

A Review of Damage by Mammals in North Temperate Forests: 3. Impact on Trees and Forests

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SUMMARY

The impact of mammals on trees and forest crops is examined by reviewing the scientific literature. The degree of growth loss, stem deformation and the likelihood of death from browsing all increase with the severity of damage. The effect of the damage depends very much on the tree species, age and season. Many studies reveal that some compensatory growth occurs after browsing, but there is a serious lack of long-term data and more work that links the incidence of damage to ultimate yield loss is required. Browsing can also make trees more or less palatable and this could have a marked effect on the likelihood of recovery, but this subject requires further research for trees growing in British conditions.

Bark stripping results in timber staining and decay but does not appear to cause serious growth loss. The amount of stem decay usually increases with wound size and tree vigour but a considerable amount of residual variation remains to be explained.

The success of natural regeneration depends on both herbivore and seedling density. Changes in tree species composition reflect the palatability of seedlings as well as their ability to recover. Browsing by deer usually causes a decrease in shrub and herbaceous plant biomass in the ground vegetation and an increase in grasses, ferns and mosses.

INTRODUCTION

Mammalian herbivores influence the development of temperate forests by retarding growth and succession (Crawley, 1983). Through the action of browsing or bark stripping, deer and other mammals can kill trees or retard their growth as well as bring about changes in the composition of forest vegetation. In stands managed for timber production, browsing and bark stripping can also reduce timber quality by causing stem deformation, callousing or staining.

Although browsing mammals are well known to be capable of eliminating tree regeneration, this is not the only effect they have. More commonly, browsing causes less conspicuous but none the less important changes in composition or reductions in productivity. Unfortunately there is very little quantitative data available on the ultimate loss in yield or on changes in

species composition of the trees and ground flora. This paper reviews the impact of browsing and bark stripping with a view to understanding the long-term changes in forests managed for both timber production and conservation objectives.

This review is the final part of a series of papers covering the impact of mammals in forests. Part 1 (Gill, 1992a) examined the causes of damage inflicted by deer (tree species preferences, deer population density, habitat use and food availability) and part 2 (Gill, 1992b) covered similar aspects of damage by small mammals. The effect of seed dispersal and predation by mammals is omitted and the impact of livestock has recently been reviewed elsewhere (Mitchell and Kirby, 1990). All three papers focus on the problems of wildlife damage in Britain but draw heavily on examples from north temperate ecosystems. Collection of relevant published literature ceased after April 1992.

THE IMPACT OF BROWSING 1. THE EFFECT ON INDIVIDUAL TREES

Effect of severity, frequency and tree size

Browsing has been widely reported to reduce growth or slow the rate of increment (Kulman, 1971; Crawley, 1989). Furthermore, the rate of subsequent growth is dependent on the severity of damage (Holloway, 1967; Kuznetsov and Lozinov, 1983; Bergström and Danell, 1987; Piene and Little, 1990) and repetitive browsing is worse than one attack (Roy, 1960; Eiberle, 1975 and 1978) and may keep trees within browsing height for several years or even decades (Holloway, 1967; Eiberle, 1980; Lavsund, 1987).

Many of the factors that result in reduced growth also raise the likelihood of death. Increased severity and increased frequency of clipping have both been found to influence mortality independently (Holloway, 1967; Tsiouvaras, 1988). Eiberle and Nigg (1987a) found a positive correlation between average height increment loss and mortality among a range of European tree species. Survival began to be affected when height increment loss exceeded 25 per cent.

The age or size of the tree is likely to determine whether browsing causes death or merely reduces growth rate. Younger or smaller trees appear to have poorer survival after damage than older or larger ones (Krefting and Stoeckeler, 1953; Hartwell, 1973; Hartwell and Johnson, 1983). Several authors have concluded that mortality after browsing declines to almost zero after a certain age, although the age at which this occurs is likely to depend on both species and local conditions. For Scots pine (*Pinus sylvestris*) in the Scottish highlands this was found to be about 3 years (Holloway, 1967) and about 1 year for Douglas fir (*Pseudotsuga menziesii*) and slash pine (*Pinus elliottii*) in the USA (Dimock, 1970; Lewis, 1980b).

There are clear differences between species in their resilience to browsing. Eiberle (1975) compared the growth of 18 species to simulated browsing in

spring and autumn and found that white pine (*Pinus strobus*), Scots pine and silver fir (*Abies alba*) were the most severely affected and larch (*Larix decidua*), Norway spruce (*Picea abies*), aspen (*Populus tremula*) and oak (*Quercus petraea*) were the least affected. Other studies have shown that Scots pine is more likely to die than birch (*Betula* sp.), willow (*Salix* sp.) or rowan (*Sorbus aucuparia*) (Miller *et al.*, 1982; Kuznetsov, 1987). Rowan appears to be particularly resilient, often surviving clipping to ground level. Holloway (1967) found that larch grew more rapidly than Scots pine after both dormant and growing-season clipping. The difference between species in their ability to survive browsing is at least partly due to the distribution of dormant buds which can be activated after shoot loss (Krefting and Stoeckeler, 1953; Piene, 1989). Holloway (1967) found that Scots pine was more likely to survive if the apical shoot was undamaged.

Once established, trees can sometimes withstand frequent or repeated browsing with little effect on survival (Bergerud and Manuel, 1968) although this may depend very critically on the severity and frequency of damage. Kermes oak (*Quercus coccifera*), for example has been found to be capable of surviving removal of 80 per cent, but not 100 per cent, of the length of current growth on twigs every 15 days during the growing season (Tsiouvaras, 1988).

The influence of environmental conditions on growth and survival after browsing does not seem to have been widely reported. Crouch (1966) however found that the growth (measured in total weight) of shaded Douglas fir seedlings was affected less by clipping than unshaded, suggesting partial compensation, although a combination of shading and clipping clearly reduced survival more than either shading or clipping alone.

The influence of season or type of damage

Trees appear to be most affected by the type or timing of browsing that most severely depletes nutrient or carbohydrate reserves. Deciduous trees store reserves in stems and roots in winter whereas evergreens retain reserves in needles (Ericsson *et al.*, 1985; Kozlowski *et al.*, 1991). Winter damage is therefore relatively more serious to evergreens than broadleaves (Carter, 1977; Eiberle, 1978) whereas summer browsing is more serious than winter browsing to broadleaves (Miller *et al.*, 1982; Kindschy, 1989; Kays and Canham, 1991). Among conifers, losing young needles is usually reported to be more serious than losing older ones (Kulman, 1971). The fact that most mammals browse evergreens in winter and broadleaves in summer (see parts 1 and 2) suggests that damage usually occurs when it is most serious for the tree.

The age of foliage removed is an important determinant of the cost of damage to a tree. ¹⁴C studies of carbon allocation have revealed that young leaves are net importers of photosynthate, whereas mature leaves are exporters (Bassman and Dickmann, 1985). Furthermore, tree leaves and needles contain higher concentrations of nitrogen during periods of active

growth (Archer and Tieszen, 1980). Foliage loss is therefore likely to be most costly during or immediately after leaf expansion, particularly for species which grow leaves throughout the season from photosynthate produced from initial leaves (Harper, 1989). Kays and Canham (1991) found that species with determinate growth (e.g. white ash *Fraxinus americana*) had a shorter growing season and were vulnerable to cutting for a shorter period during the summer than species with indeterminate growth (e.g. gray birch, *Betula populifolia*).

The upper leaves and shoots of trees generally contain more nitrogen (Harper, 1989) and have a faster growth rate than lower shoots. The loss of leading shoot has been found to affect growth more than removal of laterals in several species of pine (*Pinus taeda*, *P. densiflora*, *P. thunbergii*; Furuno and Yamazaki, 1973; Scots pine; Ericsson *et al.*, 1985). Browsing on side shoots alone has however been shown to reduce height growth in Norway spruce (Kampmann, 1983). Loss of foliage on the lower branches may even be beneficial to growth, because shading may reduce photosynthesis to the level at which it does not compensate respiration (Kozłowski *et al.*, 1991). Lower branches are however not selected preferentially by browsing mammals (Bryant and Kuropat, 1980), and are therefore unlikely to attract much feeding.

Browsing may alter relative growth in stem and leaders giving a misleading impression of the effect on overall growth. Ericsson *et al.* (1985) found that leader length of higher order shoots were positively affected by clipping, but girth increment was negatively affected. Several studies indicate that girth increment after browsing is not affected in the same way as height (Mitscherlich and Weise, 1982; Piene and Little, 1990; Welch *et al.*, 1992). In conifers, reduced growth can occur with a lag of 1–3 years after defoliation (Kulman, 1971; Ericsson *et al.*, 1980; Britton, 1988).

Browsing can alter resource allocation within the tree resulting in some unexpected effects. Birch has been found to produce more long shoots, buds per shoot and larger seeds after clipping (Bergström and Danell, 1987). Clipping has also been found to result in increased average shoot length in Scots pine (Kuznetsov and Lozinov, 1983). In oak, xylem tissues laid down after defoliation were found to contain larger cells and fewer fibres (Hilton *et al.*, 1987).

Loss of apical dominance

Browsing by mammals commonly results in the loss of the leading shoot. Although browsed leaders are eventually replaced from a lateral shoot or adventitious bud, the loss can result in the formation of multiple leaders, severe stem forking or stem sweep (Eiberle, 1975; Eiberle and Nigg, 1983; Staines and Welch, 1984; Maizeret and Ballon, 1990; Welch *et al.*, 1992). The proportion of trees developing multiple leaders after browsing is rather

variable but is often regarded as a more serious consequence of browsing than growth loss.

There are several examples indicating that the degree of deformation can depend on the severity of damage, but the influence of genetic or environmental factors have not been widely reported. Furuno and Yamazaki (1973) found that removal of the whole leader was more serious than removal of just the top half of the leader and that removal of both leader and laterals on the top whorl was even worse. Increasing the frequency of leader browsing has also been reported to increase the likelihood of multiple stemming (Eiberle, 1978; Mitscherlich and Weise, 1982). In Scots pine stands, the degree of deformation after stem breakage was found to be worst on the most fertile sites (Löyttyniemi, 1983). Although stem straightness is well known to be under genetic control (Kozlowski *et al.*, 1991), there do not appear to be any reports of genotypic differences in the severity of multiple stemming after browsing.

There is very little data available to indicate the effect of leader browsing on timber quality, but Lavsund (1987) cites one example where the proportion of good quality stems was reduced from 63 per cent to 18 per cent after a stand of Scots pine had been exposed to moose (*Alces alces*) browsing. Welch *et al.* (1992) found that 45 per cent of trees in a formerly damaged Sitka spruce stand developed multiple trunks. The problem is unfortunately complicated by other factors. Wind, frost and insect damage, which may not be as conspicuous as browsing, can also cause multiple leaders to develop (Holopainen, 1990), and in closely-spaced stands stem form has been found to improve with stand age in both aspen (Martynov, 1982) and Sitka spruce (*Picea sitchensis*) (Welch *et al.*, 1992).

Compensatory growth

Defoliated plants have been widely reported to show some degree of compensation after damage (Crawley, 1983). Browsing creates an imbalance in the shoot:root ratio which can be corrected by altering allocation of photosynthetate and nutrients to the shoot at the expense of roots (Bassman and Dickman, 1985; Kozlowski *et al.*, 1991). This results in an increased relative growth rate in the shoot following damage. Plants can also show increased growth if a competitor is damaged and therefore compensatory growth can occur between neighbours in stands (Crawley, 1983).

The mechanisms involved in compensation within a tree are still not fully understood. Browsing or clipping has been reported to reduce the shoot:root ratio in Douglas fir (Crouch, 1966), oak (Shaw, 1974) and lodgepole pine (*Pinus contorta*) seedlings (Britton, 1988). Correction of the shoot:root ratio however may not be achieved solely by shoot growth. The reallocation of resources to the shoots results in restricted new root growth as well (Carlson, 1977). Ericsson *et al.* (1985) suggested that compensation in Scots pine is achieved because the remaining needles obtain more light, water and

nitrogen. Compensatory growth may therefore be the result of a combination of resource allocation and improved photosynthetic efficiency.

The evidence for compensation by trees to browsing is varied and unfortunately limited by the lack of long-term studies. Compensation has been reported on Sitka spruce following leader damage by deer but after 10–15 years' growth was still retarded by about 1 year (Welch *et al.*, 1992). Similar partial compensation was also reported in lodgepole pine after vole damage (Hansson, 1984). Norway spruce has shown partial recovery from side-shoot browsing after 8 years (Kampmann, 1983) and both leader and side shoot clipping after 3–6 years (Mitscherlich and Weise, 1982), although in the latter case height growth lagged behind diameter growth. Stout (1986) found almost complete compensation after 22 years growth from simulated browsing on both leaders and laterals in four broadleaved species (white ash, red maple (*Acer rubrum*), sugar maple (*Acer saccharum*) and black cherry (*Prunus serotina*) in Pennsylvania.

The degree of compensation may also be affected by environmental conditions. Experiments with grasses have shown that fertilization or competition can respectively increase, or decrease relative shoot growth after defoliation (Polley and Detling, 1989). There do not appear to be any studies which have investigated these effects in trees, nor the degree to which neighbours in a stand may compensate browsing losses.

The effect of damage on palatability

Browsing results in a number of structural and chemical changes that can both increase and decrease palatability. Many of the changes involve an increase or decrease in levels of secondary metabolites (phenols and terpenes) which are known to be toxic or to reduce digestibility in many mammals (see parts 1 and 2). Although there is increasing evidence that some of these compounds are produced as a defence against mammals, many of the reductions in palatability may simply be a fortuitous consequence of resource allocation after damage.

In Scots pine, new needles growing after a previous defoliation have been found to contain higher nitrogen and phosphorus concentrations and lower levels of carbohydrates than undamaged needles (Löyttyneimi, 1985; Ericsson *et al.*, 1985). Similar observations have been made on balsam fir (*Abies balsamea*) growing on poor sites (Bergerud and Manuel, 1968). These nutritional changes can provoke still further browsing, resulting in some trees repeatedly browsed while neighbours are avoided. Bryant *et al.* (1988) suggest that an improvement in palatability may be typical of all evergreens because these species store reserves in foliage which is depleted by browsing. The subsequent redistribution of nutrients into new foliage results in a low carbon:nitrogen ratio and therefore unfavourable conditions for the synthesis of unpalatable secondary metabolites.

The response in deciduous trees appears to be more varied. Several studies

of birch suggest that palatability declines after browsing, but a few examples indicate the opposite. Both *Betula pendula* and *B. pubescens* have been reported to produce shoots with a lower mineral and higher fibre content after damage, and in *B. pendula* the new shoots also have also a lower nitrogen concentration (Danell and Bergström, 1989). In *B. pubescens* the foliage can have lower nitrogen and higher phenolic concentrations for up to 4 years after defoliation (Tuomi *et al.*, 1990), although removal of the apical bud can actually improve the quality of extant leaves on the same shoot (Haukioja *et al.*, 1990).

Several tree species (e.g. sugar maple and birch) have been found to respond quickly (within hours or days) to damage by producing phenols in existing foliage which are often local to the wound (Schultz, 1988; Tuomi *et al.*, 1990). Such responses are often referred to as short-term induced responses and are distinct from delayed induced responses which refer to chemical changes in regrown shoots. Short-term responses are likely to be more effective against pathogens or invertebrates than mammals which inflict damage rapidly and may not return to feed on the plant for a long time, if ever (Karban and Myers, 1989). However these possible interactions between pathogen, insect and mammal feeding on trees appear not to have been investigated.

Mammalian browsing can cause a reversion to the juvenile state and in some species this can result in a marked reduction in palatability (Bryant and Kuropat, 1980). The juvenile twigs of these species have high concentrations of secondary metabolites and are much less palatable than mature twigs from the same plant. In each species, and sometimes each part of the shoot, a different chemical is responsible for reducing palatability. Juvenile twigs of green alder (*Alnus crispa*) for example contain pinosylvins (Clausen *et al.*, 1986), balsam poplar (*Populus balsamifera*) contains salicaldehyde (Reichardt *et al.*, 1990), birch (*Betula resinifera* and *B. pendula*) contain papyferic acid in resin droplets (Rousi *et al.*, 1991) and several willow species contain phenolic glycosides (Palo, 1984; Tahvanainen *et al.*, 1985). In each case the deterrent or toxic effect of the metabolite has been verified in feeding trials. All of these examples are tree species growing in sub-arctic ecosystems which can experience severe damage in winter particularly when hare (*Lepus americana* or *L. timidus*) populations are highest. Juvenile twigs are most unpalatable in species and varieties which originate from areas where populations are most cyclic (Alaska and Siberia) and relatively palatable where there are no hares or where they are acyclic (Bryant *et al.*, 1989; Rousi *et al.*, 1991). This association between palatability and hare populations, together with the fact that specific chemicals have a deterrent effect whereas similar compounds found in the plant do not deter feeding has been proposed as strong evidence for the evolution of defences against herbivores (Bryant *et al.*, 1992).

The production of secondary metabolites both before and in response to browsing appears to be very dependent on nutrient availability. Bryant *et al.*

(1983) proposed that carbon-based compounds, such as terpenes and phenols should be produced where growth was restricted by a relative shortage of nitrogen to carbon and would serve to protect the plant against further nitrogen loss. Where carbon:nitrogen ratio is low, nitrogen-based toxic compounds (alkaloids) may be produced. There is evidence both for and against this theory. Fertilization has been found to reduce the concentration of secondary metabolites and increase palatability in birch in some experiments (Bryant *et al.*, 1987; Tuomi *et al.*, 1990), but not others (Rousi *et al.*, 1991). Furthermore, it is clear that the synthesis of secondary metabolites is not yet well enough understood. Some compounds that reduce palatability appear to be intermediate metabolites (e.g. the phenolic glycosides) and their role in restricting herbivory may therefore be limited (Reichardt *et al.*, 1991).

The evidence shows that trees may respond to browsing by either increasing or decreasing palatability and that both of these responses could even occur on the same tree (Haukioja *et al.*, 1990). A reduction in palatability may be a fortuitous consequence of nutrient loss and redistribution after damage and does not necessarily imply a defence, although Haukioja *et al.* (1991) argue that such a trait could be favoured by natural selection if it reduced mortality due to browsing. The most convincing examples of active resistance to mammalian herbivores are on trees growing in severe, sub-arctic conditions. In temperate regions, especially where nutrients are not limiting, compensation may be more important than defence.

THE IMPACT OF BROWSING 2. THE EFFECT ON TREE REGENERATION AND GROUND VEGETATION

Impact on understorey vegetation

Vertebrate herbivores have long been recognized as agents of vegetation change (Crawley, 1989). There are however relatively few studies which have looked at their impact on woodland understorey vegetation and most of these have concentrated on the impact of deer. Voles and rabbits can also influence the composition of woodland plant communities (Charles, 1956; Sumption and Flowerdew, 1985; Bergeron and Jodoin, 1989).

Deer browsing can reduce the biomass of shrubs and herbaceous plants (Bobek *et al.*, 1979) as well as bring about changes in species composition. In general, trees and preferred browse plants like bramble (*Rubus* sp.) and ivy (*Hedera* sp.) decrease under the influence of deer browsing and grasses, sedges or browse resistant plants like ferns increase (Table 1; Picard, 1976; Horsley and Marquis, 1984; Peterken and Jones, 1989). Picard (1976) found that red (*Cervus elaphus*) and roe (*Capreolus capreolus*) deer appeared to have less effect on the vegetation at a lowland site in eastern France than at an upland site where some minor species disappeared altogether. The domination by bracken (*Pteridium aquilinum*) or grasses may also make tree regeneration more difficult (Picard, 1976; Horsley and Marquis, 1984).

TABLE 1: *The response of woodland vegetation to deer at different densities*

Deer species	Density No. km ⁻²	Tree species	Effect	Reference and location
Red deer	2 4 25	SP*	Effects negligible. Survival and growth reduced. Regeneration prevented.	Holloway, 1967 Scotland
Red deer	33–50	SP BI	Tree survival considered unlikely.	Cummins and Miller, 1982 Scotland
Red deer	1.5 [†] 3 4.5 8.5		Change in relative cover of some plant species. Tree and shrub cover reduced. Some tree species lost. Marked reduction in trees, shrubs and herbs. Grass cover increased.	Kraus, 1987 Eifel, Germany
Roe deer	10		Tree survival unaffected.	Holloway, 1967 Scotland
Roe deer	6–8 [†]		Tree survival unaffected.	Stehle, 1986 W. Germany
Roe deer	20		Decrease in ivy (<i>Hedera helix</i>) Increase in moss & butcher's broom <i>Ruscus aculeatus</i>	Cibien <i>et al.</i> , 1988 W. France
Fallow deer	100		Tree survival severely reduced. <i>Rubus</i> and ivy decreased, and grasses and ferns increased.	Putman <i>et al.</i> , 1989 S. England
White-tailed deer	7 15.5 31		Vegetation little affected. Seedling height, tree species diversity and <i>Rubus</i> cover reduced. Fern cover increased. Similar effects, but more marked.	Tilghman, 1989 Pennsylvania, USA
White-tailed deer	8.6		Reduction in tree seedling height and density. Decrease in <i>Rubus</i> and increase in grasses and sedges.	Trumbull <i>et al.</i> , 1989 Pennsylvania, USA

*SP Scots pine; BI Birch.

[†]Densities may be underestimated (Gill, 1990).

Few authors have commented on the permanency of these vegetation changes. Horsley and Marquis (1984) noted that the cover of bramble appeared to be easily reversible, declining under deer pressure but increasing again after fencing. Other changes may be more permanent, for

example the cover of bracken may not decrease again after a reduction in browsing pressure.

It is often thought that deer decrease the species richness of woodland herbaceous vegetation but this has not yet been clearly shown. Where browsing avoids the dominant plants or favours colonization of an aggressive species then deer may cause a reduction in richness (Crawley, 1983), but because deer restrict regeneration of woody plants so effectively, the reverse may occur where palatable trees or shrubs are becoming dominant. Peterken and Jones (1989) noted that fallow deer (*Dama dama*) had a patchy impact and helped to maintain small openings. This effect could contribute to structural diversity. It is however important to obtain information on the vulnerability of rare plant species because these may be adversely affected by deer.

The effect on tree regeneration and species composition

Deer browsing is widely reported to reduce the size and number of tree seedlings (Table 1). Tree survival generally declines with increasing deer density resulting in complete failure of regeneration when numbers are too high (Table 1; Peterken and Tubbs, 1965; Miller and Cummins, 1982).

Deer populations have increased throughout North America and Europe during the twentieth century (Gill, 1990) and many temperate forests are now suffering a loss of browse-sensitive species. Thus silver fir (*Abies alba*) is declining in central European forests (Mayer, 1975; Kammerlander, 1978; Zeltner, 1979; König and Baumann, 1990) and Eastern hemlock (*Tsuga canadensis*), Canadian yew (*Taxus canadensis*) and white cedar (*Thuja occidentalis*) are being depleted by white-tailed deer (*Odocoileus virginianus*) in forests in Wisconsin and Michigan (Beals *et al.*, 1960; Anderson and Loucks, 1979; Frelich and Lorimer, 1985; Alverson *et al.*, 1988; Allison, 1990a and 1990b). Losses of some broadleaved species have also been reported from hardwood forests in Pennsylvania (Marquis, 1974; Marquis and Brenneman, 1981). Frelich and Lorimer (1985) estimated that it would take about 150 years for Eastern hemlock to decline from dominance to rarity under the existing browsing pressure in Michigan. In some cases, deer have been reported to browse the less palatable species more heavily after the most preferred have been depleted (Beals *et al.*, 1960).

Table 1 however also shows that the success of regeneration at a given deer density is very varied; it is not possible without knowing more about the other factors that affect regeneration to identify a density above which it is bound to fail nor one below which it will definitely succeed. Many reports reveal that a simple decline of some tree species is not the only outcome. Dzieciolowski (1980) investigated seedling recruitment in three Polish forests and found that several species were depleted by browsing in every site (aspen, willow and rowan and oak), others were usually

unaffected (beech (*Fagus sylvatica*) and larch) and some appeared to always benefit (alder (*Alnus glutinosa*) and juniper (*Juniperus communis*)). Other studies have also shown that some species benefit from browsing. Beals *et al.* (1960) and Anderson and Loucks (1979) found that sugar maple replaced eastern hemlock and Tilghman (1989) found that black cherry increased with increasing browsing pressure. Kuznezov (1987) reported that broadleaved trees and Norway spruce usually replace Scots pine under the influence of moose browsing in Russia. Seedlings of species that are negatively affected may still continue to recruit and increase in numbers during several years of exposure to browsing (Dzieciolowski, 1980). Because trees as a group are so vulnerable, browsing is likely to reduce tree species diversity, particularly if the pressure is high (Tilghman, 1989), but Dzieciolowski's (1980) results suggest that diversity may occasionally increase.

Several studies show that tree recruitment can be successful if the initial number and density of seedlings is high enough. The average rate of damage by moose has been found to decline with increasing stem density in young birch and Scots pine (Heikkila, 1992) and aspen stands (Martynov, 1982). Barandun (1983) reported that regeneration of Norway spruce in the presence of red and roe deer was possible in small groups with 7000–8000 stems ha⁻¹, because only trees on the edges of the groups were damaged. Riemenschneider (1987) reported success with a similar technique for establishing beech in areas where roe deer occur. The reason for the reduction in damage with increasing tree density has not been investigated but may be because crowding reduces foliage nutrient levels and therefore palatability (Thompson, 1988).

Mechanisms of change

When a species declines in abundance it is usually thought to be because it is preferred by deer rather than being less able to tolerate the damage, although many studies make no attempt to separate these factors. Silver fir however has been found to be both more palatable than Norway spruce (Eiberle and Nigg, 1983) as well as more susceptible to damage (Eiberle, 1975). The fact that several authors have reported that a broadleaved species increases under browsing whereas a conifer decreases suggests that compensation, or changes in palatability may be important aspects of a species' ability to survive and compete under browsing pressure.

Recent studies indicate that regeneration can also be retarded by mechanisms other than diminished growth or survival due to browsing directly. The survival of balsam fir seedlings has been found to be adversely affected by allelopathic plants which are also browse resistant and increase under browsing pressure (Thompson and Mallik, 1989). In Sweden, voles have been reported to attack male dioecious willows in preference to

female (Danell *et al.*, 1985; Elmqvist *et al.*, 1988) and where vole densities are high the population sex ratio becomes strongly female biased (Elmqvist *et al.*, 1988). Flowering and pollination success in Canadian yew (*Taxus canadensis*) has also been found to be reduced by browsing (Allison, 1990a, 1990b).

The increases in abundance of some tree species may occur as a result of release from competition, either from other trees or herbaceous plants. After excluding deer or livestock, regeneration often increases and then declines again when competition from other plants becomes more intense (Pigott, 1983; Welch *et al.*, 1992; Sykes, 1992). Birch, ash (*Fraxinus excelsior*) and Scots pine appear to be very susceptible to weed competition (Linhart and Whelan, 1980; Pigott, 1983; Gong *et al.*, 1991), but oak, having larger seeds, can withstand more competition and can even grow through brambles (Worrell and Nixon, 1991). Grazing animals can facilitate regeneration because they create germination sites by trampling and scraping (Miles and Kinnaird, 1979; Vinther, 1983; Mitchell and Kirby, 1990). In spite of these beneficial effects, fencing has still been found to be necessary to achieve adequate regeneration in native Scottish pinewoods, where the seed supply is very poor (Gong *et al.*, 1991; Sykes, 1992).

THE IMPACT OF BARK STRIPPING

Bark stripping involves the loss of tissues which perform a protective or translocation function. Phloem and outer bark are removed; cambial cells are either removed or exposed and xylem tissue is exposed and possibly scored by teeth. This has a variety of consequences for the tree. Apart from interrupting translocation bark stripping weakens the stem and exposes it to fungal infection and dessication. Indirectly, photosynthesis and respiration may also be affected (Noel, 1970; Ebell, 1971).

The effect on growth

Complete girdling usually kills trees by preventing photosynthesis reaching the roots. Most bark stripping however results only in partial girdling and therefore translocation is not completely interrupted. There are differing views as to whether this affects tree growth or not.

The problems arising from red deer bark stripping on Norway spruce have been reviewed by Roeder (1971) and Roeder and Knigge (1972). They cited several early European studies which reported that growth losses could occur, and if damage was serious these could be as high as 35 per cent. Unfortunately many of these studies were poorly designed, with either inadequate replication or a lack of control for environmental effects and therefore their conclusions can be largely discounted. More recent investigations have failed to reveal any significant effect (Heger *et al.*, 1955;

Krauter, 1964; Záruba and Snajdr, 1966). Other studies have examined the effect on height growth of other European tree species, namely Scots pine (Rijcken, 1965; Lavsund, 1974), Corsican pine (*Pinus nigra*) (Luitjes, 1971) and oak (*Quercus robur*) and ash (Borowski and Van Vuure, 1974), also concluding that growth was largely unaffected.

There are however several reports from North America addressing bark removal by other animals, all of which claim that bark stripping does reduce growth. These studies have included an examination of porcupine (*Erethizon dorsatum*) damage to sugar maple (Krefting *et al.*, 1962) and ponderosa pine (*Pinus ponderosa*) (Storm and Halvorson, 1967), simulated cattle damage to slash pine (Lewis, 1980a), snowshoe hare damage to balsam fir (Lloyd-Smith and Piene, 1981) and snowshoe hare and squirrel (*Tamasciurus hudsonicus*) damage to lodgepole pine (Sullivan and Sullivan, 1986; Sullivan and Vyse, 1987). One additional study examined simulated weevil (*Hylobius warreni*) damage (removal of bark on the root collar) to lodgepole pine (Cerezke, 1974).

Unfortunately some of the more recent studies have also suffered from methodological problems. Animals select stems on the basis of size, nutritional quality or growth rate (see parts 1 and 2) and damaged trees do not therefore constitute a random sample against which growth can be compared with undamaged trees (Strauss, 1988). Some of the claims of growth loss based on studies of natural damage are therefore unconvincing (Sullivan and Sullivan, 1986; Sullivan and Vyse, 1987). Sullivan and Vyse (1987) for example show that squirrels select stems of above average diameter and that some trees maintain higher increment rates even after damage.

Studies based on simulated damage however overcome this problem and show that a growth loss can occur (Cerezke, 1974; Lewis, 1980a). The amount of growth reduction appears to be dependent on the severity of damage (Storm and Halvorson, 1967; Cerezke, 1974; Lewis, 1980a). In the second case, both diameter and height growth were clearly non-linearly related to wound size, becoming most affected at only the most severe levels of damage. Many of the other studies did not report wound sizes; in any case the most significant factor would probably be wound size relative to tree size.

The position of the wound may also be important. Girth increment appears to be most affected immediately beneath the wound (Storm and Halvorson, 1967). Cerezke's (1974) results indicate that radial responses to damage at the root collar can be greater higher up the stem than lower down. Damage in the crown can result in branch and foliage loss, in which case the loss of growth may of course be very severe. Storm and Halvorson's (1967) results show that the effect of bark removal on radial growth is largely temporary, decreasing rapidly two or more years after damage.

There is no clear association between studies reporting a significant effect and the size of tree under investigation. Lewis (1980a) found that growth was affected only on severely damaged (75 per cent circumference girdled) 6-month seedlings, but (Luitjes, 1971) found no effect for either small

(< 150 cm height) or large (> 150 cm height) trees. Some authors (Heger *et al.*, 1955) have suggested that suppressed trees are affected more than dominants, but both Storm and Halvorson (1967) and Cerezke (1974) found a significant response from both dominant and co-dominant trees.

There is not yet sufficient evidence to say how growth loss after stripping differs between tree species, or under conditions of stress such as drought or disease. Although it is difficult to make generalizations from these studies, it appears that bark stripping can reduce growth although the effect will probably be negligible unless a lot of bark is removed. In this event, stem breakage, death or infection are likely to be more serious than growth loss.

The effect on tree survival

The majority of trees appear to survive partial girdling. Cerezke (1974) for example reported 100 per cent survival on trees with as much as 90 per cent of the circumference de-barked. Where death has been reported, it has largely been confined to trees with 66 per cent or more of the stem girdled (Luitjes, 1971; Lewis, 1980a; Miquelle and Van Ballenberghe, 1989). Because smaller stems are more easily girdled than larger stems, death from bark stripping is more common on small trees attacked by small mammals than larger trees stripped by deer.

Death from partial girdling often occurs simply as a result of breakage at the wound. Lodgepole pine appears to be more susceptible to this than most other conifers commonly grown in Britain (Holloway, 1968). The risk of breakage at the wound on any species can of course be aggravated by conditions that apply physical stress, such as high winds or snow (Fruhman and Roeder, 1981).

The effect on timber quality

Bark stripping can result in serious losses due to reductions in timber quality. These arise from the wound itself, stem deformation, breaks in the crown and most importantly, the development of strain and rot.

Although bark wounds gradually heal by callus formation, the wound leaves a fissure under the callus which breaks when the stem is sectioned into planks. The weakness is confined to the wound itself and therefore the timber loss is proportional to the size of the wound and the age of the tree when damaged. Wounds inflicted when the tree is young or old are likely to be the least serious because they are smaller or near the stem periphery respectively.

Stem breakage in the crown is a common consequence of squirrel (*Sciurus* sp.) or edible dormouse (*Glis glis*) damage (White, 1962; Platt and Rowe, 1964), especially if the main stem has been nearly or completely girdled. It can result in side branches assuming dominance, forking, or ultimate suppression of the tree by undamaged neighbours. Bark stripping by red deer can also result in stem deformation, but the only species which appears to be

commonly affected in this way is Scots pine (Soest and Stefels, 1965; Lavsund, 1974), possibly because it is damaged at such an early age that leader dominance is affected (Strandgaard, 1967).

The most important form of timber degrade is usually stain or rot developing from the wound. Staining normally refers to discolouration but not structural deterioration of the wood, but it none the less results in timber devaluation. Rot usually involves structural deterioration by micro-organisms as well as staining.

The majority of studies of stain and rot development have concentrated on spruces, because these appear to be more seriously affected than other timber-producing species. Pines in general produce more resin in the region of the wound than spruces and this helps to limit stain advance (Rijcken, 1965).

Staining is associated with most wounds and usually extends some distance above and below the wound. There are several types of stain which develop for different reasons and vary in intensity, rate of spread and distance away from the wound. Understandably therefore, the amount of variation in stain and rot arising from wounds is considerable and the factors that govern their development are rather complicated.

Stain can develop in stems either as a reaction by the tree to wounding or from micro-organisms colonizing the wood (Kallio, 1973; Gregory, 1986). Reaction stain is usually lighter in coloration than stain directly associated with fungal colonization and may not form a noticeable depreciation in timber quality (Gregory, 1986). Lightly stained wood has been found to have a lower microbial population than heavily stained wood (Gregory, 1984).

The majority of wounds develop rot of some kind, but it may remain local to the wound area. The probability that a tree will develop rot after bark stripping depends on the size of the wound and the amount of damage to the exposed surface (Pawsey and Gladman, 1965; Pawsey and Stankovikova, 1974; Bonnemann, 1979). In Norway spruce, the proportion of stems developing decay has been reported to range from 73 per cent (Bazzigher, 1973) to 99.7 per cent Roeder (1971). If rot does develop, it is usually confined to the wound face rather than extending to the stem interior (Holloway, 1968; Gregory, 1986), although Atta and Hayes (1987) isolated *Stereum sanguinolentum* with increasing frequency from the outside of the stem inwards, whereas the opposite was the case for the other micro-organisms. Lateral development of rot can sometimes be effectively restricted by the tree, for example decay in beech has been found to be confined to a few growth rings (Mercer, 1984) and staining in Norway spruce to be contained within the growth ring formed when bark stripping took place (Roeder, 1971).

There appears to be general agreement that stain and rot in spruces advance with time and can extend well above and below the wound (Roeder and Knigge, 1972; Bazzigher, 1973; Mayer, 1983; Gregory, 1986). Lighter stain extends further than heavy stain or rot, but in Sitka spruce heavy stain

has been reported to develop beyond the wound in only a minority of cases (Gregory, 1986). The extent of stain development has been found to be positively correlated with wound size (Roeder and Knigge, 1972; Löffler, 1975; Bonnemann, 1979; Gregory, 1986; Atta and Hayes, 1987), but light stain shows a better correlation than heavy stain, perhaps reflecting the fact that it is determined more by wounding than fungal activity (Gregory, 1986). The relationship of wound size to stain extent is curvilinear, with larger wounds developing disproportionately more stain (Roeder and Knigge, 1972; Gregory, 1986). In yellow poplar (*Liriodendron tulipifera*) stain development has also been found to be more severe from wounds positioned nearer the ground (Lowerts and Kellison, 1981).

Stain development is sometimes reported to be most rapid after wounding, after which it then slows and may cease altogether (Isomäki and Kallio, 1974; Löffler, 1975). Bonnemann (1979) however found a delay of several months before some fungal species began to advance from the site of infection. Since trees have to be killed to measure stain advance, changes in rate have to be detected by fitting a non-linear response curve taken from a large sample of damaged trees. Most investigators have been unable to do this and consequently simply quote an average rate. These rates are rather variable, ranging from 0.5 cm yr^{-1} to 46 cm yr^{-1} , with higher rates quoted for Norway in contrast to Sitka spruce, and for larger wounds or light rather than heavy stain (Isomäki and Kallio, 1974; Mayer, 1983; Gregory, 1986).

Some investigations have revealed that stain advances more rapidly in faster growing trees (Isomäki and Kallio, 1974; Löffler, 1975; Bonnemann, 1979, Atta and Hayes, 1987) and that fertilization increases the rate of stain extension (Isomäki and Kallio, 1974). This is thought to be either because wider rings provide more favourable conditions for fungal advance or because the sapwood area is greater (Bonnemann, 1979). The rate of wound callusing is also dependent on tree growth rate (Lavsund, 1974; Mercer, 1984) and species (Girompaire, 1990) and may counteract the effect of growth rate on stain advance if the wound heals over more quickly. There is no consensus on the influence of season of wounding. Bonnemann (1979) found February to be the worst month but Sylvestre and Delatour (1990) found higher infection rates after late spring damage to larch. Others report little or no effect (Isomäki and Kallio, 1974; Pawsey and Stankovikova, 1974).

The species of fungi infecting the wound can also affect stain development, because some species move faster than others (Pawsey and Gladman, 1965; Gregory, 1984; Bonnemann, 1979). At least 15 species of fungi as well as bacteria have been isolated from bark wounds inflicted by mammals (Holloway, 1968; Bazzigher, 1973; Gregory, 1984). The most serious is considered to be *S. sanguinolentum*, even though some authors find it relatively uncommon in wounded Norway and Sitka spruce stems (Bazzigher, 1973; Gregory, 1984).

Even after allowing for the effects of wound size, age, tree growth rate or pathogen, many authors report considerable individual or between-site

variation in the extent of stain development (Pawsey and Gladman, 1965; Pawsey and Stankovikova, 1974; Löffler, 1975; Bonnemann, 1979; Gregory, 1986). The reasons for this may be due to differences in spore populations or to genetic differences in the fungus (Pawsey and Gladman, 1965). Interactions may also occur between fungi entering the wound, because some species, once established, inhibit the development of others (Gregory, 1984). In some tree species (e.g. yellow poplar) stain development is under genetic control (Lowerts and Kellison, 1981). There may therefore be opportunities to limit stain development by tree breeding.

DISCUSSION

Mammals can clearly have a major impact on forest trees ranging from the complete destruction of regeneration to varying degrees of growth delay and timber devaluation. In order to manage the problem effectively foresters need to be able to relate an observed impact (which may be on trees as young as seedlings) to the effect the damage will have on the mature stand or ultimate reduction in yield. An adequate knowledge of the long-term consequences of damage is clearly important for effective wildlife management but unfortunately lacking from the literature on wildlife impact.

Some attempts have been made to assess the cost of browsing and bark stripping to timber production. However, the variability in the results serves to underlie the difficulties in accurately assessing the cost. After adjusting for inflation and exchange rates, estimates of the costs of browsing range from £0.73–0.98 ha⁻¹ yr⁻¹ for browsing by moose in Sweden (Jantz, 1982) to £85.23 ha⁻¹ yr⁻¹ for red and roe deer browsing in Germany (Spiedel, 1980). Both of these estimates were intended to represent serious, but not catastrophic damage, but the difference of two orders of magnitude is much greater than that which would be expected from differences in timber production or growth loss. As yet, there appear to be no examples of direct measurements of growth delay or deformation from browsing for anything longer than 22 years after the damage occurred.

The cost of bark stripping is easier to estimate because it occurs later in the rotation and is readily quantifiable (Speidel, 1980). Even this however requires making assumptions about the volume of stain and rate of stain extension which are only partly explained by readily assessable characteristics such as wound size and tree growth rate.

Obtaining long-term data is of course costly and there is likely to be considerable variability between stands in the response to damage. It is likely that models could be applied to predicting the long-term consequences of browsing but effective modelling will require more information on growth rates after damage than presently available.

Although there are distinct differences between tree species, the response to browsing appears to follow a general pattern. The risk of death is high during the first 1 or 2 years after which browsing mainly reduces growth. Light

levels of browsing are likely to be partially or even entirely compensated for by later growth. Heavier browsing is likely to impose an unrecoverable delay and increased risk of stem deformity but growth may be very rapid when release occurs. This suggests that it would be useful to know more about the levels and types of damage that are largely recoverable as distinct from those that inflict mortality or stem deformity. It is also important to know more about the amount of compensation that will occur between trees as the stand closes canopy. Eiberle and Nigg (1987b) showed that it is possible to develop field survey methods that predict mortality and growth loss from the frequency of visible browse marks on a sample of sycamore (*Acer pseudoplatanus*) stems. Studies of this kind could be applied to making damage assessments much more informative.

In spite of a number of anecdotal reports of differences in palatability between planted and naturally regenerated seedlings, there do not appear to be any studies that have directly compared their performance in response to browsing. The reports indicating that the rate of damage declines with increasing seedling density suggest that under certain conditions natural seeding may be more successful and require less protection than planting. Nevertheless, it would still be important to know more about the critical seedling densities required and the appropriate age for respacing.

The fact that many studies of the impact of deer browsing on regeneration show that a broadleaved species often increases and a coniferous species decreases is a little surprising, since broadleaves are usually considered to be more susceptible (see part 1). Although the most palatable species may be sought after first by deer, a seedling's resilience or resistance to subsequent damage may be crucial to survival if the initial attack does not cause death. Although investigations have so far covered only a limited range of species, it appears that many broadleaved species can tolerate more browsing than conifers, either because they can withstand removal of a greater proportion of the current annual growth or because the new foliage is *less* palatable after damage (e.g. birch) rather than *more* palatable (e.g. Scots pine). Chemical changes in twigs and foliage are now known to be an important aspect of the resilience of trees subject to browsing by hares in subarctic regions, but they may be significant at lower latitudes as well. The defensive as well as compensatory responses of British trees to browsing deserves much wider investigation.

There is abundant evidence of genotypic variation in the susceptibility of trees to several mammals, including deer, voles and hares (see parts 1 and 2). For some forms of damage (for example bark stripping by deer) these differences can be associated with morphological characters such as bark thickness, but many differences appear to be based on the concentration of terpenes or phenols. These chemicals are widely reported to deter feeding (see parts 1 and 2); and can vary in concentration between clones or origins (Forrest, 1980) and in some cases genotypic differences in palatability have been directly associated with terpene or resin content (Radwan and Ellis,

1975; Hansson *et al.*, 1986; Danell *et al.*, 1990; Rousi *et al.*, 1991). There is also evidence that browsing resistance is greatest among trees growing in regions subject to severe browsing pressure (Bryant *et al.*, 1989; Rousi *et al.*, 1991). This evidence indicates that breeding for resistance is possible and that trees from regions with a high historical browsing pressure should form the focus of an initial search for resistant varieties (Rousi, 1990).

There are however potential problems with attempting to breed for resistance. Preferences usually decrease when herbivore densities increase, so protection may be lost if numbers cannot be controlled (see part 2). It may also be difficult to find varieties resistant to all mammals and with suitable growth characteristics. However, varieties which are fast-growing and resistant to vole damage have been reported (Rousi, 1990). It may also be possible to select varieties that are less prone to forking or recover quickly after damage. The possibilities for breeding should therefore not be dismissed without an initial assessment of the variability in resistance or tolerance which could form the basis for selecting varieties.

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REFERENCES

- Allison, T. D. 1990a The influence of deer browsing on the reproductive biology of Canada yew (*Taxus canadensis* Marsh) .1. Direct effect on pollen, ovule, and seed production. *Oecologia* **83**, 523–529.
- Allison, T. D. 1990b The influence of deer browsing on the reproductive biology of Canada yew (*Taxus canadensis* Marsh.) .2. Pollen limitation: an indirect effect. *Oecologia* **83**, 530–534.
- Alverson, W. S., Waller, D. M. and Solheim, S. L. 1988 Forests too deer: edge effects in Northern Wisconsin. *Conserv. Biol.* **2**, 348–358.
- Anderson, R. C. and Loucks, O. L. 1979 White-tail deer (*Odocoileus virginianus*) influence on structure and composition of *Tsuga canadensis* forests. *J. Appl. Ecol.* **16**, 855–861.
- Archer, S. and Tieszen, L. L. 1980 Growth and physiological responses of tundra plants to defoliation. *Arc. Alp. Res.* **12**, 531–552.
- Atta, A. H. and Hayes, A. J. 1987 Decay in Norway spruce caused by *Stereum sanguinolentum* Alb. & Schw. ex Fr. developing from extraction wounds. *Forestry* **60**, 101–111.
- Barandun, J. 1983 Afforestation at high altitudes. *Schweiz. Z. Forstwes.* **134**, 431–441.
- Bassman, J. H. and Dickmann, D. I. 1985 Effects of defoliation in the developing leaf zone on young *Populus × euamericana* plants .2. Distribution of 14-C photosynthesate after defoliation. *For. Sci.* **31**, 358–366.
- Bazzigher, G. 1973 Wound rot in spruce stands after bark stripping. *Eur. J. For. Pathol.* **3**, 71–82.
- Beals, E. W., Cottam, G. and Vogl, R. J. 1960 Influence of deer on vegetation of the Apostle islands, Wisconsin. *J. Wildl. Manage.* **24**, 68–80.

- Bergeron, J. and Jodoin, L. 1989 Patterns of resource use, food quality and health status of voles (*Microtus pennsylvanicus*) trapped from fluctuating populations. *Oecologia* **79**, 306–314.
- Bergerud, A. T. and Manuel, F. 1968 Moose damage to balsam fir – white birch forests in central Newfoundland. *J. Wildl. Manage.* **32**, 729–746.
- 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.
- Bobek, B., Perzanowski, K., Siwanowicz, J. and Zielinski, J. 1979 Deer pressure on forage in a deciduous forest. *Oikos* **32**, 373–380.
- Bonnemann, I. 1979 Investigations into the occurrence and prevention of wound decay in Norway spruce. *Doctoral Thesis*. University of Gottingen.
- Borowski, S. and Van Vuure, T. 1974 Effect of bark peeling on the height increment of oak and ash. *Sylvan* **2**, 30–36.
- Britton, R. J. 1988 Physiological effects of natural and artificial defoliation on the growth of young crops of Lodgepole pine. *Forestry* **61**, 165–175.
- Bryant, J. P., Chapin, F. S. III and Klein, D. R. 1983 Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos* **40**, 357–368.
- Bryant, J. P., Chapin, F. S. III, Reichardt, P. B. and Clausen, T. P. 1987 Response of winter chemical defense in Alaska paper birch and green alder to manipulation of plant carbon/nutrient balance. *Oecologia* **72**, 510–514.
- Bryant, J. P. and Kuropat, P. J. 1980 Selection of winter forage by subarctic browsing vertebrates: The role of plant chemistry. *Annu. Rev. Ecol. Syst.* **11**, 261–285.
- Bryant, J. P., Reichardt, P. B. and Clausen, T. P. 1992 Chemically mediated interactions between woody plants and browsing mammals. *J. Range Manage* **45**, 18–24.
- Bryant, J. P., Tahvanainen, J., Sulkinoja, M., Julkunttiitto, R., Reichardt, P. and Green, T. 1989 Biogeographic evidence for the evolution of chemical defense by boreal birch and willow against mammalian browsing. *Am. Nat.* **134**, 20–34.
- Bryant, J. P., Tuomi, J. and Niemala, P. 1988 Environmental constraint of constitutive and long-term inducible defenses in woody plants. In *Chemical Mediation of Coevolution*. K. C. Spencer (ed.). American Institute of Biological Sciences, Academic Press, New York, 367–389.
- Carlson, L. W. 1977 The effect of defoliation on conifer seedling root initiation. *Bi-monthly Research Notes* **33**, 1.
- Carter, C. I. 1977 Impact of green spruce aphid on growth. *Forestry Commission Research and Development Paper No. 116*. HMSO, London. 8 pp.
- Cerezke, H. F. 1974 Effects of partial girdling on growth in Lodgepole pine with application to damage by the weevil *Hylobius warreni* wood. *Can. J. For. Res.* **4**, 312–320.
- Charles W. N. 1956 The effects of a vole plague in the Carron Valley, Stirlingshire. *Scott. For.* **10**, 201–204.
- Cibien, C., Boutin, J. M. and Maizeret, C. 1988 Impact of roe deer (*Capreolus capreolus*) on vegetation in relation to population density and type of woodland. *Z. Jagdwiss.* **34**, 232–241.
- Clausen, T. P., Reichardt, P. B. and Bryant, J. P. 1986 Pinosylvins and pinosylvins methyl ether as feeding deterrents in green alder. *J. Chem. Ecol.* **12**, 2117–2131.
- Crawley, M. J. 1983 *Herbivory – the dynamics of plant–animal interactions*. Studies in Ecology 10. Blackwells, Oxford.
- Crawley, M. J. 1989 The relative importance of vertebrate and invertebrate herbivores in plant population dynamics. *Insect–Plant Interactions*. E. A. Bernays (ed.). CRC press, Boca Raton, Florida, 45–71.
- Crouch, G. L. 1966 Effects of simulated deer browsing on Douglas fir seedlings. *J. For.* **64**, 322–326.

- Cummins, R. P. and Miller, G. R. 1982 Damage by red deer (*Cervus elaphus*) enclosed in planted woodland. *Scott. For.* **36**, 1–8.
- Danell, K. and Bergström, R. 1989 Winter browsing by moose on two birch species: impact on food resources. *Oikos* **55**, 11–18.
- Danell, K., Elmqvist, T., Ericson, L. and Salomonson, A. 1985 Sexuality in willows and preference by bark-eating voles: defence or not? *Oikos* **44**, 82–90.
- Danell, K., Gref, R. and Yazdani, R. 1990 Effects of mono and diterpenes in Scots pine needles on moose browsing. *Scand. J. For. Res.* **5**, 535–539.
- Dimock, E. J. 1970 Ten year height growth of Douglas fir damaged by hare and deer. *J. For.* **68**, 285–288.
- Dzięciolowski, R. 1980 Impact of deer browsing upon forest regeneration and undergrowth. *Ekol. Pol.* **28**, 583–599.
- Ebell, L. F. 1971 Girdling: its effect on carbohydrate status and on reproductive bud and cone development of Douglas fir. *Can. J. Bot.* **49**, 453–466.
- Eiberle, K. 1975 Results of a simulation of game damage by cutting the shoots. *Schweiz. Z. Forstwes.* **126**, 821–839.
- Eiberle, K. 1978 The consequential effects of simulated deer browsing damage on the development of young forest trees. *Schweiz. Z. Forstwes.* **129**, 757–768.
- Eiberle, K. 1980 Evaluating silviculturally acceptable browsing rates. *Schweiz. Z. Forstwes.* **131**, 311–326.
- Eiberle, K. and Nigg, H. 1983 Consequences of browsing damage to Norway spruce and silver fir at montane sites. *Schweiz. Z. Forstwes.* **134**, 361–372.
- Eiberle, K. and Nigg, H. 1987a Basis for assessing game browsing in montane forests. *Schweiz. Z. Forstwes.* **138**, 747–785.
- Eiberle, K. and Nigg, H. 1987b Criteria for permissible browse impact on sycamore maple (*Acer pseudoplatanus*) in mountain forests. *Experimentia* **43**, 127–133.
- Elmqvist, T., Ericson, L., Danell, K. and Salomonson, A. 1988 Latitudinal sex ratio variation in willows, *Salix* spp., and gradients in vole herbivory. *Oikos* **51**, 259–266.
- Ericsson, A., Hellqvist, C., Langstrom, B., Larsson, S. and 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.
- Ericsson, A., Larsson, S. and Tenow, O. 1980 Effects of early and late season defoliation on growth and carbohydrate dynamics in Scots pine. *J. Appl. Ecol.* **17**, 747–769.
- Forrest, G. I. 1980 Variation in monoterpene composition of the shoot cortical oleoresin within and between trees of *Pinus contorta*. *Biochem. Syst. Ecol.* **8**, 337–341.
- Frelich, L. E. and Lorimer, C. G. 1985 Current and predicted long-term effects of deer browsing in hemlock forests in Michigan, USA. *Biol. Conserv.* **34**, 99–120.
- Fruhmann, M. and Roeder, A. 1981 Increased risk of snow breakage in Norway spruce stands caused by red deer bark-stripping damage. *Allg. Forstzeitschr.* **21**, 528–529.
- Furuno, T. and Yamazaki, T. 1973 Effects of artificial deprival of shoots on stem upon the growth of some Pine species. *Bull. Kyoto Univ. For.* **45**, 9–26.
- Gill, R. M. A. 1990 Monitoring the status of European and North American cervids. *GEMS Information Series* No. 8. Global Environment Monitoring System, United Nations Environment Programme, Nairobi, Kenya. 277 pp.
- Gill, R. M. A. 1992a A review of damage by mammals in north temperate forests: 1. Deer. *Forestry* **65**, 145–169.
- Gill, R. M. A. 1992b A review of damage by mammals in north temperate forests: 2. Small mammals. *Forestry* **65**, 281–308.
- Girompaire, L. 1990 *Assessment of the Consequences of Bark Stripping by Red Deer in the Alsatian Vosges*. CEMAGREF, Nogent sur Vernisson, France. 102 pp.

- Gong, Y. L., Swaine, M. D. and Miller, H. D. 1991 Effects of fencing and ground preparation in natural regeneration Glen Tanar, Aberdeenshire. *Forestry* **64**, 157–168.
- Gregory, S. C. 1984 Micro-organisms isolated from wounded stems of *Picea sitchensis*. *Trans. Br. Mycol. Soc.* **83**, 683–686.
- Gregory, S. C. 1986 The development of stain in wounded Sitka spruce stems. *Forestry* **59**, 199–208.
- Hansson, L. 1984 Regeneration capacity of *Pinus contorta* seedlings after vole attacks. *Sver. Skogsvardsforb. Tidskr.* **6**, 13–16.
- Hansson, L., Gref, R., Lundgren, L. and Theander, O. 1986 Susceptibility to vole attacks due to bark phenols and terpenes in *Pinus contorta* provenances introduced into Sweden. *J. Chem. Ecol.* **12**, 1569–1578.
- Harper, J. L. 1989 The value of a leaf. *Oecologia* **80**, 53–58.
- Hartwell, H. D. 1973 A comparison of large and small Douglas-fir nursery stock outplanted in potential wildlife damage areas. *DNR Notes* **6**, Department of Natural Resources, State of Washington.
- Hartwell, H. D. and Johnson, L. E. 1983 Survival and height of large and small Douglas fir seedlings in relation to animal damage six years after planting. *DNR Notes* **19**, Department of Natural Resources, State of Washington.
- Haukioja, E., Ruokomäki, K., Senn, J., Suomela, J. and Walls, M. 1990 Consequences of herbivory in the mountain birch (*Betula pubescens* ssp. *tortuosa*) – importance of the functional organization of the tree. *Oecologia* **82**, 238–247.
- Haukioja, E., Ruohomäki, K., Suomela, J. and Vuorisalo, T. 1991 Nutritional quality as a defense against herbivores. *For. Ecol. Manage.* **39**, 237–245.
- Heger, A., Kurth, H. and Fassel, B. 1955 A report on the problem of dealing with damaged spruce stands. *Arch. Forstwes.* **4**, 309–362.
- Heikkilä, R. 1992 Moose browsing in a Scots pine plantation mixed with deciduous tree species. *Acta For. Fenn.* **224**, 1–13.
- Hilton, G. M., Packham, J. R. and Willis, A. J. 1987 Effects of experimental defoliation on a population of pedunculate oak (*Quercus robur* L.). *New Phytol.* **107**, 603–612.
- Holloway, C. W. 1967 The effect of red deer and other animals on naturally regenerated Scots pine. *PhD Thesis*. University of Aberdeen.
- Holloway, C. W. 1968 *A survey of Bark Damage by Deer in Keillour Forest, Perthshire*. Forestry Commission, Unpublished Report.
- Holopainen, J. K. 1990 The relationship between multiple leaders and mechanical and frost damage to the apical meristem of Scots pine seedlings. *Can. J. For. Res.* **20**, 280–284.
- Horsley, S. B. and Marquis, D. A. 1984 Interference by weeds and deer with Allegheny hardwood reproduction. *Can. J. For. Res.* **13**, 61–69.
- Isomäki, A. and Kallio, T. 1974 Consequences of injury caused by timber harvesting machines on the growth and decay of spruce (*Picea abies* (L.) Karst.). *Acta For. Fenn.* **136**, 1–25.
- Jantz, K. 1982 What does elk damage cost? *Sver. Skogsvardsforb. Tidskr.* **4**, 41–42.
- Kallio, T. 1973 *Peniophora gigantea* (Fr) Massee and wounded spruce (*Picea abies* L. Karst.) *Acta For. Fenn.* **133**, 1–28.
- Kammerlander, H. 1978 Structure and regeneration of 'Forets Jardinees' in Kufstein (Tirol) and their vulnerability to browsing. *Schweiz. Zeitschr. Forstwes.* **129**, 711–726.
- Kampmann, H. 1983 Investigations on the effects of gnawing side shoots by roe deer on the growth of spruce trees. *Z. Jagdwiss.* **29**, 235–243.
- Karban, R. and Myers, J. H. 1989 Induced plant responses to herbivory. *Annu. Rev. Ecol. Syst.* **20**, 331–348.

- Kays, J. S. and Canham, C. D. 1991 Effects of time and frequency of cutting on hardwood root reserves and sprout growth. *For. Sci.* **37**, 524–539.
- Kindschy, R. R. 1989 Regrowth of willow following simulated beaver cutting. *Wildl. Soc. Bull.* **17**, 290–294.
- König, E. and Baumann, B. 1990 The influence of roe deer browse on the natural regeneration in mixed-conifer stands. *Allg. Forst Jagdztg.* **161**, 170–176.
- Kozlowski, T. T., Kramer, P. J. and Pallardy, S. G. 1991 *The Physiological Ecology of Woody Plants*. Academic Press, London.
- Kraus, P. 1987 The use of vegetation by red deer as an indicator of their population density. *Z. Jagdwiss.* **33**, 42–59.
- Krauter, G. 1964 The ways of determining diameters and diameter increments of spruce peeled by red deer. *Archiv. Forstwes.* **13**, 363–381.
- Krefting, L. W. and Stoeckeler, J. H. 1953 Effect of simulated snowshoe hare and deer damage on planted conifers in the Lake States. *J. Wildl. Manage.* **17**, 487–494.
- Krefting, L. W., Stoeckeler, J. H., Bradle, B. J. and Fitzwater, W. D. 1962 Porcupine–timber relationships in the Lake States. *J. For.* **60**, 325–330.
- Kulman, H. M. 1971 Effects of insect defoliation on growth and mortality of trees. *Annu. Rev. Entomol.* **16**, 289–329.
- Kuznetsov, G. V. 1987 Habitats, movements and interactions of moose with forest vegetation in the USSR. *Proceedings 2nd International Moose Symposium*. 1 *Viltrevy*, Supplement 1, Stockholm. 201–212.
- Kuznetsov, G. V. and Lozinov, G. L. 1983 Experimental removal of plant mass to study the effect of ungulates on woody vegetation. *Ekologiya* **2**, 34–38.
- Lav Sund, S. 1974 Damage to Scots pine (*Pinus sylvestris* L.) from red deer (*Cervus elaphus* L.). *Inst. For. Zool. Res. Notes* **15**, 1–56.
- Lav Sund, S. 1987 Moose relationships to forestry in Finland, Norway and Sweden. *Proceedings of the 2nd International Moose Symposium*. 1 *Viltrevy*, Supplement 1, Stockholm. 229–246.
- Lewis, C. 1980a Simulated cattle injury to planted slash pine: girdling. *J. Range Manage.* **33**, 337–340.
- Lewis, C. 1980b Simulated cattle injury to planted slash pine: defoliation. *J. Range Manage.* **33**, 345–348.
- Linhart, Y. B. and Whelan, R. J. 1980 Woodland regeneration in relation to grazing and fencing in Coed Gorswen, North Wales. *J. Appl. Ecol.* **17**, 827–840.
- Lloyd-Smith, J. and Piene, H. 1981 Snowshoe hare girdling of balsam fir on the Cape Breton Highlands. *Maritime Forest Research Centre, Information Report M-X-124*. Canadian Forestry Service.
- Löffler, H. 1975 The spreading of wound rot in Norway spruce. *Forstwiss. Centralbl.* **94**, 175–183.
- Lowerts, G. A. and Kellison, R. C. 1981 Genetically controlled resistance to discoloration and decay in wounded trees in Yellow poplar. *Silvae Genet.* **30**, 98–101.
- Löyttyniemi, K. 1983 Recovery of young Scots pines from stem breakage. *Folia For.* **560**, 11 pp.
- Löyttyniemi, K. 1985 On repeated browsing of Scots pine saplings by moose (*Alces alces*). *Silva Fenn.* **19**, 387–391.
- Luitjes, J. 1971 The effect of barking by red deer on height growth and mortality of Corsican pine. *Ned. Bosbouw Tijdschr.* **43**, 112–118.
- Maizeret, C. and Ballon, P. 1990 Analysis of causal factors behind cervid damage on the cluster pine in the landes of Gascony. *Gibier Faune Sauvage* **7**, 275–291.
- Marquis, D. A. 1974 The impact of deer browsing on allegheny hardwood regeneration. *Research Paper NE-308*. Northeastern Forest Research Station, USDA Forest Service.

- Marquis, D. A. and Brenneman, R. 1981 The impact of deer on forest vegetation in Pennsylvania. *General Technical Report NE-65*. Northeastern Forest Research Station, USDA Forest Service.
- Martynov, E. 1982 Effect of elk on the formation of young *Populus tremula* stands. *Lesovodstvo, Lesnye Kul'tury i Pochvovedenie* **11**, 34–45.
- Mayer, H. 1975 The effect of ungulate game on the regeneration and conservation of natural forest reserves. *Forstwiss. Centralbl.* **94**, 209–224.
- Mayer, H. 1983 Short and long-term effects of severe bark-stripping damage on Norway spruce. *Allg. Forstztg.* **94**, 52–53.
- Mercer, P. C. 1984 The effect on beech of bark-stripping by grey squirrels. *Forestry* **57**, 199–203.
- Miles, J. and Kinnaird, J. W. 1979 Grazing: with particular reference to birch, juniper and Scots pine in the Scottish highlands. *Scott. For.* **34**, 280–289.
- Miller, G. R. and Cummins, R. P. 1982 Regeneration of Scots pine (*Pinus sylvestris*) at a natural tree-line in the Cairngorm mountains, Scotland. *Holarct. Ecol.* **5**, 27–34.
- Miller, G. R., Kinnaird, J. W. and Cummins, R. P. 1982 Liability of saplings to browsing on a red deer range in the Scottish Highlands. *J. Appl. Ecol.* **19**, 941–951.
- Miquelle, D. G. and Van Ballenberghe, V. 1989 Impact of bark stripping by moose on aspen-spruce communities. *J. Wildl. Manage* **53**, 577–586.
- Mitchell, F. and Kirby, K. 1990 The impact of large herbivores on the conservation of semi-natural woods in the British uplands. *Forestry* **63**, 333–353.
- Mitscherlich, G. and Weise, U. 1982 Growth restriction (simulated browsing) trials with spruce in Abtsgmund and Crailsheim. *Allgemeine Forst Jagdztg* **153**, 97–104.
- Noel, A. 1970 The girdled tree. *Bot. Rev.* **36**, 162–195.
- Palo, R. T. 1984 Distribution of birch (*Betula* spp.), willow (*Salix* spp.) and poplar (*Populus* spp.) secondary metabolites and their potential role as chemical defense against herbivores. *J. Chem. Ecol.* **10**, 499–521.
- Pawsey, R. G. and Gladman, R. J. 1965 Decay in standing conifers developing from extraction damage. *Forestry Commission Forest Record* No. **54**. Forestry Commission, Edinburgh.
- Pawsey, R. G. and Stankovikova, L. 1974 Studies of extraction damage decay in crops of *Picea abies* in southern England: II The development of *stereum sanguinolentum* following experimental wounding and inoculation. *Eur. J. For. Pathol.* **4**, 203–214.
- Peterken, G. F. and Jones, E. W. 1989 Forty years of change in Lady Park Wood: the young-growth stands. *J. Ecol.* **77**, 401–429.
- Peterken, G. F. and Tubbs, C. R. 1965 Woodland regeneration in the New Forest, Hampshire, since 1650. *J. Appl. Ecol.* **2**, 159–170.
- Picard, J. 1976 Feeding preferences of deer and their consequences: first conclusions from two years' experimentation. *Rev. For. Fr.* **28**, 106–114.
- Piene, H. 1989 Spruce budworm defoliation and growth loss in young balsam fir – recovery of growth in spaced stands. *Can. J. For. Res.* **19**, 1616–1624.
- Piene, H. and Little, C. H. A. 1990 Spruce budworm defoliation and growth loss in young balsam fir – artificial defoliation of potted trees. *Can. J. For. Res.* **20**, 902–909.
- Pigott, C. D. 1983 Regeneration of oak-birch woodland following exclusion of sheep. *J. Ecol.* **71**, 629–646.
- Platt, F. B. W. and Rowe, J. J. 1964 Damage by the edible dormouse (*Glis glis* L.) at Wendover Forest (Chilterns). *Q. J. For.* **58**, 228–233.
- Polley, H. W. and Detling, J. K. 1989 Defoliation, nitrogen and competition: effects on plant growth and nitrogen nutrition. *Ecology* **70**, 721–727.
- Putman, R. J., Edwards, P. J., Mann, J. E. E., Howe, R. C. and Hill, S. D. 1989 Vegetational and faunal change in an area of heavily grazed woodland following relief from grazing. *Biological Conservation* **47**, 13–32.

- Radwan, M. and Ellis, W. 1975 Clonal variation in monoterpene hydrocarbons of vapor of Douglas-fir foliage. *Forest Science* **21**, 63–67.
- Reichardt, P. B., Bryant, J. P., Mattes, B. R., Clausen, T. P., Chapin, F. S. and Meyer, M. 1990 Winter chemical defense of Alaskan balsam poplar against snowshoe hares. *J. Chem. Ecol.* **16**, 1941–1959.
- Reichardt, P. B., Chapin III, F. S., Bryant, J. P., Mattes, B. R. and Clausen, T. P. 1991 Carbon/nutrient balance as a predictor of plant defense in Alaskan balsam poplar: potential importance of metabolite turnover. *Oecologia* **88**, 401–406.
- Riemenschneider, K. 1987 Planting beech saplings replaces roe deer fences. *Allg. Forstzeitschr.* **19**, 492.
- Rijcken, P. H. 1965 Bark-stripping damage to Scots pine by red deer. *Ned. Boschbouw Tijdschr.* **37**, 32–65.
- Roeder, A. 1971 Surprising experimental results of the effects of red deer peeling damage to spruce. *Allg. Forstzeitschr.* **26**, 907–909.
- Roeder, A. and Knigge, W. 1972 Is red deer peeling damage really so serious? *Forstarchiv* **43**, 109–114.
- Rousi, M. 1990 Breeding forest trees for resistance to mammalian herbivores – a study based on European white birch. *Acta For. Fenn.* **210**, 1–20.
- Rousi, M., Tahvanainen, J. and Uotila, I. 1991 A mechanism of resistance to hare browsing in winter-dormant European white birch (*Betula pendula*). *Am. Nat.* **137**, 64–82.
- Roy, D. F. 1960 Deer browsing and Douglas fir seedling growth in northwestern California. *J. For.* **58**, 518–522.
- Schultz, J. 1988 Plant responses induced by herbivores. *Trends in Ecology and Evolution* **3**, 45–49.
- Shaw, M. W. 1974 The reproductive characteristics of oak. *The British Oak: Its History and Natural History*. M. G. Morris and F. H. Perring (eds). Conference Report 14. The Botanical Society of the British Isles, Classey, Farringdon, Berks.
- Soest, J. and Stefels, C. J. 1965 Some notes on bark injuries by red deer to trees. *Ned. Boschbouw Tijdschr.* **37**, 266–273.
- Speidel, G. 1980 Methods of evaluating the economic consequences of game damage in the forest, and ways of regulating it. *Forstwiss. Centralbl.* **99**, 76–85.
- Staines, B. W. and Welch, D. 1984 Habitat selection and impact of red deer and roe deer in a Sitka spruce plantation. *Proc. R. Soc. Edinb.* **82**, 303–319.
- Stehle, K. 1986 Silviculture and roe deer: a successful synthesis on a private estate. *Allg. Forstzeitschr.* **49**, 1224–1227.
- Storm, G. and Halvorson, C. 1967 Effect of injury by porcupines on radial growth of Ponderosa pine. *J. For.* **65**, 740–743.
- Stout, S. 1986 22-year growth of four planted hardwoods. *Northern J. Appl. For.* **3**, 69–72.
- Strandgaard, H. 1967 A study of the relationship of red deer to the modern, cultivated landscape of Denmark. *Dansk Vildt Undersøgelser* **13**, 20–49.
- Strauss, S. Y. 1988 Determining the effects of herbivory using naturally damaged plants. *Ecology* **69**, 1628–1630.
- Sullivan, T. P. and Sullivan, D. S. 1986 Impact of feeding damage by snowshoe hares on growth rates of juvenile Lodgepole pine in central British Columbia. *Can. J. For. Res.* **16**, 1145–1149.
- Sullivan, T. P. and Vyse, A. 1987 Impact of red squirrel feeding damage on spaced stands of Lodgepole pine in the Cariboo region of British Columbia. *Can. J. For. Res.* **17**, 666–674.
- Sumption, K. J. and Flowerdew, J. R. 1985 The ecological effects of the decline in rabbits (*Oryctolagus cuniculus* L.) due to myxomatosis. *Mammal Rev.* **15**, 151–186.
- Sykes, J. M. 1992 Caledonian pinewood regeneration: progress after sixteen years of enclosure at Coile Coire Chuilc, Perthshire. *Arboric. J.* **16**, 61–67.

- Sylvestre, G. and Delatour, C. 1990 Wound susceptibility of *Larix decidua* to *Lachnellula willkommii* (Hartig). *Ann. Sci. For.* **47**, 57–66.
- Tahvanainen, J., Helle, E., Julkunen-Tiito, R. and Lavola, A. 1985 Phenolic compounds of willow bark as deterrents against feeding by mountain hare. *Oecologia* **65**, 319–323.
- Thompson, I. D. 1988 Moose damage to pre-commercially thinned balsam fir stands in Newfoundland. *Alces* **24**, 56–61.
- Thompson, I. D. and Mallik, A. U. 1989 Moose browsing and allelopathic effects of *Kalmia augustifolia* on Balsam fir regeneration in central Newfoundland. *Can. J. For. Res.* **19**, 524–526.
- Tilghman, N. G. 1989 Impacts of white-tailed deer on forest regeneration in Northwestern Pennsylvania. *J. Wildl. Manage* **53**, 524–532.
- Trumbull, V. L., Zielinski, E. J. and Aharrah, E. C. 1989 The impact of deer browsing on the Allegheny forest type. *Northern J. Appl. For.* **6**, 162–165.
- Tsiouvaras, C. N. 1988 Long-term effects on production and vigor of kermes oak (*Quercus coccifera*). *For. Ecol. Manage* **24**, 159–166.
- Tuomi, J., Niemela, P. and Siren, S. 1990 The panglossian paradigm and delayed inducible accumulation of foliar phenolics in mountain birch. *Oikos* **59**, 399–410.
- Vinther, E. 1983 Invasion of *Alnus glutinosa* (L.) Gaertn. in a former grazed meadow in relation to different grazing intensities. *Biol. Conserv.* **25**, 75–89.
- Welch, D., Staines, B., Scott, D. and French, D. 1992 Leader browsing by red and roe deer on young sitka spruce trees in western Scotland .2. Effects on growth in tree form. *Forestry* **65**, 309–330.
- White, J. 1962 Damage by red squirrel to larch in Perthshire. *Scott. For.* **16**, 59–60.
- Worrell, R. and Nixon, C. J. 1991 Factors affecting the natural regeneration of oak in upland Britain – a literature review. *Forestry Commission Occasional Paper* No. **31**, Forestry Commission Edinburgh 1–28.
- Zaruba, C. and Snadjr, J. 1966 Effect of bark-scaling by red deer on timber production. *Lesnický Casopis* **12**, 81–98.
- Zeltner, J. 1979 Impoverishment of tree species mixtures as a result of roe deer populations. *Schweiz. Z. Forstwes.* **130**, 81–84.

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