to be examined as an important component of (over)compensation.) Reviews by Belsky (1986), drawing attention to the imperfect experimental design and statistical analyses of studies that claim overcompensation, and by Verkaar (1988), directing attention to the physiological background of overcompensation, demonstrate that beneficial effects of herbivores on individual plants are seldom found. Although numerous studies have shown a constant or increased yield in attacked plants, these studies have almost invariably focused on a single organ. Field experiments, in which removal of stem apices from *Ipomopsis aggregata* resulted in a 2.4-fold increase in seed production, did, however, focus on above-ground as well as below-ground plant parts. Comparable laboratory experiments showed that seed production was also significantly increased, though to a smaller extent. The plant seems to have evolved to depend on herbivory to achieve its greater fitness. In this special case, herbivory was restricted to only a short period at the start of the growing season, but more than 70% of plants were severely damaged (Paige and Whitham, 1987).

As pointed out by Crawley (1987), it may be unclear at first why ungrazed plants do not also have a comparable, second burst of flowering after the period of herbivory has passed. However, a simple model by van der Meijden (1990) illustrates the advantage to a genotype which does not invest all its resources in early season growth, but is able to accelerate stem growth after herbivory, compared with a genotype that invests all its resources in growth before herbivory. Herbivory simply seems to be a trigger for growth in this species (van der Meijden, 1990). Ungrazed plants do not have such a trigger, so do not respond with a second burst of flowering.

Maschinsky and Whitham (1989) found evidence for a continuum of compensatory responses to vertebrate herbivory in *Ipomopsis arizonica*. In their study, the most

common response to herbivory was compensation. Overcompensation was found in grazed plants that were supplied with additional nutrients and moreover were not competing with neighbours. Undercompensation was found when nutrient availability was low and *I. arizonica* was growing in mixture with grasses. This concept of a continuum in reactions of plants to herbivory (Maschinsky and Whitham, 1989) is an important contribution to the debate concerning a possible beneficial effect of herbivores to plants.

Until now, most physiological studies on the plant's reaction to herbivory have been concerned with single mechanisms, such as increased photosynthesis or a changed allocation pattern. We challenge plant physiologists to join this discussion by extending their studies to the physiological mechanisms that may lead to overcompensation. This would give an important stimulus to the debate on overcompensation.

Acknowledgements

We wish to thank Tom de Jong, Peter Klinkhamer, Rinny Kooi, Thom van Rossum and Geert van Wirdum for critically reading the manuscript.

References

- Alcock, M.B. (1964) The physiological significance of defoliation on the subsequent regrowth of grass-clover mixtures and cereals. In: *Grazing in Terrestrial and Marine Environments*. Symposium British Ecological Society. Blackwell, Oxford, pp. 25–41.
- Ayres, P.G. (1991) Growth responses induced by pathogens and other stresses. In: *Responses of Plants to Multiple Stresses* (eds H.J. Mooney, E.J. Pell and W.E. Winner). Academic Press, London, pp. 227–248.
- Baur-Hösch, B., Mächler, F. and Nösberger, J. (1990) Effect of carbohydrate demand on the remobilization of starch in stolons and roots of white clover (*Trifolium repens* L.) after defoliation. *J. Exp. Bot.* **41**, 573–578.
- Belsky, A.J. (1986) Does herbivory benefit plants? A review of the evidence. *Am. Nat.* **127**, 870–892.
- Benner, B.L. (1988) Effects of apex removal and nutrient supplementation on branching and seed production in *Thlaspi arvense* (Brassicaceae). *Am. J. Bot.* **75**, 645–651.
- Bentley, S. and Whittaker, J.B. (1979) Effects of grazing by a chrysomelid beetle, *Gastrophysa viridula*, on competition between *Rumex obtusifolius* and *Rumex crispus*. *J. Ecol.* **67**, 79–90.
- Bergström, R. and Danell, K. (1987) Effects of simulated winter browsing by moose on morphology and biomass of two birch species. *J. Ecol.* **75**, 533–544.
- Brouwer, R. (1962a) Distribution of dry matter in the plant. *Neth. J. Agric. Sci.* **10**, 361–376.
- Brouwer, R. (1962b) Influence of temperature of the root medium on the growth of seedlings of various crop plants. *Mededel. I.B.S.* **175**, 11–18.
- Brouwer, R. (1963) Some aspects of the equilibrium between overground and underground plant parts. *Mededel. I.B.S.* **213**, 31–39.
- Brouwer, R. (1983) Functional equilibrium: sense or nonsense? *Neth. J. Agric. Sci.* **31**, 335–348.
- Caldwell, M.M., Richards, J.H., Johnson, D.A., Nowak, R.S. and Dzurec, R.J. (1981) Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. *Oecologia* **50**, 14–24.
- Cockfield, S.D. and Potter, D.A. (1986) Interaction of *Euonymus* scale (Homoptera: Diaspididae)

- feeding damage and severe water stress on leaf abscission and growth of *Euonymus fortunei*. *Oecologia* **71**, 41–46.
- Cottam, D.A., Whittaker, J.B. and Malloch, A.J.C. (1986) The effects of chrysomelid beetle grazing and plant competition on the growth of *Rumex obtusifolius*. *Oecologia* **70**, 452–456.
- Coughenor, M.B., McNaughton, S.J. and Wallace, L.L. (1985) Responses of an African tall-grass (*Hyparrhenia filipendula* Stapf.) to defoliation and limitations of water and nitrogen. *Oecologia* **68**, 80–86.
- Cox, C.S. and McEvoy, P.B. (1983) Effect of summer moisture stress on the capacity of tansy ragwort (*Senecio jacobaea*) to compensate for defoliation by the cinnabar moth (*Tyria jacobaeae*). *J. Appl. Ecol.* **20**, 225–234.
- Crawley, M.J. (1987) Benevolent herbivores? *Trends Ecol. Evol.* **2**, 167–168.
- Culvenor, R.A., Davidson, I.A. and Simpson, R.J. (1989) Regrowth by swards of subterranean clover. 2. Carbon exchange in shoot, root and nodule. *Ann. Bot.* **64**, 557–567.
- Culvenor, R.A. and Simpson, R.P. (1991) Mobilization of nitrogen in swards of *Trifolium subterraneum* L. during regrowth after defoliation. *New Phytol.* **117**, 81–90.
- Cyr, D.A. and Bewley, D.J. (1990) Seasonal variation in nitrogen storage reserves in the roots of leafy spurge (*Euphorbia esula*) and responses to decapitation and defoliation. *Physiol. Plant* **78**, 361–366.
- Danell, K., Huss-Danell, K. and Bergström, R. (1985) Interactions between browsing moose and two species of birch in Sweden. *Ecology* **66**, 1867–1878.
- Doak, D.F. (1991) The consequences of herbivory for dwarf fireweed: different time scales, different morphological scales. *Ecology* **72**, 1397–1407.
- Dyer, M.I., Acra, M.A., Wang, G.M., Coleman, D.C., Freckman, D.W., McNaughton, S.J. and Strain, B.R. (1991) Source-sink carbon relations in two *Panicum coloratum* ecotypes in response to herbivory. *Ecology* **72**, 1472–1483.
- Eaton, F.M. (1931) Early defoliation as a method of increasing cotton yield, and the relation of fruitfulness to fiber and boll characters. *J. Agric. Res.* **42**, 447–462.
- van Emden, H.F. (1990) The effect of *Brevicoryne brassicae* on leaf area, dry matter distribution and amino acids of the Brussels sprout plant. *Ann. Appl. Biol.* **116**, 199–204.
- Fajer, E.D., Bowers, M.D. and Bazzaz, F.A. (1991) Performance and allocation patterns of the perennial herb, *Plantago lanceolata* in response to simulated herbivory and elevated CO₂ environments. *Oecologia* **87**, 37–42.
- Harris, P. (1973) Insects in the population dynamics of plants. In: *Insect/plant relationships*. Symposia of the Royal Entomological Society of London, Volume 6 (ed. H.F. van Emden). Blackwell, Oxford, pp. 201–209.
- Harris, P., Thomson, L.S., Wilkinson, A.T.S. and Neary, M.E. (1978) Reproductive biology of tansy ragwort, climate and biological control by the cinnabar moth. In: *Proceedings IV International Symposium on Biological Control of Weeds* (ed. I.E. Freeman), pp. 163–173.
- Ingham, R.E. and Detling, J.K. (1986) Effects of defoliation and nematode consumption on growth and leaf gas exchange in *Bouteloua curtipendula*. *Oikos* **46**, 23–28.
- Inouye, D.W. (1982) The consequences of herbivory: a mixed blessing for *Jurinea mollis* (Asteraceae). *Oikos* **39**, 269–272.
- Islam, Z. and Crawley, M.J. (1983) Compensation and regrowth in ragwort (*Senecio jacobaea*) attacked by cinnabar moth (*Tyria jacobaeae*). *J. Ecol.* **71**, 829–843.
- Jaramillo, V.J. and Detling, J.K. (1988) Grazing history, defoliation, and competition: effects on shortgrass production and nitrogen accumulation. *Ecology* **69**, 1599–1608.
- de Jong, T.J. and Klinkhamer, P.G.L. (1991) Early flowering in *Cynoglossum officinale* L. constraint or adaptation? *Func. Ecol.* **5**, 750–756.
- Kolodny-Hirsch, D.M., Saunders, J.A. and Harrison, F.P. (1986) Effects of simulated tobacco

- hornworm (Lepidoptera: Sphingidae) defoliation on growth dynamics and physiology of tobacco as evidence of plant tolerance to leaf consumption. *Environ. Entomol.* **15**, 1137–1144.
- Larsson, S. (1983) Effects of artificial defoliation on stem growth in *Salix smithiana* grown under intensive culture. *Acta Oecol. Oecol. Applic.* **4**, 343–349.
- Leather, S.R. (1986) Insects on bird cherry. I. The bird cherry ermine moth, *Yponomeuta evonymellus*. *Entomol. Gaz.* **37**, 209–213.
- Leather, S.R. (1988) Consumers and plant fitness: coevolution or competition? *Oikos* **53**, 285–288.
- Louda, S.M. (1984) Herbivore effect on stature, fruiting, and leaf dynamics of a native crucifer. *Ecology* **65**, 1379–1386.
- Marriot, C.A. and Haystead, A. (1990) The effect of defoliation on the nitrogen economy of white clover: regrowth and the remobilization of plant organic nitrogen. *Ann. Bot.* **66**, 465–474.
- Maschinsky, J. and 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.
- van der Meijden, E. (1990) Herbivory as a trigger for growth. *Funct. Ecol.* **4**, 597–598.
- Michaud, J.P. (1989) Nectar accumulation in flowers of fireweed, *Epilobium angustifolium* (Onograceae), in response to simulated defoliation. *J. Apic. Res.* **28**, 181–186.
- Neales, T.F. and Incoll, L.D. (1968) The control of leaf photosynthesis rate by the level of assimilate concentration in the leaf: a review of the hypothesis. *Bot. Rev.* **34**, 107–125.
- Nooden, L.D. (1980) Senescence in the whole plant. In: *Senescence in Plants* (ed. K.V. Thimann). CRC Press, Boca Raton, FL, pp. 219–258.
- Nowak, R.S. and Caldwell, M.M. (1984) A test of compensatory photosynthesis in the field: implications for herbivory tolerance. *Oecologia* **61**, 311–318.
- Oesterheld, M. and McNaughton, S.J. (1991a) Effect of stress and time for recovery on the amount of compensatory growth after grazing. *Oecologia* **85**, 305–313.
- Oesterheld, M. and McNaughton, S.J. (1991b) Interactive effect of flooding and grazing on the growth of Serengeti grasses. *Oecologia* **88**, 153–156.
- Olson, B.E. and Richards, J.H. (1988a) Annual replacement of the tillers of *Agropyron desertorum* following grazing. *Oecologia* **76**, 1–6.
- Olson, B.E. and Richards, J.H. (1988b) Spatial arrangement of tiller replacement in *Agropyron desertorum* following grazing. *Oecologia* **76**, 7–10.
- Owen, D.F. and Wiegert, R.G. (1976) Do consumers maximize plant fitness? *Oikos* **27**, 488–492.
- Paige, K.N. and Whitham, T.G. (1987) Overcompensation in response to mammalian herbivory: the advantage of being eaten. *Am. Nat.* **129**, 407–416.
- Paul, N.D. and Ayres, P.G. (1986) The effects of infection by rust (*Puccinia lagenophorae* Cooke) on the growth of groundsel (*Senecio vulgaris* L.) cultivated under a range of nutrient concentrations. *Ann. Bot.* **58**, 321–331.
- Polley, H.W. and Detling, J.K. (1989) Defoliation, nitrogen and competition: effects on plant growth and nitrogen nutrition. *Ecology* **70**, 721–727.
- Prins, A.H., Verkaar, H.J. and M. van den Herik (1989) Responses of *Cynoglossum officinale* L. and *Senecio jacobaea* L. to various degrees of defoliation. *New Phytol.* **111**, 725–731.
- Reichman, O.J. and Smith, S.C. (1991) Responses to simulated leaf and root herbivory by a biennial, *Tragopogon dubius*. *Ecology* **72**, 116–124.
- Richards, J.H. (1984) Root growth response to defoliation in two *Agropyron* bunchgrasses: field observations with an improved root periscope. *Oecologia* **64**, 21–25.
- Royalty, R.N. and Perring, T.M. (1989) Reduction in photosynthesis of tomato leaflets caused by tomato russet mite (Acari: Eriophyidae). *Environ. Entomol.* **18**, 256–260.

- Ruess, R.W. (1988) The interaction of defoliation and nutrient uptake in *Sporobolus kentrophyllus*, a short grass species from the Serengeti Plains. *Oecologia* **77**, 550–556.
- Salisbury, F.B. and Ross, C.W. (1985) *Plant Physiology*, 3rd edition. Wadsworth, Belmont, CA.
- Seastedt, T.R., Crossley, D.A. Jr. and Hargrove, W.J. (1983) The effect of low-level consumption by canopy arthropods on the growth and nutrient dynamics of black locust and red maple trees in the southern Appalachians. *Ecology* **64**, 1040–1048.
- Shields, E.J. and Wyman, J.A. (1984) Effects of defoliation at specific growth stages on potato yields. *J. Econ. Entomol.* **77**, 1194–1199.
- Simoes, M. and Baruch, Z. (1991) Responses to simulated herbivory and water stress in two tropical C₄ grasses. *Oecologia* **88**, 173–180.
- Smith, D. and Silva, J.P. (1969) Use of carbohydrate and nitrogen root reserves in the regrowth of alfalfa from greenhouse experiments under light and dark conditions. *Crop Sci.* **9**, 464–467.
- Solomon, B.P. (1983) Compensatory production in *Solanum carolinense* following attack by a host-specific herbivore. *J. Ecol.* **71**, 681–690.
- Stamp, N.E. (1984) Effect of defoliation by checkerspot caterpillars (*Euphydryas phaeton*) and sawfly larvae (*Macrophya nigra* and *Tenthredo grandis*) on their host plants (*Cbelone* spp.). *Oecologia* **63**, 275–280.
- Sweet, G.B. and Wareing, P.F. (1966) Role of plant growth in regulating photosynthesis. *Nature* **210**, 77–79.
- Taylor, W.E. and Bardner, R. (1968) Effect of feeding by larvae of *Phaedon cochleariae* (F.) and *Plutella maculipennis* (Curt.) on the yield of radish and turnip plants. *Ann. Appl. Biol.* **62**, 249–252.
- Thimann, K.V. (1980) The senescence of leaves. In: *Senescence in Plants* (ed. K.V. Thimann). CRC Press, Boca Raton, Florida, pp. 86–115.
- Thimann, K.V. (1987) Plant senescence: a proposed integration of the constituent processes. In: *Plant Senescence: Its Biochemistry and Physiology* (eds W.W. Thomson, E.A. Nothnagel and R.C. Huffaker). Proc. X Annual Symposium in Plant Physiology, pp. 1–19.
- Verkaar, H.J. (1988) Are defoliators beneficial for their host plants in terrestrial ecosystems – a review. *Acta Bot. Neerl.* **37**, 137–152.
- Verkaar, H.J., van der Meijden, E. and Breebaart, L. (1986) The responses of *Cynoglossum officinale* L. and *Verbascum thapsus* to defoliation in relation to nitrogen supply. *New Phytol.* **104**, 121–129.
- Vranjic, J.A. and Gullan, P.J. (1990) The effect of a sap-sucking herbivore, *Eriococcus coriaceus* (Homoptera: Eriococcidae), on seedling growth and architecture in *Eucalyptus blakelyi*. *Oikos* **59**, 157–162.
- Wallace, L.L., McNaughton, S.J. and Coughenor, M.B. (1984) Compensatory photosynthetic responses of three African grassland species to different fertilization, watering, and clipping regimes. *Bot. Gaz.* **145**, 151–156.
- Walters, D.R. and Ayres, P.G. (1983) Changes in nitrogen utilization and enzyme activities associated with CO₂ exchanges in healthy leaves of powdery mildew-infected barley. *Physiol. Plant Pathol.* **23**, 447–459.
- Wareing, P.F., Khalifa, M.M. and Treharne, K.J. (1968) Rate limiting processes in photosynthesis at saturating light intensities. *Nature* **220**, 453–457.
- Wareing, P.F. and Patrick, J. (1975) Source-sink relations and the partition of assimilates in the plant. In: *Photosynthesis and Productivity in Different Environments* (ed. J.P. Cooper). Cambridge University Press, Cambridge, pp. 481–499.
- Westoby, M. (1989) Selective forces exerted by vertebrate herbivores on plants. *Trends Ecol. Evol.* **4**, 115–117.
- Whittaker, J.B. (1979) Invertebrate grazing, competition and plant dynamics. In: *Population*

- Dynamics* (eds R.M. Anderson, B.D. Turner, L.R. Taylor). Volume 20, Symposia of the British Ecological Society. Blackwell Scientific Publications, Oxford, pp. 207–222.
- Williams, P.F. (1978) Growth of broad beans infected by *Uromyces viciae-fabae*. *Ann. Appl. Biol.* **90**, 329–334.
- Wit, A.K.H. (1985) The relation between partial defoliation during the preheading stages of spring cabbage and yield, as a method to assess the quantitative damage induced by leaf-eating insects. *Z. Ang. Entomol.* **100**, 96–100.
- Woolhouse, H.W. (1967) The nature of senescence in plants. In: *Aspects of the Biology of Aging*, Volume 21, Symposium for the Society for Experimental Biology (ed. H.W. Woolhouse). Cambridge University Press, Cambridge, pp. 179–213.