Acta Bot. Neerl. 37(2), June 1988, p. 137–152

Are defoliators beneficial for their host plants in terrestrial ecosystems—a review?

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Key-words: compensatory (re)growth, defoliation, herbivory, physiological and morphological responses, vegetation.

INTRODUCTION

The impact of herbivory on food plants has engaged mankind for millennia. The detrimental impact of browsing by cattle on the performance of seedlings and young trees of species other than crop plants was noticed long ago, e.g. for Scotch pine on Surrey heaths (Darwin 1859). For more than a century physiologists have studied the responses of defoliated plants (Vöchting 1884, Reinke 1884, Kny 1894). Since the seventies ecologists have developed a number of hypotheses to describe the responses of plants to defoliation under field conditions.

It has been hypothesized that under certain conditions herbivory may result in better growth and/or higher fitness (Harris 1973, Owen & Wiegert 1976, Owen 1980, McNaughton 1983a). In this paper these hypotheses, especially those on the possible beneficial impact of defoliation, are discussed, a survey of possible responses is given, and finally the conditions under which beneficial effects may occur are summarized.

Recently, Belsky (1986) has argued that unequivocal evidence of beneficial effects has failed and that most studies show serious imperfections in experimental design and statistical analysis. Apart from those imperfections there are also biological arguments

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to support the idea that beneficial effects after grazing are exceptional and may occur in only a few peculiar conditions. Crawley (1983) stated: 'There is no evidence at all that the genetic fitness of an individual grass plant is ever enhanced by defoliation, when compared to an individual plant nearby'.

Most of the discussion does not discriminate between the effects of herbivores on plant organs, total plant, plant population and ecosystems. This review will only consider the impact of defoliators on plant organs and individual plants, as recent reviews have treated the effects on populations and ecosystems (Drent & Prins 1987, Fresco *et al.* 1987, Thalen *et al.* 1987).

TYPOLOGY OF DEFOLIATORS

In this paper defoliation is defined as all activities that result in the removal of leaf tissue. Among defoliators many types can be distinguished. Typology is generally based on the various leaf parts that are destroyed, e.g. by leaf punchers and skeletonizers (throughout the leaf or only superficially, upper side or underside), e.g. beetles, sawflies, capsid bugs, moths, weevils, pigeons, slugs and leaf edge eaters, and leaf tip eaters, e.g. ungulates, slugs, snails, sawflies and butterflies, and leaf miners, e.g. Microlepidoptera and Diptera (Crawley 1983). Apart from patterns of grazing in the leaves a number of other differences among grazers can be noticed. Compared to invertebrates, grazing mammals have an important impact on the abiotic environment and may influence the plant's responses. Due to defoliation soil bulk density and bearing capacity increase, while hydraulic conductivity and gas exchange decrease (Blom 1979, Willatt & Pullar 1983). Soil compaction can strongly affect germination and seedling establishment (Blom 1979). Above-ground, the temperature profile and light transmission through the leaf canopy can also be changed.

HYPOTHESES ON THE BENEFICIAL EFFECTS AFTER DEFOLIATION

Several ideas about the responses of plants to defoliation have been developed (Harris 1973, Owen & Wiegert 1976, Owen 1980, McNaughton 1983a). Apart from examples of inhibition of plant growth after herbivory, the examples of stimulation of plant growth and reproduction after herbivore attack, mentioned by Harris (1973), deal with both the positive effects of early pruning of cotton flowers, which results in a prolonged period of vegetative expansion and therefore higher and quantitatively better yield (Eaton 1931), and a number of positive effects due to defoliation.

One of the positive effects of defoliation consists of a stimulated herbage and flower stalk production of *Potentilla gracilis* (Mueggler 1967). This study, however, concerned the effects of clipping a whole grassland vegetation, and the improved regrowth of *P. gracilis* is ascribed to the more ready response to the removal of dead plant material by the clipping treatment earlier in the growing season than in the other species (Mueggler 1967). There is no evidence that *P. gracilis* responds positively to defoliation as an individual plant, but the competitive ability of the plants might increase relatively to plants of other species after clipping. Therefore, serious criticisms have been formulated on this conception (Lam & Dudgeon 1985).

Another example of positive effects as a result of defoliation may be the response of one particular variety of late potato from Czechoslovakia to artificial defoliation (50%)

(Skuhravý 1968). Tuber yield and shoot fresh weight seem to profit from artificial defoliation from the latter half of June to the end of July. Infestation by Colorado Potato Beetles, however, results in detrimental effects.

A further example given by Harris (1973) is based on the work of Ellison (1960) on the effects of light browsing in rangelands. Some shrubs show a stimulated twig production from grazing, but at the same time flower and fruit production decrease, and possibly also root growth. In contrast to Harris' argument Ellison (1960) concludes: 'The benefits of grazing, if any, would appear to accrue to the ecosystem, to the range as a whole, instead of to the palatable species of plants that are grazed most.'

The only relevant example with a positive effect is the higher vegetative growth of turnip (*Brassica rapa*) after defoliation (Taylor & Bardner 1968). The average figures indicate a slightly stimulated growth after grazing by the larvae *Plutella maculipennis*. This growth stimulation is attributed to the formation of lateral shoots. If the attack is, however, more concerted, e.g. due to *Phaedon cochleariae* grazing, the final consequences are negative. Sufficient statistical analysis is lacking.

Owen & Wiegert (1976) and Owen (1980) did not mention examples dealing with defoliation that entail evidence for a possible positive impact of herbivores on their host plants. Since these studies are beyond the scope of this paper and the evidence might be doubtful, they will not be discussed here.

McNaughton (1983a) formulated three alternative hypotheses about how herbivory may affect both plant growth and fitness. Unfortunately, he did not separate clearly the term 'growth' from the term 'fitness'. Since fitness deals with the degree of maintenance of a certain genotype in a population, it is too complex to be equated to an equivalent of growth (Wall & Begon 1985).

Compensatory (re)growth (McNaughton 1983a) of a grazed plant is a growth response that leads to a higher relative growth rate and/or a longer period of growth. This compensatory regrowth does not necessarily compensate for all detrimental effects of herbivory, but diminishes them. An extension of the life of a plant due to a delay in reproduction may result in increased risk of mortality and/or in a change in reproductive output and thus most likely in fitness depending on local circumstances. Although compensation *sensu stricto* must be defined as bringing the fitness of an attacked plant into balance relative to an intact plant, effects of herbivory so far have been described in terms of temporal growth responses or in seed production in the same generation (Verkaar 1987). Although there may be a temporal higher relative growth rate, it is questionable whether this growth rate persists over long periods, and how defoliation affects plant fitness.

If we overcome this a priori objection against McNaughton's (1983a) formulation, and read growth or seed production instead of fitness, the three alternative hypotheses are: (1) that plant growth declines consistently as the intensity of herbivory increases; (2) that effects of herbivory are absent up to some level ('threshold level'), then growth declines with increasing herbivory; (3) that growth increases by moderate levels of herbivory, then declines and becomes negative, relative to unaffected plants, at higher levels of herbivory. McNaughton's (1983a) evidence for the existence of case 3 consists of three studies, i.e. Dyer (1975), McNaughton (1979) and Dyer *et al.* (1982).

Dyer's (1975) study deals with the effects of Red-winged Blackbird *Agelaius phoenicus* attack on corn grain (*Zea mays*) production. The length and weight of ears per plant increased with increasing herbivory to a certain level (about 60% of all ears damaged). Surprisingly, the number of ears per plant was not counted in this study. It is likely that, due to Blackbird attack, part of the carbohydrate sinks (the ears) are removed. Then, competition for nutrients—carbohydrates and/or mineral elements—among ears diminishes and the amount of carbohydrates available for the remaining sinks increases (Stanton 1984a). Similar effects have been found in *Rumex crispus* (Maun & Cavers 1971). When 75% of the flowers were removed, mean weight per seed in the remaining flowers was about 30% higher than in the controls. As a result, remaining ears may develop better and weigh more, but it is doubtful whether, in attacked corn fields, the total yield of ears per plant or per area exceeds that of undamaged stands.

McNaughton (1979) and Dyer *et al.* (1982) report upon the effects of grazing on relative growth rate of shoots in grasslands; unfortunately, the scope of both these studies has been limited to above-ground production. Grassland production has often been expressed as standing crop from an agricultural point of view, or as edible food from the point of view of studies on animal intake (Dyer & Bokhari 1976, Prins *et al.* (1980). The effects of grazing are not limited to the shoot performance, but may affect below-ground plant parts in a radical way (Weinmann 1948, Throughton 1956, Brouwer 1962a, 1962b, 1983, Harper 1977).

Certainly, shoot growth may be enhanced as a result of grazing, but it might be at the cost of the root's reserves, and therefore of increasing the risk of mortality (Bentley & Whittaker 1979). For instance, *Senecio jacobaea* plants attacked by *Tyria jacobaeae* became more vulnerable to frost during winter (Harris *et al.* 1978) and to drought in summer (Cox & McEvoy 1983) than undamaged plants. Detrimental effects from shoot grazing that deplete these reserves might induce the partial dying-off of the roots and therefore an insufficient uptake of water and other hazards in root functioning. Whittaker (1982) has demonstrated that shoot grazing by the chrysomelid beetle *Gastrophysa viridula* negatively affected root development in *Rumex crispus*, inducing a considerable mortality due to flooding during winter. Hence, from an ecological point of view whole plant behaviour must be considered, roots included.

Paige & Whitham (1987), advocating the concepts of McNaughton (1983a), revealed overcompensation of seed production of the biennial *Ipomopsis aggregata* after grazing by large mammals in North American montane grassland. This overcompensation might amount to a 2·4-fold increase in seed production compared to ungrazed plants. No significant differences in germination and seedling survival between seeds from grazed and ungrazed plants were found. Here again, the competitive ability of *I. aggregata* may increase relative to other species after grazing, as was found in the biennial *Cirsium vulgare*. In pastures grazed by sheep these plants showed increased growth, flowering, seed production and survival of seedlings (Forcella & Wood 1986).

The possibility of achieving compensatory regrowth depends on the intensity and type of grazing and the physiological responses of the attacked plant in relation to environmental factors. Defoliators might also influence plant response due to the release of secretory products from their salivary glands. Some authors reported the release of hormone analogs from saliva, e.g. thiamine, and its effects on plant performance (Dyer & Bokhari 1976, Detling *et al.* 1980, Dyer *et al.* 1982, McNaughton 1983b, 1985). In McNaughton's (1985) study the significant effects were found after an application of pure thiamine solution instead of real saliva. Hence, we must conclude that the suggested positive effects from saliva on regrowth have not been demonstrated until now; sometimes the effects are negative (Rhoades 1985a). Toxic effects of saliva of spider mites have also been reported (Tomczyk & Kropczýnska 1985). These effects might be caused by one or more proteolitic enzymes (Storms 1971).

PHYSIOLOGICAL AND MORPHOLOGICAL MECHANISMS UNDERLYING THE RESPONSE TO DEFOLIATION

Many responses to defoliation are known. These responses can deal with recovery from defoliation itself or with the defence against new attacks of herbivores. This section treats the mechanisms underlying recovery from grazing itself.

Defoliation interferes directly with plant morphology: the leaf area is reduced and hence the amount of carbon dioxide fixation. The effect also depends on the reserves of the plant, e.g. the higher the shoot:root ratio the more plant performance is generally affected by a certain degree of defoliation (Verkaar *et al.* 1986). Both physiological and morphological responses will be discussed.

Leaf photosynthesis

When leaf tissue is damaged by herbivores, the efficiency of photosynthesis is affected in general, probably linked to changes in the water status of the leaf (Whittaker 1984, Trumble *et al.* 1985). Trumble *et al.* (1985) reported that leaf-mining *Liriomyza trifolii* causes a disruption of the vascular system of *Apium graveolens*, affecting the movement of water, which in turn causes changes in turgor pressure. As guard cells collapse, a reduction in stomatal conductance occurs which reduces transpiration and photosynthesis. On the other hand, when *Acer pseudoplatanus* leaves are infected by the leaf hopper *Ossiannilssonola callosa*, abaxial leaf surface is punched resulting in punctures of about the same density and order of magnitude as the stomata. Stomatal conductance then increases and the photosynthetic apparatus is damaged due to excessive water loss (Whittaker 1984).

Conversely, the remaining and newly formed leaf tissue often shows a higher rate of photosynthesis (Sweet & Wareing 1966, Wareing *et al.* 1968, Detling *et al.* 1979, Painter & Detling 1981, McNaughton *et al.* 1982, Heichel & Turner 1983, Nowak & Caldwell 1984, Wallace *et al.* 1984), although a decrease in photosynthetic rate has been mentioned when very young leaf tissue was removed, which probably acts as a carbohydrate sink (Ryle & Powell 1975).

Several mechanisms are held responsible for the increase in photosynthetic rate (Mooney & Chiariello 1984). This response has been interpreted as a product accumulation and thus a result of increased sink strength relative to source strength (Gifford & Evans 1981, Mayoral *et al.* 1985). Housley & Pollock (1985) argued that carbohydrates in detached *Lolium temulentum* leaves are rapidly converted partly to cytoplasmatic fructan and partly to sucrose and fructan in the vacuoles resulting in a maintenance of cytoplasmatic sucrose concentrations within limits that do not seriously constrain the overall rate of carbon fixation.

Nowak & Caldwell (1984) stated that decreased leaf senescence and increased soluble protein content, probably resulting in a higher content of photosynthetically active enzymes, but not in an improved water status, lead to a higher photosynthetic rate. Gifford & Marshall (1973) and Wallace *et al.* (1984) found that an increased stomatal opening is mainly responsible for an enhanced rate of photosynthesis. An increased stomatal opening generally affects the leaf's water balance which may be unfavourable under dry conditions. Wareing *et al.* (1968) have observed that partial defoliation resulted in increased photosynthetic rates and increased activities of carboxylating enzymes in the remaining leaves, suggesting that in normal field conditions photosynthetic rates are at least partly limited by the levels of carboxylating enzyme-activity. Moreover, they mentioned the effect of high cytokinin concentration, since spraying 20 mg l^{-1} kinetin on the shoot enhanced photosynthesis. They argued that part of the increase in photosynthetic rate after defoliation may be induced by an improved supply of endogeneous cytokinins from the roots to the remaining leaves.

In spite of an increase in photosynthetic rate of the remaining leaves, the total amount of fixed carbohydrates in severely defoliated plants is reduced, compared to control plants (Parsons *et al.* 1983a, 1983b, Ryle *et al.* 1985). This may have a tremendous impact on root functioning. Therefore, it is not useful to limit the scope of studies on the effects of grazing to single leaf measurements (Mooney & Chiariello 1984).

If plants are high and the canopy is closed, self-shading may result in low net assimilation rates (Vickery, 1972); it cannot be ruled out that defoliation of part of the shoot may result in improved carbon balance due to higher net assimilation rates.

Carbon balance and root functioning

When leaf photosynthesis is limited due to (partial) defoliation, levels of soluble carbohydrates, especially fructosan and sucrose, decrease (Alcock 1964, Harris *et al.* 1978, Valentine *et al.* 1983, Ericsson *et al.* 1985). Carbohydrates stored in the stubble and/or below-ground tissue are translocated to new leaves and the rate of leaf expansion is generally related to the total amount of stored carbohydrates (Davidson & Milthorpe 1966a,b), although such a relation could not be ascertained by Richards & Caldwell (1985), who compared two *Agropyron* species. When defoliation is severe, even large carbohydrate pools are inadequate and other substances, presumably proteins, may be remobilized for use in new growth and respiration (Davidson & Milthorpe 1966b).

In the remaining leaves the export of carbohydrates to new tissue increases after partial defoliation (Marshall & Sagar 1968, Ryle & Powell 1975), and in some species, e.g. *Lolium multiflorum* and *Hordeum vulgare,* the diversion of assimilates is mainly at the expense of other parts of the shoot, if defoliation is mild (Gifford & Marshall 1973, Ryle & Powell 1975). In *L. multiflorum* carbohydrate export from the leaves to the root is unaffected after defoliation (Marshall & Sagar 1968), resulting in maintenance of the root weight relative to control plants (Brouwer 1963, Whitehead 1983). In general, the rate of root respiration is not affected by defoliation (Detling *et al.* 1979, Richards & Caldwell 1985).

Insufficient supply of carbohydrates to the roots and translocation from the roots result in the inhibition of root growth in many species, and sometimes in the dying of parts of the root system (Detling *et al.* 1979, Painter & Detling 1981, Whitehead 1983, Richards 1984, Richards & Caldwell 1985). The degree of root weight loss may also depend on the physiological activity of the root system as affected by environmental factors. Root dying may have an important impact on uptake capacity for some mineral nutrients and water.

Uptake of nutrients

In spite of the above mentioned possible losses of roots the specific root uptake of nutrients, e.g. nitrogen, might sometimes increase depending on the nitrogen source applied in response to defoliation (Ruess 1984, Ruess & McNaughton 1984). But when the nutrient supply partly depends on *Rhizobium, Frankia* or other nitrogen-fixing micro-organisms, these micro-organisms form an important sink for carbohydrates from the plant. Because defoliation strongly limits the supply of carbohydrates to this sink, nodulation, nodule activity and therefore nitrogen fixation decrease drastically (Whitehead 1983, Bayne *et al.* 1984, Huss-Danell & Sellstedt 1985, Ryle *et al.* 1985). At light and moderate levels of defoliation vesicular-arbuscular mycorrhizal activity is obviously not affected (Wallace *et al.* 1982).

Water status

Water status may be strongly affected by defoliation. Immediately after damage bleeding may occur and it might cause considerable water loss. This water loss is linearly related to the length of the cut edge (Ostlie & Pedigo 1984). When a cicatrice and a periderm have been formed (Esau 1960) bleeding stops and water loss decreases. Water supply to the leaves may then be improved if the stomatal regulation of the leaf water conductance and the supply of water from the vessels are unimpaired. Consequently, leaf transpiration increases along with an increase in photosynthetic rate (Gifford & Marshall 1973, Wallace *et al.* 1984). When the regulatory mechanisms of the cuticula and stomata are damaged, e.g. by puncturing the leaf surface, water loss can be considerable (Whittaker 1984). Under field conditions the impact of defoliation on the water balance will depend on the water status of the soil and on the air humidity.

Morphological effects

Plant morphology can be changed drastically due to defoliation (White 1984). When apical meristems are damaged, lateral shoots become important and form a completely different stature (Taylor & Bardner 1968, van der Meijden & van der Waals-Kooi 1979, Augspurger *et al.* 1985). When shoot parts other than the apical meristems are also affected, various morphological effects might occur, i.e. small internode length, changes in leaf size, changes in leaf angles, etc. (Coughenour 1984, Coughenour *et al.* 1984, Etherington 1984, Fliervoet 1984, Louda 1984, McNaughton 1984). Leaf demography shows that changes which depend on the level of defoliation generally result in higher turnover rates (Dirzo 1984, Louda 1984).

Since relative growth rate is determined by both physiological (net assimilation rate) and morphological (leaf area ratio) features (Evans 1972), recovery of the leaf area forms an important aspect of the plant's changes for (compensatory) regrowth. Surprisingly, leaf area ratio of defoliated plants can exceed that of control plants during several weeks resulting in a higher relative growth rate than control plants (Alcock, 1964, Verkaar *et al.* 1986). On the other hand, Brouwer (1963) reported that in *L. perenne* the proportion of shoot weight did not increase after attaining a new equilibrium between shoots and roots after artificial defoliation. In all these studies final weight of the damaged plants was never higher than that of the control plants.

DO PLANTS GENERALLY BENEFIT FROM GRAZERS?

The review of possible physiological responses to defoliation entails some processes that might result in a better plant performance compared to ungrazed plants. A survey of the literature, mainly from the last decade, supports this view (Table 1). The survey comprises a great variety of studies, some of which covered a few weeks and others several years. Therefore, the term 'final' should be understood here as the total plant weight or total seed yield at the end of the study and not at the end of the plant's life. The rate of defoliation in these studies differed from scanty to 100%. In 53% of the studies the intensity of defoliation was not mentioned, particularly if responses of graminoids were investigated. All these studies are omitted in Table 1. Although most studies mentioned deserve some critical comments on their experimental design or the interpretation of the results (e.g. see Belsky 1986), only the studies where beneficial effects due to grazing were found will be discussed.

Table 1. Final effects of defoliation found in a review of the literature. Citations only consider literature mentioning the percentage of leaf damage

Plant species	% leaf area removed	Herbivore	Condition*	Author(s)†	Note
(a) FINAL EFFECTS POSITIVE					
Cynoglossum officinale	100	Artificial	f	6	Effects probably not significant
Solanum tuberosum	50	Artificial	f	27	cv. Sperber; no statistical analysis
(b) FINAL EFFECTS NOT SIGNIFICANTLY DIFFERENT FROM GRAZING					
Acer rubrum	4	Arthropoda	f	25	
Agropyron spicatum	0–>75	Small mammals	f	21	
Robinia pseudoacacia	10	Arthropoda	f	25	
(c) FINAL EFFECTS NOT SIGNIFICANT FROM CONTROL PLANTS UP TO SOME LEVEL, AND THEN NEGATIVE WITH INCREASING DEFOLIATION					
Astrocaryum mexicanum	0–100	Artificial	f	20	Threshold level at *c.* 33%
(d) FINAL EFFECTS NEGATIVE WITH INCREASING RATE OF DEFOLIATION					
TREES					
Abies balsamea	100	*Choristoneura fumiferana*	f	5	
Acacia farnesiana	100	Artificial	f	23	
Acer pseudoplatanus	10	Various insects	f	32	Roots also damaged
Bauhinia ungulata	100	Artificial	f	23	
Betula pendula and *B. pubescens*	0–100	Artificial	f	4	Simulated moose browsing
Cochlospermum vitifolium	100	Artificial	f	23	
Crescentia alata	100	Artificial	f	23	Effects 1 year after defoliation still measurable
Gliricidia sepium	100	Artificial	f	23	
Picea glauca	100	*Choristoneura fumiferana*	f	5	
Pinus contorta	10–32	*Recurvaria starki*	f	30	
Quercus robur	8–12	Various invertebrates	f	9	
Salix smithiana	0–100	Artificial	f	19	
Spondias purpures	100	Artificial	f	23	

HERBACEOUS MONOCOTYLEDONS					
Agropyron desertorum	85	Artificial	f	22	Clipping height 5–7 cm
Agropyron spicatum	85	Artificial	f	22	Clipping height 5–7 cm
Bouteloua curtipendula	52–57	Artificial	1	17	Clipping height 4 cm
Bouteloua gracilis	62	Artificial	1	10	Clipping height 4 cm
Bromus tectorum	0–>75	Small mammals	f	21	
HERBACEOUS DICOTYLEDONS					
Ambrosia trifida	100	Artificial	1	2	
Arachis hypogeae	3–28	*Empoasca fabae*	f	28	
Aralia nudicaulis	33–66	*Alces alces*/artificial	f	11	
Aristolochia reticulata	100	Artificial	1	14	
Artemisia nova	67	Sheep	f	12	
Ceanothus griseus	80	*Tischeria immaculata*	f	13	
Chelone glabra	66–100	*Euphydryas phaeton* *Macrophyra nigra* *Tenthredo grandis*	f	29	
Chelone obliqua	66–100	Idem	f	29	
Chrysothamnus stenophyllus	10	Sheep	f	12	
Glycine max	22–66	Artificial	1	1	
Lactuca virosa	100	Artificial	f	6	
Rumex crispus	25	Artificial/*Gastrophysa viridula*	1	3	
Rumex obtusifolius	25	Idem	1	3	
Solanum tuberosum	25–100	*Leptinotarsa decemlineata*	f	16	cv. Katahdin
	0–50	Idem	f	18	cv. Katahdin
	10–75	Idem and *Peridroma saucia*	f	26	cv. Superior and cv. Russet Burbank
	50–100	*Leptinotarsa decemlineata*/artificial	f	27	cv. Krasawa and cv. Tschaika
Trifolium repens	50	Artificial	1	24	
Vicia hirsuta	0–100	Insect herbivores	f	8	Also many stem and sap-feeding insects
Vicia sativa	0–100	Insect herbivores	f	8	Predominantly chewing insects
Five Australian species	76–89	Artificial	1	7	Clipping height 3 cm
Pasture vegetation	40–60	*Alauda arvensis*	f	15	

*a, artificially defoliated; 1, laboratory study; f, field study; m, model study.

†1, Bayne *et al.* (1984); 2, Bazzaz & Carlson (1979); 3, Bentley & Whittaker (1979); 4, Bergström & Danel (1987); 5, Blais (1958); 6, Boorman & Fuller (1984); 7, Brown (1985); 8, Brown *et al.* (1987); 9, Crawley (1985); 10, Detling *et al.* (1979); 11, Edwards (1985); 12, Ellison (1960); 13, Fasoranti (1984); 14, Fowler & Rauscher (1985); 15, Halse & Trevenen (1985); 16, Hare (1980); 17, Ingham & Detling (1986); 18, Jansson & Smilowitz (1985); 19, Larsson (1983); 20, Mendoza *et al.* (1987); 21, Pyke 1986; 22, Richards & Caldwell (1985); 23, Rockwood (1973); 24, Ryle *et al.* (1985); 25, Seastedt *et al.* (1983); 26, Shields & Wyman (1984); 27, Skuhravý (1968); 28, Smith *et al.* (1985); 29, Stamp (1984); 30, Stark & Cook (1957); 31, Whittaker (1982) and 32, Whittaker & Warrington (1985).

Of more than one hundred plant species (species included of which the rate of defoliation is not mentioned) only four may achieve beneficial effects from grazing or clipping. The results of two of these four are not tested statistically, and for one (*Cynoglossum officinale*) of the latter the results of defoliated plants do not differ from the control plants (Boorman, personal communication).

One study in which the intensity of defoliation was not given and in which a positive effect of grazing was mentioned deserves some attention. If *Trichosirocalus horridus* grazed on *Carduus nutans*, the apical meristem was primarily damaged (Cartwright & Kok 1985). Then lateral shoots also formed, sometimes yielding heavier plants. Large damaged plants gave approximately the same number of seeds compared to control plants, but small- and medium-sized infested plants showed a reduction in plant weight and seed production. Moreover, seed weight was sometimes reduced slightly but not significantly after damage. If so, seedling growth and even adult fitness may also be affected (Cideciyan & Malloch 1982, Dolan 1984, Hendrix 1984, Stanton 1984b, 1985, Crawley & Nachapong 1985, Schaal 1985). On the other hand, it is clear that, if defoliation is limited to only some buds and/or young leaves, the effects are not detrimental.

Table 1 reveals that the majority of the studies indicates the adverse effects of defoliation. Hence, we must conclude that, in general, consumers are not beneficial but detrimental for their host plants in contrast with the hypothesis of Owen & Wiegert (1976) and Owen (1980). Although no differentiation is made within various phases of life history, the trend is common. Seedlings generally die after defoliation because reserves are limited, whereas most rosettes survive complete defoliation. But in every life phase defoliation is generally detrimental.

WHEN COULD GRAZING BE BENEFICIAL?

Compensatory regrowth can be *de facto* based on two principles. Firstly, the relative growth rate of the damaged plant is higher than that of the control plant; secondly, the period of growth is longer than that of the control plant (e.g. Eaton 1931).

Although in partly defoliated plants the relative growth rate of remaining tissue is often temporarily increased after the recovery of the carbon balance, there are few examples known that indicate a higher final plant weight or seed production, compared to ungrazed plants without extension of the period of vegetative growth. Innate restrictions to growth are eliminated by defoliator activity, e.g. if the dominance of the apical meristem is broken no environmental factors limit lateral expansion, which is the case in open habitats, and therefore this expansion permits a higher net carbon gain, and, finally, the plant's life length is not increased for another growing season or more (e.g. Taylor & Bardner 1968, Cartwright & Kok 1985).

There are, however, particular situations conceivable in which the plant's fitness is enhanced by grazing, although the relative growth rate of the grazed plant is lower than that of the ungrazed plant (Verkaar 1986). One might expect that under field conditions plants may benefit from grazing. If a cicatrice and a periderm are formed at the damaged surface under conditions of ample water supply and high air humidity, and if grazing animals reduce the amount of transpiring leaf area, and no excessive water loss occurs, grazed plants may survive subsequent drought while control plants desiccate.

Previous moderate herbivory could result in less edible food for successive, more disastrous, grazers. Recently, evidence has been found for both the accumulation of plant defence substances and degradation of nutritional quality after defoliation, although there is some confusion whether these responses depend on either wound repair or an evolved defence response (Myers & Williams 1984, Edwards & Wratten 1985).

On the one hand Valentine *et al.* (1983), Myers & Williams (1984) and Danell & Hus-Danell (1985) did not find much evidence for a strong defence response. Danell & Hus-Danell (1985) observed a decrease in content of secondary plant substances, an increased protein content and an increased dry matter digestibility in birch after moose browsing. Myers & Williams (1984) mentioned a deterioration of food quality after three years of caterpillar attack on Red Alder foliage and after almost complete defoliation.

On the other hand, wound-induced changes in food quality and plant defence are often reported (Raupp & Denno 1984, Williams & Myers 1984, Haukioja & Hanhimäki 1985, West 1985). Undamaged leaves belonging to the same plant show improved herbivore defence (Edwards 1985). In Red Alder the reduced palatability is ascribed to a deterioration in nutritional quality, but not to plant defensive chemicals (Williams & Myers 1984). On the contrary, a strong increase in phenolic substances and procyanidins is found (Tuomi *et al.* 1984, Wagner & Evans 1985). In nitrogen-poor habitats, mainly carbon-based substances, e.g. lignin and phenolics, are produced in large amounts, whereas plant protein content decreases (Bryant *et al.* 1983, 1985, Tuomi *et al.* 1984).

In Britain a few acorns of oak attacked by cynipid gall wasps Hymenopterans or curculionid weevils Coleopterons, survive infestation. In contrast with sound acorns, the first acorns are completely ignored by small mammals which may be due to changes in the content of secondary metabolites. In years of heavy attack of small mammals the weevily oaks benefit from earlier attacks, since they may spoil the food of possible successors.

Beneficial effects after defoliation are probably rare. If they occurred more often, it could be speculated why plants have evolved so many defence mechanisms to avoid being grazed entirely, or to reduce grazing to certain levels (like hairs and thorns) and energy-demanding production of secondary metabolites, etc. (Rhoades & Cates 1976). Due to the described daily rhythm in alkaloid concentration and its variation during life history (Hartmann & Zimmer 1986, Wink & Witte 1984) among other considerations the real impact of secondary metabolism on defoliators should be reinvestigated.

CONCLUSIONS

Few examples of increased fitness as a result of defoliation mentioned by Harris (1973), Owen & Wiegert (1976), Owen (1980) and McNaughton (1983a) have convincing evidence. Sometimes the term ‘fitness’ has been confused with ‘growth’. In studies on the effects of defoliation on plant performance, inadequate attention has been paid to the integrated functioning of the whole plant. The effects of defoliation on root development have particularly been ignored. Both a higher photosynthetic rate and a higher leaf area ratio may account for a temporal increase in relative growth rate as a result of defoliation. As well as improved nutrient and water supply, changes in hormonal status could cause this increase in rate of photosynthesis and leaf area ratio. Nutrient quality deteriorates as a result of defoliation, owing to an increased accumulation of toxic secondary metabolites, though in some cases food quality is improved as a result of a higher nitrogen content of freshly regrown leaves. Extensive tillering or an extension of the period of vegetative growth after defoliation may promote final dry weight and seed output. In particular situations, e.g. when irregular disturbances take place, or when previous attacks provide a defence against later more serious attacks, fitness may be enhanced due to defoliation.

ACKNOWLEDGEMENTS

I wish to thank Dr E. van der Meijden for his encouragement throughout this study and for all his constructive suggestions on earlier drafts of the manuscript. I am also grateful to the other members of the research group 'Plants and herbivores' for providing the opportunity of discussing all the above-mentioned topics, especially Drs T.J. de Jong, P.G.L. Klinkhamer, R.E. Kooi and A.H. Prins. The critical comments of Professor K. Bakker and Professor W.H.O. Ernst are gratefully acknowledged.

REFERENCES

Alcock, M.B. (1964): The physiological significance of defoliation on the subsequent regrowth of grass-clover mixtures and cereals. In: D.J. Crisp (ed.): *Grazing in Terrestrial and Marine Environments.* 25–41. Symp. Brit. Ecol. Soc., Blackwell Scientific Publications, Oxford.

Augspurger, C.K., Greber, M.A. & Evans, J.P. (1985): Reproductive output and biomass allocation in *Sesbania emerus* in a tropical swamp. *Am. J. Bot.* **72:** 1136–1143.

Bayne, H.G., Brown, M.S. & Bethlenfalvay, G.L. (1984): Defoliation effects on mycorrhizal colonization, nitrogen fixation and photosynthesis in the *Glycine-Glomus-Rhizobium* symbiosis. *Physiol. Plant.* **62:** 576–580.

Bazzaz, F.A. & Carlson, R.W. (1979): Photosynthetic contribution of flowers and seeds to reproductive effort of an annual colonizer. *New Phytol.* **82:** 233–244.

Belsky, A.J. (1986): Does herbivory benefit plants? A review of the evidence. *Am. Nat.* **127:** 870–892.

Bentley, S. & 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. & Danell, K. (1987): Effects of simulated winter browsing by moose on morphology and biomass of two birch species. *J. Ecol.* **75:** 533–544.

Blais, J.R. (1958): Effects of defoliation by Spruce budworm on radial growth at breast height of balsam fir and white spruce. *For. Chron.* **34:** 39–47.

Blom, C.W.P.M. (1979): *Effects of trampling and soil compaction on the occurrence of some Plantago species in coastal sand dunes.* Thesis, University of Nijmegen.

Boorman, L.A. & Fuller, R.M. (1984): The comparative ecology of two sand dune biennials: *Lactuca virosa* L. and *Cynoglossum officinale* L. *New Phytol.* **69:** 609–629.

Brouwer, R. (1962a): Distribution of dry matter in the plant. *Neth. J. Agric. Sci.* **10:** 361–376.

— (1962b): Influence of temperature of the root medium on the growth of seedlings of various crop plants. *Mededel. I.B.S.* **175:** 11–18.

— (1963): Some aspects of the equilibrium between overground and underground plant parts. *Mededel. I.B.S.* **213:** 31–39.

— (1983): Functional equilibrium: sense or nonsense? *Neth. J. Agric. Sci.* **31:** 335–348.

Brown, R. F. (1985): The effect of severe defoliation on the subsequent growth and development of five rangeland pasture grasses of south-western Queensland. *Austr. J. Ecol.* **10:** 335–343.

Brown, V.K., Gange, A.C., Evans, I.M. & Storr, A.L. (1987): The effect of insect herbivory on the growth and reproduction of two annual *Vicia* species at different stages in plant succession. *J. Ecol.* **75:** 1173–1189.

Bryant, J.P., Chapin, F.S. & Klein, D.R. (1983): Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos* **40:** 357–368.

—, Wieland, G.D., Clausen, T. & Kuropat, P. (1985): Interactions of snowshoe hare and feltleaf willow in Alaska. *Ecology* **66:** 1564–1573.

Cartwright, B. & Kok, L.T. (1985): Growth responses of musk and plumeless thistles *(Cardus nutans* and *C. acanthoides*) to damage by *Trichosirocalus horridus* (Coleoptera: Curculiomidae). *Weed Sci.* **33:** 57–62.

Cideciyan, M.A. & Malloch, A.J.C. (1982): Effects of seed size on germination, growth and competitive ability of *Rumex crispus* and *Rumex obtusifolius. J. Ecol.* **70:** 227–232.

Coughenour, M.B. (1984): A mechanistic simulation analysis of water use, leaf angles, and grazing in East African graminoids. *Ecol. Modell.* **26:** 203–230.

—, McNaughton, S.J. & Wallace, L.L. (1984): Simulation study of East African perennial graminoid responses to defoliation. *Ecol. Modell.* **26:** 177–201.

Cox, C.S. & 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. (1983): Herbivory, the dynamics of animal-plant interaction. In: *Studies in Ecology,* Vol. 10. Blackwell Scientific Publications, Oxford.

— (1985): Reduction of oak fecundity by low-density herbivore populations. *Nature* **314:** 163–164.

— (1987): Benevolent herbivores? *TREE* **2:** 167–168.

— & Nachapong, M. (1985): The establishment of seedlings from primary and regrowth seeds of ragwort (*Senecio jacobaea*). *J. Ecol.* **73:** 255–261.

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

Darwin, C. (1859): *The Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life.* Murray, London.

Davidson, J.L. & Milthorpe, F.L. (1966a): Leaf growth in *Dactylis glomerata* following defoliation. *Ann. Bot.* **30:** 173–184.

— & — (1966b): The effect of defoliation on the carbon balance in *Dactylis glomerata. Ann. Bot.* **30:** 185–198.

Detling, J.K., Dyer, M.I. & Winn, D.T. (1979): Net photosynthesis, root respiration, and regrowth of *Bouteloua gracilis* following simulated grazing. *Oecologia (Berl.)* **41:** 127–134.

— & —, Procter-Gregg, C. & Winn, D. T. (1980): Plant–herbivore interactions: examination of potential effects of bison saliva on regrowth of *Bouteloua gracilis* (H.B.K.) Lag. *Oecologia (Berl.)* **45:** 26–31.

Dirzo, R. (1984): Herbivory: a phytocentric overview. In: R. Dirzo and J. Sarukhán (eds): *Perspectives on Plant Population Ecology.* 141–165. Sinauer, Sunderland MA.

Dolan, R.W. (1984): The effect of seed size and maternal source on individual size in a population of *Ludwigia leptocarpa* (Onagraceae). *Am. J. Bot.* **71:** 1302–1307.

Drent, R.H. & Prins, H.H.T. (1987): The herbivore as prisoner of its food supply. In: J. van Andel, J.P. Bakker and R.W. Snaydon, (eds): *Disturbance in Grasslands. Causes, Effects and Processes.* 131–147. Junk Publ., Dordrecht.

Dyer, M.I. (1975): The effects of red-winged blackbirds (*Agelaius phoeniceus* L.) on biomass production of corn grains (*Zea mays* L.). *J. appl. Ecol.* **12:** 719–726.

— & Bokhari, U.G. (1976): Plant-animal interactions on the effects of grasshopper grazing on blue grama grass. *Ecology* **57:** 762–772.

—, Detling, J.K., Coleman, D.C. & Hilbert, D.W. (1982): The role of herbivores in grasslands. In: J.R. Estes, R.J. Tyrl and J.N. Brunken (eds.): *Grasses and Grasslands, Systematics and Ecology.* 255–295. University of Oklahoma Press, Norman.

Eaton, F. M. (1931): Early defloration as a method of increasing cotton yields, and the relation of fruitfulness to fiber and boll characters. *J. Agric. Res.* **42:** 447–462.

Edwards, J. (1985): Effects of herbivory by moose on flower and fruit production of *Aralia nudicaulis. J. Ecol.* **73:** 861–868.

Edwards, P.J. & Wratten, S.D. (1985): Induced plant defences against insect grazing: fact or artefact? *Oikos* **44:** 70–74.

Ellison, L. (1960): Influence of grazing on plant succession of rangelands. *Bot. Rev.* **26:** 1–78.

Ericsson, A., Hellqvist, C., Längström, B., Larsson, S. & Tenow, O. (1985): Effects on growth of simulated and induced shoot pruning by *Tomicus piniperda* as related to carbohydrate and nitrogen dynamics in Scots pine. *J. appl. Ecol.* **22:** 105–124.

Ernst, W.H.O. (1987): Population differentiation in grassland vegetation. In: J. van Andel, J.P. Bakker and R.W. Snaydon (eds): *Disturbance in Grasslands. Causes, Effects and Processes.* 213–228. Junk Publ., Dordrecht.

Esau, K. (1960): *Anatomy of Seed Plants.* Wiley, New York.

Etherington, J.R. (1984): Relationship between morphological adaptation to grazing, carbon balance and water logging tolerance in clones of *Dactylis glomerata* L. *New Phytol.* **98:** 47–658.

Evans, G.C. (1972): *The Quantitative Analysis of Plant Growth.* Blackwell Scientific Publications, Oxford.

Fasoranti, J.O. (1984): Mining of *Tischeria immaculata* (Braun) (Lepidoptera: Tischeriidae) in the leaves of *Ceanothus griseus* L. *J. Econ. Entomol.* **77:** 1127–1129.

Fliervoet, L.M. (1984): *Canopy structure of Dutch grasslands.* Thesis, University of Utrecht.

Forcella, F. & Wood, H. (1986): Demography and control of *Cirsium vulgare* (Savi) Ten. in relation to grazing. *Weed Res.* **26:** 199–206.

Fowler, N.L. & Rauscher, M.D. (1985): Joint effects of competitors and herbivores on growth and reproduction in *Aristolochia reticulata. Ecology* **66:** 1580–1587.

Fresco, L.F.M., van Laarhoven, H.P.M., Loonen, M.J.J.E. & Moesker, T. (1987): Ecological modelling of short-term plant community dynamics under grazing with and without disturbance. In: J. van Andel, J.P. Bakker and R.W. Snaydon (eds): *Disturbance in Grasslands. Causes, Effects and Processes.* 149–165. Junk Publ., Dodrecht.

Gifford, R.M. & Marshall, C. (1973): Photosynthesis and assimilate distribution in *Lolium multiflorum* Lam. following differential tiller defoliation. *Austr. J. Biol. Sci.* **26:** 517–526.

— & Evans, L.T. (1981): Photosynthesis, carbon partitioning, and yield. *Ann. Rev. Plant Physiol.* **32:** 485–509.

Halse, S.A. & Trevenen, H.J. (1985): Damage to medic pastures by skylarks in North-Western Iraq. *J. appl. Ecol.* **22:** 337–346.

Hare, J.D. (1980): Impact of defoliation by the Colorado potato beetle on potato yields. *J. Econ. Entomol.* **73:** 369–373.

Harper, J.L. (1977): *Population Biology of Plants.* Academic Press, London.

Harris, P. (1973): Insects in the population dynamics of plants. In: H.F. van Emden (ed.): *Insect/Plant Relationships. Symp. Roy. Entomol. Soc. London* **6:** 201–209. Blackwell Scientific Publications, Oxford.

—, Thompson, L.S., Wilkinson, A.T.S. & Neary, M.E. (1978): Reproductive biology of tansy ragwort, climate and biological control by the cinnabar moth in Canada. In: T.E. Freeman (ed): *Proceedings of the 4th International Symposium on the Biological Control of Weeds.* 163–173. University of Florida, Gainesville.

Hartmann, T. & Zimmer, M. (1986): Organic-specific distribution and accumulation of pyrrolozidine alkaloids during the life history of two annual *Senecio* species. *J. Plant Physiol.* **122:** 67–80.

Haukioja, E. & Hanhimäki, S. (1985): Rapid wound-induced resistance in white birch (*Betula pubescens*) foliage to the geometrid *Epirrita autumnata*: a comparison of trees and moths within and outside the outbreak range of the moth. *Oecologia* (Berl.) **65:** 223–228.

Heichel, G.H. & Turner, N.C. (1983): CO_2 assimilation of primary and regrowth foliage of red maple (*Acer rubrum* L.) and red oak (*Quercus rubra* L.): response to defoliation. *Oecologia (Berl.)* **57:** 14–19.

Hendrix, S.D. (1984): Variation in seed weight and its effects on germination in *Pastinaca sativa* L. (Umbellifera). *Am. J. Bot.* **71:** 795–802.

Housley, T.L. & Pollock, C.J. (1985): Photosynthesis and carbohydrate metabolism in detached leaves of *Lolium temulentum* L. *New Phytol.* **99:** 499–507.

Huss-Danell, K. & Sellstedt, A. (1985): Nitrogenase activity in response to darkening and defoliation of *Alnus incana. J. Exp. Bot.* **36:** 1352–1358.

Ingham, R.E. & Detling, J.K. (1986): Effects of defoliation and nematode consumption on growth and leaf gas exchange in *Bouteloua curtipendula. Oikos* **46:** 23–28.

Jansson, R.K. & Smilowitz, Z. (1985): Influence of nitrogen on population parameters of potato insects: abundance, development, and damage of the Colorado potato beetle, *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae). *Envir. Entomol.* **14:** 500–506.

Kny, L. (1894): On correlation in the growth of roots and shoots. *Ann. Bot.* **8:** 265–280.

Lam, P.K.S. & Dudgeon, D. (1985): Fitness implications of plant-herbivore 'mutualism'. *Oikos* **44:** 360–361.

Larsson, S. (1983): Effects of artificial defoliation on stem growth in *Salix smithiana* grown under intensive culture. *Acta Oecol., Oecol. Appl.* **4:** 343–349.

Louda, S.M. (1984): Herbivore effect on stature, fruiting, and leaf dynamics of a native crucifer. *Ecology* **65:** 1379–1386.

Marshall, C. & Sagar, G.R. (1968): The distribution of assimilates in *Lolium multiflorum* Lam. following differential defoliation. *Ann. Bot.* **32:** 715–719.

Maun, M.A. & Cavers, P.B. (1971): Seed production and dormancy in *Rumex crispus.* II. The effects of removal of various proportions of flowers at anthesis. *Can. J. Bot.* **49:** 1841–1848.

Mayoral, M.L., Plant, Z. & Reinhold, L. (1985): Effect of sink-source manipulations on the photosynthetic rate and carbohydrate control of cucumber cotyledons. *J. Exp. Bot.* **36:** 1551–1558.

McNaughton, S. J. (1979): Grazing as an optimization process: grass-ungulate relationships in the Serengeti. *Am. Nat.* **113:** 691–703.

— (1983a): Compensatory plant growth as a response to herbivory. *Oikos* **40:** 329–336.

— (1983b): Physiological and ecological implication of herbivory. In: O.L. Lange, P.S. Nobel, C.B. Osmond and H. Ziegler (eds): *Physiological Plant Ecology III. Responses to the Chemical and Biological Environment, N.S. 12 C.* 657–677. Springer-Verlag, Berlin.

— (1984): Grazing lawns: animals in herds, plant form, and coevolution. *Am. Nat.* **124:** 863–886.

— (1985): Interactive regulation of grass yield and chemical properties by defoliation, a salivary, chemical and inorganic nutrition. *Oecologia (Berl.)* **65:** 478–486.

—, Coughenour, M.B. & Wallace, L.L. (1982): Interactive processes in grassland ecosystems. In: J.R. Estes, R.J. Tyrl and J.N. Brunken (eds): *Grasses and Grasslands: Systematics and Ecology.* 167–193. University of Oklahoma Press, Norman.

Meijden, E. van der, & van der Waals-Kooi, R.E. (1979): The population ecology of *Senecio jacobaea* in a sand dune system. I. Reproduction strategy and biennial habit. *J. Ecol.* **67:** 131–153.

Mendoza, A., Piñero, D. & Sarukhán, J. (1987): Effects of experimental defoliation on growth, reproduction and survival of *Astrocaryum mexicanum. J. Ecol.* **75:** 545–554.

Mooney, H.A. & Chiariello, N.R. (1984): The study of plant function—the plant as a balanced system. In: R. Dirzo & J. Sarukhán (eds): *Perspectives on Plant Population Ecology.* 305–323. Sinauer, Sunderland MA.

Mueggler, W.F. (1967): Response of mountain grassland vegetation to clipping in southwestern Montana. *Ecology* **48:** 942–949.

Myers, J.H. & Williams, K.S. (1984): Does tent caterpillar attack reduce the food quality of red alder foliage? *Oecologia (Berl.)* **62:** 74–79.

Nowak, R.S. & Caldwell, M.M. (1984): A test of compensatory photosynthesis in the field: implications for herbivory tolerance. *Oecologia* (*Berl.*) **61:** 311–318.

Ostlie, K.R. & Pedigo, L.P. (1984): Water loss from soybeans after simulated actual insect defoliation. *Envir. Entomol.* **13:** 1675–1680.

Owen, D.F. (1980): How plants may benefit from the animals that eat them. *Oikos* **35:** 230–235.

— & Wiegert, R.G. (1976): Do consumers maximize plant fitness? *Oikos* **27:** 488–492.

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

Painter, E.L. & Detling, J.K. (1981): Effects of defoliation on net photosynthesis and regrowth of western wheatgrass. *J. Range Managemt.* **34:** 68–71.

Parsons, A.J., Leafe, E.L., Collett, B. & Stiles, W. (1983a): The physiology of grass production under grazing. I. Characteristics of leaf and canopy photosynthesis of continuously-grazed swards. *J. appl. Ecol.* **20:** 117–126.

—, —, —, Penning, R.D. & Lewis, J. (1983b): The physiology of grass production under grazing. II. Photosynthesis, crop growth and animal intake of continuously-grazed swards. *J. appl. Ecol.* **20:** 127–139.

Prins, H.H.T., Ydenberg, R.C. & Drent, R.H. (1980): The interaction of brent geese *Branta bernicla* and sea plantain *Plantago maritima* during spring staging: field observations and experiments. *Acta Bot. Neerl.* **29:** 585–596.

Pyke, D.A. (1986): Demographic responses of *Bromus tectorum* and seedlings of *Agropyron spicatum* to grazing by small mammals: occurrence and severity of grazing. *J. Ecol.* **74:** 739–754.

Raupp, M.J. & Denno, R.F. (1984): The suitability of damaged willow leaves as food for the leaf beetle, *Plagiodera versicolora. Ecol. Entomol.* **9:** 443–448.

Reinke, J. (1884): Notiz über die Abhängigkeit der Blattenentwicklung von der Bewurzelung. *Ber. Deutsch. Bot. Gesell.* **2:** 376–378.

Rhoades, D.F. (1985): Offensive–defensive interactions between herbivores and plants: their relevance in herbivore population dynamics and ecological theory. *Am. Nat.* **125:** 205–238.

— & Cates, R.G. (1976): Toward a general theory of plant antiherbivore chemistry. *Rec. Adv. Phytochem.* **10:** 168–213.

Richards, J.H. (1984): Root growth response to defoliation in two *Agropyron* bunchgrasses: field observations with an improved root periscope. *Oecologia* (*Berl.*) **64:** 21–25.

— & Caldwell, M.M. (1985): Soluble carbohydrates, concurrent photosynthesis and efficiency in regrowth following defoliation: a field study with *Agropyron* species. *J. appl. Ecol.* **22:** 907–920.

Rockwood, L.L. (1973): The effect of defoliation on seed production of six Costa Rican tree species. *Ecology* **54:** 1363–1369.

Ruess, R.W. (1984): Nutrient movement and grazing: experimental effects of clipping and nitrogen source on nutrient uptake in *Kyllinga nervosa. Oikos* **43:** 183–188.

— & McNaughton, S.J. (1984): Urea as a promotive coupler of plant-herbivore interactions. *Oecologia* (*Berl.*) **63:** 331–337.

Ryle, G.J.A. & Powell, C.E. (1975): Defoliation and regrowth in the graminaceous plant: the role of current assimilate. *Ann. Bot.* **39:** 297–310.

—, — & Gordon, A.J. (1985): Defoliation in white clover: regrowth, photosynthesis and N2 fixation. *Ann. Bot.* **56:** 9–18.

Schaal, B.A. (1985): Genetic variation in plant populations: from demography to DNA. In: J. Haeck and J.W. Woldendorp (eds): *Structure and Functioning of Plant Populations 2.* 321–341. North-Holland Publ. Comp., Amsterdam.

Seastedt, T.R., Crossley, D.A. & Hargrove, W.W. (1983): The effects 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. & Wyman, J.A. (1984): Effect of defoliation at specific growth stages on potato yields. *J. Econ. Entomol.* **77:** 1194–1199.

Skuhravý, V. (1968): Einfluss der Entblätterung und des Kartoffelkäferfrasses auf die Kartoffelernte. *Anz. f. Schädlingskunde* **41:** 180–188.

Smith, J.W., Sams, R.L., Agnew, C.W. & Simpson, C.E. (1985): Methods for estimating damage and evaluating the reaction of selected peanut cultivars to the potato leafhopper, *Empoasca fabae* (Homoptera: Cicadellidae). *J. Econ. Entomol.* **78:** 1059–1062.

Stamp, N.E. (1984): Effect of defoliation by checkerspot caterpillars (*Euphydryas phaeton*) and sawfly larvae (*Macrophya nigra* and *Tenthredo grandis*) on their host plants (*Chelone* spp.). *Oecologia* (*Berl.*). **63:** 275–280.

Stanton, M.L. (1984a): Developmental genetic sources of seed weight variation in *Raphanus raphanistrum* L. (Brassicaceae). *Am. J. Bot.* **71:** 1090–1098.

— (1984b): Seed variation in wild radish: effect of seed size on components of seedling and adult fitness. *Ecology* **65:** 1105–1112.

— (1985): Seed size and emergence time within a stand of wild radish (*Raphanus raphanistrum* L.): the establishment of a fitness hierarchy. *Oecologia* (*Berl.*) **67:** 524–531.

Stark, A.W. & Cook, J.A. (1957): The effects of defoliation by the lodgepole needle miner. *Forest Sci.* **3:** 376–396.

Storms, J.J.H. (1971): Some physiological effects of spider mite infestations on bean plants. *Neth. J. Plant Path.* **77:** 154–167.

Sweet, G.B. & Wareing, P.F. (1966): Role of plant growth in regulating photosynthesis. *Nature* **210:** 77–79.

Taylor, W.E. & 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.

Thalen, D.C.P., Poorter, H., Lotz, L.A.P. & Oosterveld, P. (1987): Modelling the structural changes in vegetation under different grazing regimes. In: J. van Andel, J.P. Bakker and R.W. Snaydon (eds): *Disturbance in Grasslands. Causes, Effects and Processes.* 167–183. Junk Publ., Dordrecht.

Throughton, A. (1956): Studies on the growth of young grass plants with special reference to the relationship between the shoot and root systems. *J. Br. Grassl. Soc.* **11:** 56–65.

Tomczyk, A. & Kropczýnska, D. (1985): Effect of spider mites on their host plants. In: W. Helle and M.W. Sabelis (eds): *Spider Mites: Their Biology, Natural Enemies and Control, vol. 1A:* 317–329. Elsevier, Amsterdam.

Trumble, J.T., Ting, I.P. & Bates, L. (1985): Analysis of physiological, growth and yield responses of celery to *Liriomyza trifollii. Entomol. Exp. Appl.* **38:** 15–21.

Tuomi, J., Niemelä, P., Haukioja, E., Sirén, S. & Neuvonen, S. (1984): Nutrient stress: an explanation for plant anti-herbivore responses to defoliation. *Oecologia* (*Berl.*) **61:** 208–210.

Valentine, H.T., Wallner, W.E. & Wargo, P.M. (1983): Nutritional changes in host foliage during and after defoliation, and their relation to the weight of gipsy moth pupae. *Oecologia* (*Berl.*) **57:** 298–302.

Verkaar, H.J. (1986): When does grazing benefit plants? *TREE* **1:** 168–169.

— (1987): Population dynamics—the influence of herbivory. *New Phytol. (Suppl.)* **106:** 49–60.

—, van der Meijden, E. & Breebaart, L. (1986): The responses of *Cynoglossum officinale* L. and *Verbascum thapsus* L. to defoliation in relation to nitrogen supply. *New Phytol.* **104:** 121–129.

Vickery, P.J. (1972): Grazing and net primary production of a temperate grassland. *J. appl. Ecol.* **9:** 307–314.

Vöchting, H. (1884): *Über Organbildung im Pflanzenreich II.* Emil Strauss, Bonn.

Wagner, M.R. & Evans, P.D. (1985): Defoliation increases nutritional quality and allelochemics of pine seedlings. *Oecologia* (*Berl.*) **67:** 235–237.

Wall, R. & Begon, M. (1985): Competition and fitness. *Oikos* **44:** 356–360.

Wallace, L.L., McNaughton, S.J. & Coughenour, M.B. (1982): The effects of clipping and fertilization on nitrogen nutrition and allocation by mycorrhizal and nonmycorrhizal *Panicum coloratum* L., a C4 grass. *Oecologia* (*Berl.*) **54:** 68–71.

—, — & — (1984): Compensatory photosynthetic responses of three African graminoids to different fertilization, watering and clipping regimes. *Bot. Gaz.* **145:** 151–156.

Wareing, P.F., Khalifa, M.M. & Treharne, K.J. (1968): Rate-limiting processes in photosynthesis at saturating light intensities. *Nature* **220:** 453–457.

Weinmann, H. (1948): Underground development and reserves of grasses—a review. *J. Br. Grassl. Soc.* **3:** 115–140.

West, C. (1980): Factors underlying the late seasonal appearance of the lepidopterous leaf-mining guild on oak. *Ecol. Entomol.* **10:** 111–120.

White, J. (1984): Plant metamerism. In: R. Dirzo and J. Sarukhán (eds): *Perspectives on Plant Population Ecology.* 15–47. Sinauer, Sunderland MA.

Whitehead, D.C. (1983): The influence of frequent defoliation and of drought on nitrogen and sulfur in the roots of perennial ryegrass and white clover. *Ann. Bot.* **52:** 931–934.

Whittaker, J.B. (1982): The effect of grazing by a chrysomelid beetle, *Gastrophysa viridula*, on growth and survival of *Rumex crispus* on a shingle bank. *J. Ecol.* **70:** 291–296.

— (1984): Responses of sycamore (*Acer pseudoplatanus*) leaves to damage by a typhlocybine leaf hopper, *Ossiannilssonola callosa. J. Ecol.* **72:** 455–462.

— & Warrington, S. (1985): An experimental field study of different levels of insect herbivory induced by *Formica rufa* predation on sycamore (*Acer pseudoplatanus*). III. Effects on tree growth. *J. appl. Ecol.* **22:** 797–811.

Willatt, S.T. & Pullar, D.M. (1983): Changes in soil physical properties under grazed pastures. *J. Soil Res.* **22:** 343–348.

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.

Wink, M. & Witte, L. (1984): Turnover and transport of quinolizidine alkaloids. Diurnal fluctuations of lupanine in the phloem sap, leaves and fruits of *Lupinus albus* L. *Planta* **161:** 519–524.