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Browsing by deer on naturally regenerating Scots pine (*Pinus sylvestris* L.) and its effects on sapling growth

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Abstract

Browsing by deer has been identified as an important factor in preventing the regeneration of Scots pine (*Pinus sylvestris*) woodland. In this 4-year study, we monitored use by red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) and the incidence and severity of browsing to individual saplings across a range of Caledonian pinewood sites in the Highlands of Scotland and related sapling growth to browsing history and site characteristics.

Browsing incidence during winter increased with use (as indexed by dung counts) by red deer, but not roe deer, and increased with sapling height and the apparency of the sapling. The form of these relationships was influenced by the characteristics of the ground vegetation. In contrast, browsing during summer increased with use by roe deer, but not red deer, and was most frequent on saplings of around 1 m tall. In both winter and summer, saplings showing a history of previous browsing were more likely to be browsed, than saplings of the same height with little or no browsing history.

The length of the leading shoot varied with aspect, soil type and the sapling's height. Annual variation in shoot length was considerably greater than variation between sites. Saplings with a history of previous browsing showed some degree of compensatory growth, with an increased leader length, but decreased basal diameter increment. The severity of browsing had a significant effect on leader length, but much less of an effect than browsing to the leader itself. The severity of browsing had very little effect on basal diameter increment.

This study demonstrates the complexity of factors influencing the suppression of natural regeneration by deer, and we recommend combining further field studies with simulation modelling to allow predictions to be made of the conditions under which regeneration is likely to be successful in the presence of deer.

Keywords: Browsing; *Capreolus capreolus*; *Cervus elaphus*; Natural regeneration; *Pinus sylvestris*; Sapling growth

1. Introduction

Caledonian pine forests may once have covered more than 1.5 million hectares of the Highlands of Scotland (O'Sullivan, 1977), but the present area of native pinewood is now thought to be no more than about 16,000 ha, with natural regeneration often being scarce (Callander, 1995). Heavy browsing by high numbers of red deer (*Cervus elaphus* L.) has been identified as an important factor in preventing regeneration of woodlands in general (Gill, 1992) and of many of Scotland's native pinewoods in particular (Staines, 1995; Staines et al., 1995). Exclusion of deer by fencing has led to prolific regeneration in some

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areas, but many such enclosures are small, because fencing is expensive to erect and maintain. An enclosed wood lacking large herbivores will also develop a different vegetation structure from an open wood grazed by its natural herbivores. Furthermore, fencing has been shown to be a major cause of mortality of two threatened woodland grouse species, the capercaillie (*Tetrao urogallus* L.) and black grouse (*T. tetrix* L.) (Catt et al., 1994). Reducing deer numbers to enable pinewoods to regenerate without the need for fencing is therefore the preferred management option. Ideally, land managers would like to know the density of deer that a site can support whilst permitting natural regeneration to occur. However, the relationships between the density of deer and browsing rates, and the impacts of other features of the woodland habitat on those relationships, remain to be clearly understood (Putman, 1996).

Many factors influence the natural regeneration of Scots pine (*Pinus sylvestris* L.), including soil type, ground vegetation type and cover (McVean, 1963; French et al., 1997), distance to seed source (Scott et al., 2000), availability of germination niches (Miles and Kinnaird, 1979; Edwards, 1981; Low, 1988) and canopy cover (Vickers and Palmer, 2000). Growth rates of naturally regenerating Scots pine are characteristically low: mean height increments of 7.5 cm per year (Beaumont et al., 1995) and 7 cm over a 2-year period (Scott et al., 2000) have been recorded, with the increment being less for browsed saplings. Established Scots pine saplings remain vulnerable to browsing until the leading shoot is out of reach of red deer at roughly 2 m tall, and browsing incidence can be high, e.g. up to 72% recorded on Scots pine and associated broad-leaved saplings by Beaumont et al. (1995). Clearly if the leading shoot is browsed, then the time taken for a sapling to reach that height is increased, but browsing of lateral shoots might also reduce height increments owing to increased stress.

Thus the likelihood of successful natural regeneration depends on the frequency and severity of browsing to individual saplings, both of which are expected to increase with use by deer, and the rates at which saplings are able to grow to compensate for, and ultimately escape, browsing. Our aims in this study of the effects of browsing by deer on the natural regeneration of Scots pine were: (1) to make quantitative predictions of the probability and severity of browsing of saplings as a function of site characteristics and use by deer, (2) to make quantitative predictions of the effects of environmental conditions on sapling growth rates and (3) to test the hypothesis that subsequent growth is dependent on the severity of browsing. Such information is an essential pre-requisite for the development of models to aid the integrated management of deer populations and native woodlands.

2. Methods

2.1. Study areas

Twenty-two sites in eight locations throughout the Highlands of Scotland were established in autumn 1995 or spring 1996 (Fig. 1). The sites were chosen

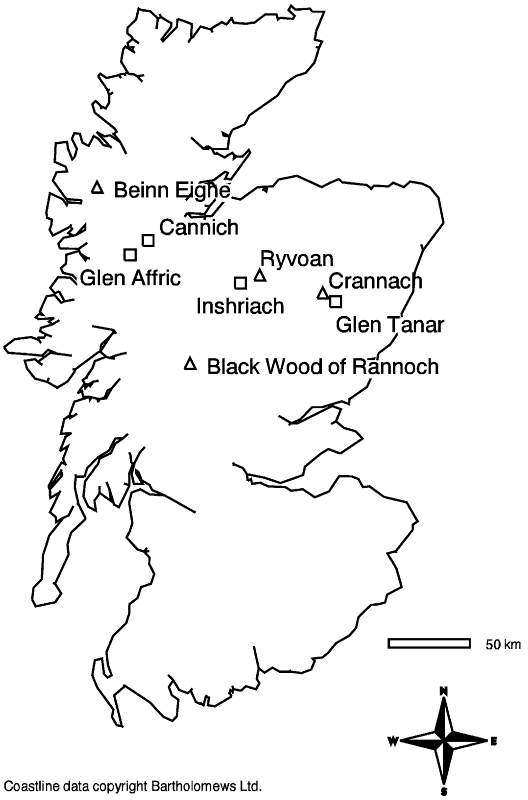

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Fig. 1. Locations of study sites within the Highlands of Scotland. Sites at locations marked by a triangle were sampled during the first year of the study only.

to be either within relatively open areas in Caledonian pine woodland or where Scots pine was colonising moorland around the periphery of woodland. Altitudes ranged from 100 to 500 m, and mean height of ground vegetation ranged from 13 cm on an exposed ridge to 60 cm in mature woodland. The sites were also selected to cover a range of red deer densities based on information available from foresters and land managers. There were no domestic stock present at any of the sites throughout the study. Browsing by deer at all 22 sites was monitored in spring and autumn 1996 (Palmer et al., 1998). Thereafter, eight of the sites in four locations (Glen Affric, Glen Cannich, Inshriach and Glen Tanar) were monitored each spring and autumn from 1997 to 1999.

2.2. *Field methods*

Three permanent 50 m transects were set up at each site through areas where Scots pine saplings <2 m tall were present (ideally with at least 30 saplings per transect). Transects were also placed to be representative of the range of conditions to be found within a site, including areas of wetter ground, where present. The slope, aspect and altitude of each transect was recorded. On the initial visit, ground cover of dwarf shrubs, grasses, sedges, herbs and bare ground was estimated visually (to the nearest 5%) in five quadrats of 1 m × 1 m, equally spaced along each transect. Soil type (peat or mineral), soil moisture (on a subjective five point scale) and 10 vegetation heights were also recorded within each quadrat.

Use of the sites by red deer and roe deer (*Capreolus capreolus* L.) was estimated by counting faecal pellet groups (minimum 10 pellets to constitute a group) in a band 2 m either side of each transect line (i.e. a total area of 600 m^2 per site) each spring and autumn.

Scots pine saplings growing within 1 m of each transect line were individually identified, and examined at each visit. The height, basal diameter and leading shoot length (the longest if there were multiple leading shoots) were measured each autumn, and saplings were classified as being above, equal to or below the ground vegetation canopy and as having single or multiple leading shoots. Browsing damage to saplings was assessed in both spring (for damage during the winter) and autumn (for damage during the summer). From spring 1997 onwards, the percentage of shoots browsed was either estimated visually or, on many saplings, measured by counting the number of shoots browsed and the total number of terminal shoots (i.e. grown in the most recent summer). The location of browsing (leader only; lateral shoots only; leader and laterals) was recorded at each visit. Other damage (thrashing by deer, insect damage, etc.) to saplings was also recorded.

2.3. *Data analysis*

2.3.1. *Relationships between browsing and deer use*

Dung counts were converted to estimates of deer use (equivalent to density, but at too small a spatial scale for density to be a meaningful term) using published defecation rates for red and roe deer (24 and 18 pellet groups per day respectively in winter, 23 and 19 pellet groups per day respectively in summer; Mitchell and McCowan, 1984; Mitchell et al., 1985; Ratcliffe and Mayle, 1992; Mayle and Staines, 1998) and dung accumulation periods of 6 months for western sites, 7 months for central sites and 8 months for eastern sites (Palmer and Truscott, 2003). Indices of ground vegetation and soil type/wetness for each transect were derived from quadrat data by principal components analysis (PCA) (Table 1).

Generalised linear mixed models (GLMM) were used to fit the proportion of trees under 2 m tall which were browsed or leader browsed along individual transects to deer use as estimated from standing crop dung counts with site and year added as random effects. Transect ground vegetation indices were then incorporated as additional explanatory variables. Saplings below the ground vegetation canopy were omitted, as they were rarely browsed, as were those subjected to ‘other damage’ during the year of measurement. Non-significant terms were dropped by sequential backwards elimination (at $\alpha = 0.05$).

The probability of browsing as a function of tree characteristics was also examined by fitting GLMM of browsing incidence and leader browsing incidence to individual tree data (height, above or equal to the ground vegetation canopy), dung counts and ground vegetation indices derived by PCA, with site, transect and year added as random effects. A quadratic height term was included to allow for maximum browsing probability at intermediate heights. For saplings that were browsed, the percentage of shoots browsed was

Table 1
Principal components ordination of ground vegetation and soil type of 345 quadrats

Axis	Positive loading	Negative loading	Eigenvalue	Variation explained (%)	Cumulative (%)
1	*Calluna vulgaris* cover *Vaccinium myrtillus* cover Vegetation height	Grass cover Sedge cover Herb cover Bare ground cover	4.44	22.2	22.2
2	Grass cover Sedge cover Moss cover Litter Vegetation maximum height Wet soil Peaty soil	*C. vulgaris* cover *E. cinerea* cover Other heath cover Bare ground cover Dry soil Mineral soil	2.78	13.9	36.1
3	Vegetation minimum height *C. vulgaris* cover *Erica tetralix* cover Mineral soil	*V. myrtillus* cover *V. vitis-idaea* cover Bare ground cover Peaty soil	1.70	8.5	44.6
4	*Erica cinerea* cover *V. myrtillus* cover Grass cover Herb cover Bracken cover Dry soil Mineral soil	*C. vulgaris* cover Sapling cover Wet soil Peaty soil	1.41	7.1	51.7

fitted by linear mixed models to the same explanatory data (but without the quadratic term).

2.3.2. Sapling growth

Two aspects of growth were analysed by fitting linear mixed models to leading shoot length (log-transformed to yield normal residuals) and annual increment in basal diameter. Because of the possible complexity of interacting environmental variables, the procedure we adopted for each was: (i) to fit a model for unbrowsed saplings only by backwards elimination (at $\alpha = 0.05$) and then (ii) to add browsed saplings to the data set, retaining the explanatory variables fitted in model (i), adding variables which might account for differences in growth due to browsing, and then discarding non-significant terms from this latter set by backwards elimination.

For model (i), growth data for pine saplings under 2 m tall, which were not browsed during the summer or the previous winter and not damaged by any other means, were modelled as functions of transect characteristics, year and tree characteristics. Transect characteristics comprised altitude, slope, aspect (easterly and northerly components) and soil index, plus first-order interactions. Tree characteristics comprised height, basal diameter, the log-ratio of height to basal diameter (all from the previous year) and height relative to the ground vegetation canopy, plus first-order interactions. Location, site and transect were included as random effects.

For model (ii), the effects of browsing damage during winter and summer comprised the percentage of shoots browsed and whether or not the leader was browsed. As the percentage of shoots browsed was not recorded in 1996, saplings that were browsed in that year were omitted (for 1996 growth only). Saplings below the ground vegetation canopy were omitted from models incorporating browsing effects as very few were browsed.

All analyses were performed using the SAS statistical package. In all cases, as many saplings were measured in more than 1 year, ‘tree’ should strictly have also been included as a random effect. However, in order to achieve model convergence, we assumed that browsing to, and growth of, individual trees was independent from year to year, and omitted the 'tree' effect.

3. Results

3.1. Browsing and deer use at the population level (transect scale)

The probability of a pine sapling under 2 m tall being browsed in winter averaged over all years and sites was 9%. Data from one site (Glen Cannich) were omitted from analyses of the relationship between browsing incidence and dung counts. This site was atypical, being a narrow band of naturally regenerated Scots pine between a forestry plantation and open moorland, where very large amounts of dung accumulated (Palmer et al., 1998), equivalent to 82 red deer/km^2. At the remaining sites, estimated red deer use ranged between 0 and 21 deer/km^2 during winter and between 0 and 16 deer/km^2 during summer. Estimated roe deer use ranged between 0 and 10 deer/km^2 during winter and between 0 and 8 deer/km^2 during summer.

The simplest model of the incidence of browsing on pine saplings under 2 m tall during winter at the transect scale showed that the proportion of trees browsed increased with red deer use ($F_{1,17} = 6.8$, $P < 0.05$) (Fig. 2). Roe deer use had no significant effect. The addition of transect ground vegetation indices resulted in a significant effect of PCA axis 1 ($F_{1,60} = 12.8$, $P < 0.001$), such that, for a given level of red deer use, higher browsing incidence was predicted for transects with tall vegetation dominated by heather (*Calluna vulgaris* (L.) Hull.) than for transects with short grassy vegetation. Finally, if interaction terms were added, there was a significant interaction between red deer use and PCA axis 2 ($F_{1,28} = 4.7$, $P < 0.05$), with the highest predicted browsing relative to deer use where woodland was colonising dry heather moorland and the lowest in mature forests on a peaty substrate with high graminoid and moss cover.

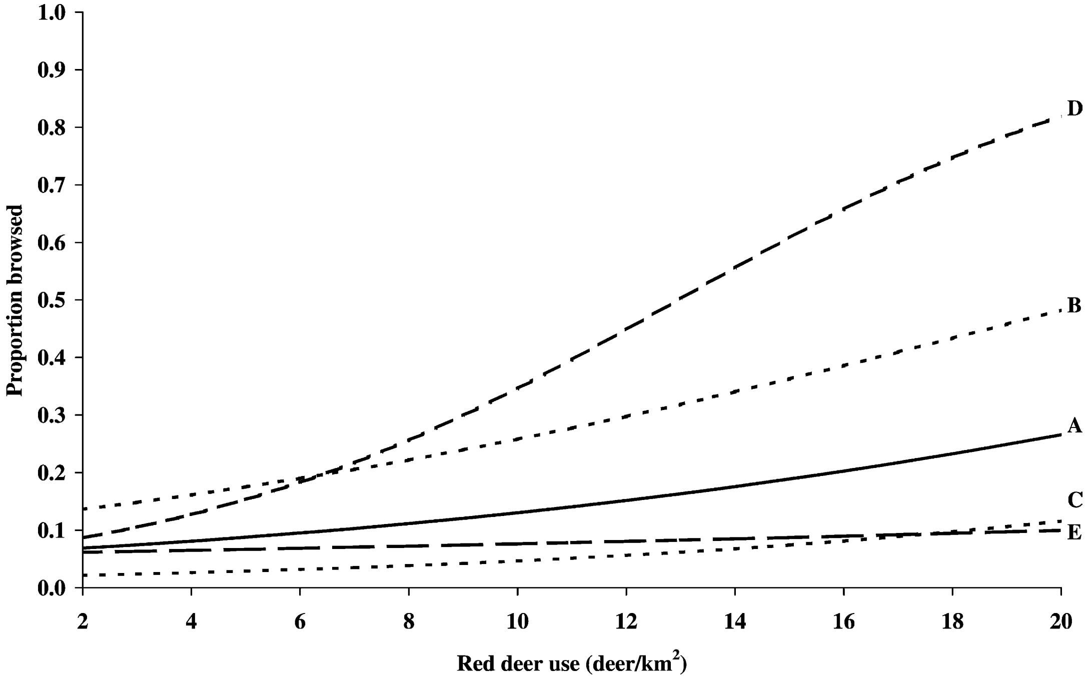


Fig. 2. Predicted proportions of Scots pine saplings browsed during winter in relation to use by red deer: (A) model with red deer use only; (B) addition of first PCA vegetation index—a typical site with tall heather; (C) as (B), but a site with shorter, grassy vegetation; (D) further addition of an interaction between red deer use and second PCA vegetation index—a typical dry moorland-edge site on mineral soil; (E) as (D), but a site typical of wetter areas on a peaty substrate with high graminoid and moss cover.

In contrast, for summer browsing at the transect scale, red deer density was not significant. The proportion of trees under 2 m tall that were browsed increased with roe deer use, albeit not quite significantly ($F_{1,17} = 2.9$, $P = 0.11$).

3.2. Variation in seasonal browsing incidence to individual trees

The probability of an individual tree being browsed during winter increased with tree height ($F_{1,2527} = 37.5$, $P < 0.001$; Fig. 3) in models including red deer use (roe deer use was not significant) and tree attributes only. At higher red deer use, the effect of sapling height on the probability of browsing was accentuated. Also, saplings of a given height were more likely to be browsed if they were above the ground vegetation than at the same height as the ground vegetation ($F_{1,2791} = 8.3$, $P < 0.005$; Fig. 3). Inclusion of the log-ratio of height to basal diameter resulted in a small but significantly increased probability of browsing for saplings with low log-ratios ($F_{1,2618} = 4.9$, $P < 0.05$). The log-ratio provided an index of previous leader browsing. Saplings with a low index were characterised by a 'bushy' form, often with multiple leading shoots (the proportion of saplings classed as having a single-leader increased with log-ratio: 14% at log-ratio = 3.0 and 69% at log-ratio = 4.0; $F_{1,2089} = 235$, $P < 0.001$). The addition of ground vegetation scores to the models accentuated the effects of the interaction between red deer use and sapling height. For saplings of a given height, there was a higher probability of browsing in tall heather-dominated vegetation than in shorter vegetation with graminoids.

If a sapling were browsed during winter, the overall probability of its leader being browsed averaged over all years and sites was 24%. The probability of leader browsing decreased with sapling height ($F_{1,388} = 38.6$, $P < 0.001$) and increased with red deer use ($F_{1,16} = 4.2$, $P < 0.1$) (Fig. 4). The probability of leader browsing also increased with the height to basal diameter log-ratio ($F_{1,378} = 8.5$, $P < 0.005$), i.e. it was greater for saplings with little previous leader browsing history.

The severity of damage, expressed as the proportion of terminal shoots browsed, to pine saplings browsed

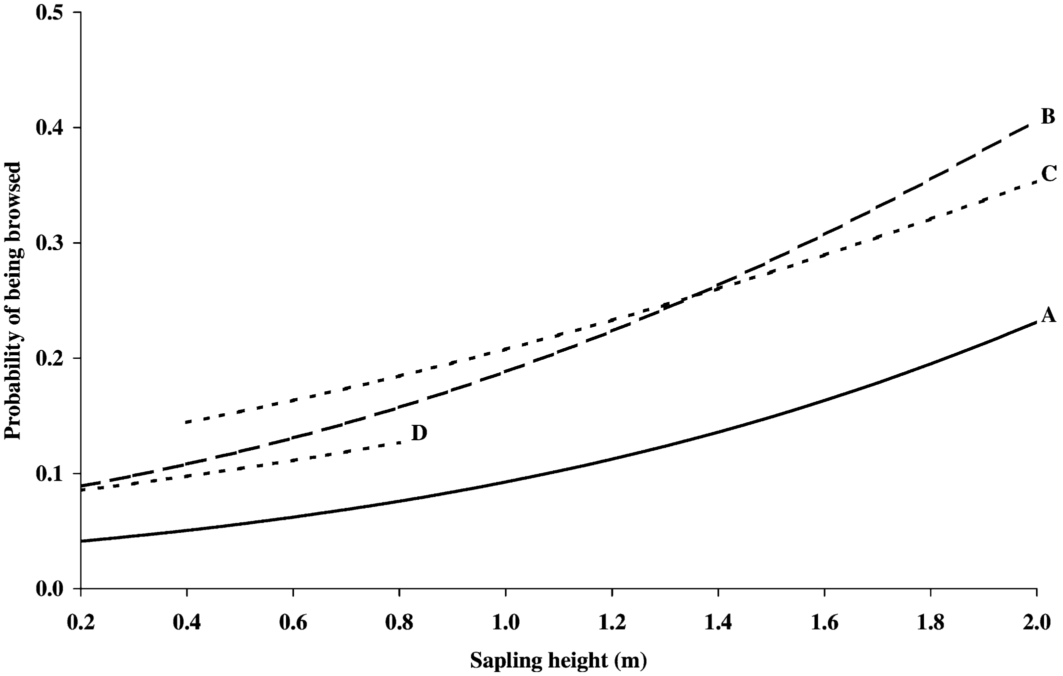


Fig. 3. Predicted probability of a Scots pine sapling being browsed during winter in relation to its height: (A) at 5 red deer/km^2; (B) at 15 red deer/km^2; (C) and (D) as (B), but separating saplings growing above the ground vegetation canopy (C) from those equal to it (D).

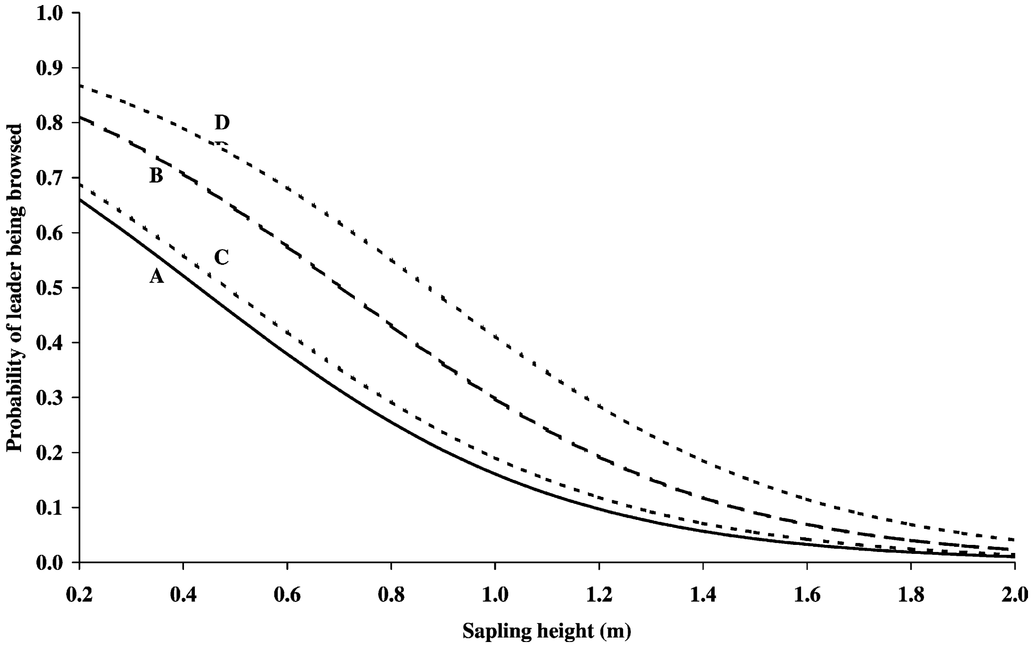


Fig. 4. Predicted probability of the leading shoot(s) being browsed if a Scots pine sapling were browsed during winter in relation to its height: (A) at 5 red deer/km^2; (B) at 15 red deer/km^2; (C) and (D) as (B), but separating saplings with a history of leader browsing ((C): height to basal diameter log-ratio, Ht:BD = 3.0) from those with little or no browsing history ((D): the ratio Ht:BD = 4.2).

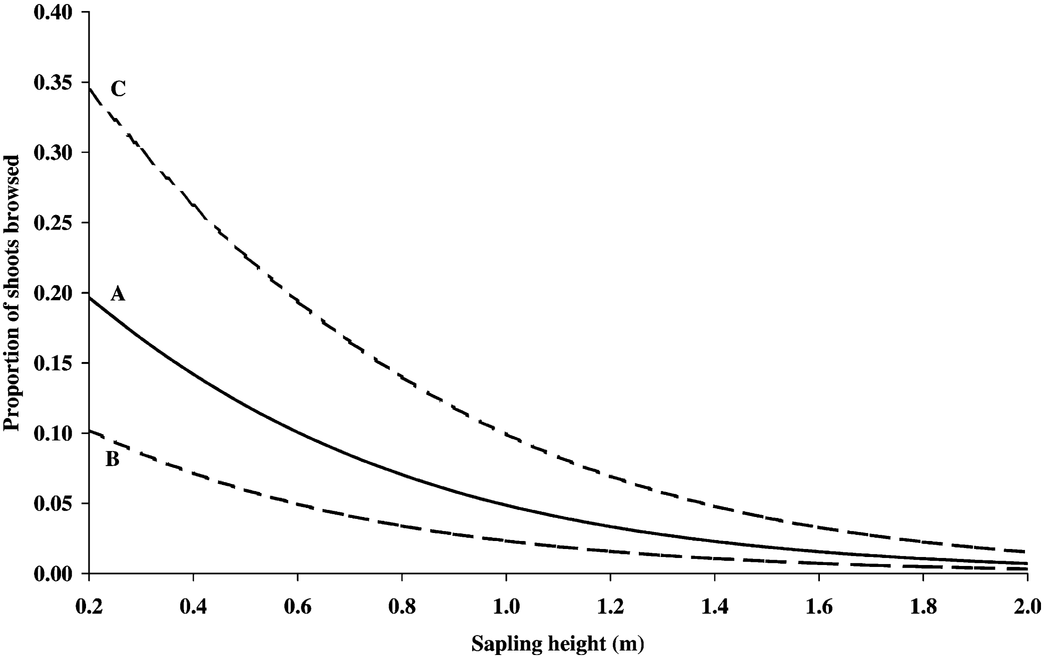
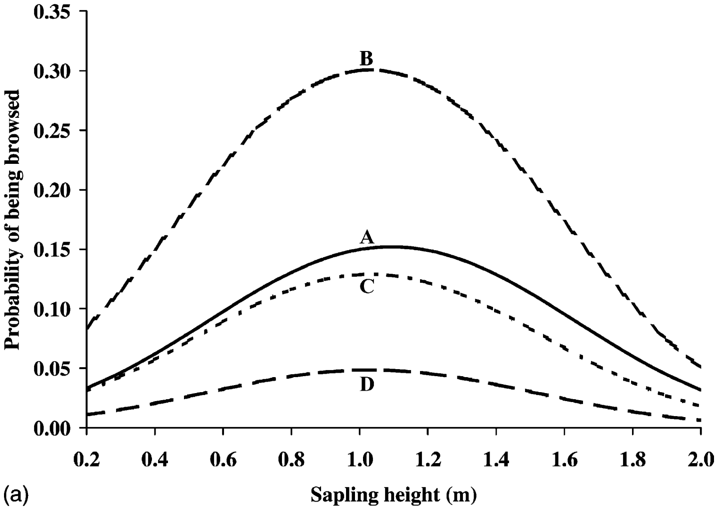


Fig. 5. Predicted proportions of shoots browsed if a Scots pine sapling were browsed during winter in relation to its height: (A) at 10 red deer/km^2 and height to basal diameter log-ratio, Ht:BD = 3.6; (B) as (A), but with Ht:BD=3.0; (C) as (A), but with Ht:BD = 4.2.

during winter decreased with sapling height ($F_{1,122} = 56.9$, $P < 0.001$) and increased with the sapling's height to basal diameter log-ratio ($F_{1,152} = 28.4$, $P < 0.001$; Fig. 5). Severity increased slightly with red deer use, but not significantly, as the analysis was restricted to the eight sites studied from 1997 onwards.

The probability of browsing during summer was greatest for saplings around 1 m tall in models including roe deer use and tree attributes ($F_{1,2519} = 39.2$, $P < 0.001$; Fig. 6a). Use by red deer was not significant. Saplings with low height to basal diameter log-ratios, i.e. with a history of repeated leader browsing, were much more likely to be browsed than were saplings with high log-ratios ($F_{1,2028} = 88.7$, $P < 0.001$).

Fifty percent of saplings browsed in summer had their leading shoot(s) browsed. The probability of leader browsing decreased with sapling height ($F_{1,176} = 28.9$, $P < 0.001$; Fig. 6b). The percentage of shoots browsed was greater at higher use by roe deer ($F_{1,96} = 11.7$, $P < 0.001$) and greater for trees with little previous browsing than trees with much previous browsing ($F_{1,106} = 8.0$, $P < 0.01$; Fig. 7).



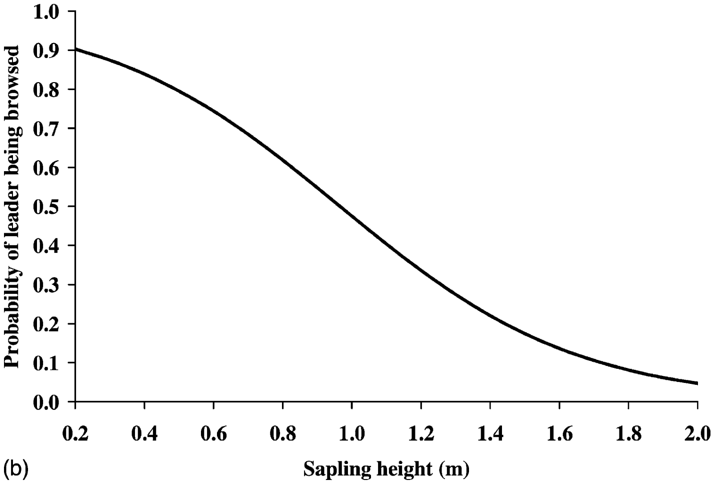


Fig. 6. (a) Predicted probability of a Scots pine sapling being browsed during summer in relation to its height: (A) at 6 roe deer/km^2 regardless of browsing history; (B) at 6 roe deer/km^2 and height to basal diameter log-ratio, Ht:BD = 3.0; (C) as (B), but with Ht:BD = 3.6; (D) as (B), but with Ht:BD = 4.2. (b) Predicted probability of the leading shoot(s) being browsed if the sapling is browsed.

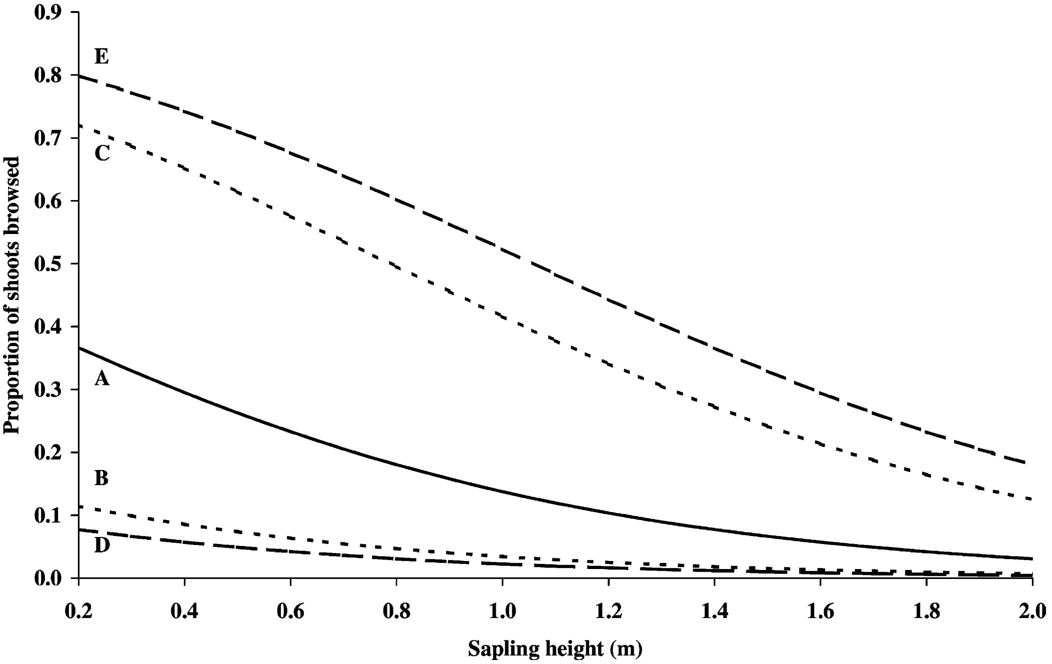


Fig. 7. Predicted proportions of shoots damaged if a Scots pine sapling were browsed during summer in relation to its height: (A) at 6 roe deer/km^2 and height to basal diameter log-ratio, Ht:BD = 3.6; (B) as (A), but at 2 roe deer/km^2; (C) as (A), but at 10 roe deer/km^2; (D) as (B), but with Ht:BD=3.0; (E) as (C), but with Ht:BD = 4.2.

3.3. Growth of pine saplings if not browsed

The length of the leading shoot was proportional to the height of the sapling in the previous year ($F_{1,1792} = 74.8$, $P < 0.001$), significantly related to the soil type ($F_{1,32} = 16.6$, $P < 0.001$) and aspect ($F_{1,66} = 4.1$, $P < 0.05$) of the site, and differed significantly between years ($F_{3,1734} = 24.7$, $P < 0.001$; Fig. 8). Leaders were longer at sites on dry mineral soil than on peaty soils and on south-facing sites. Leader length also varied significantly with the height of the sapling relative to the ground vegetation canopy ($F_{2,1773} = 4.7$, $P < 0.01$) and to the height to basal diameter ratio ($F_{1,1791} = 19.3$, $P < 0.001$; Fig. 9). Saplings growing above the ground vegetation canopy grew relatively longer leading shoots than those below or equal to it, and saplings with low height to basal diameter ratios grew longer leading shoots than those with higher ratios.

Basal diameter increments were proportional to the basal diameter in the previous year ($F_{1,1663} = 32.8$, $P < 0.001$), but there was a significant interaction with the height to basal diameter ratio ($F_{1,1688} = 61.8$, $P < 0.001$), such that saplings with higher height to basal diameter ratios had larger increments relative to their previous basal diameter than saplings with lower ratios (Fig. 10). The basal diameter increment was significantly lower for saplings growing below or equal to the ground vegetation canopy than those above it ($F_{2,1786} = 4.8$, $P < 0.01$), but the effect was small (Fig. 10). It also varied with altitude and aspect ($F_{1,48} = 4.0$, $P < 0.1$), with higher increments on south-facing sites.

3.4. Effects of browsing on sapling growth

The percentage of shoots browsed during winter had a significant detrimental effect on the subsequent summer's leading shoot growth ($F_{1,1786} = 3.3$, $P < 0.1$), but the effect was much more marked if the leading shoot(s) were browsed during winter than if not ($F_{1,1788} = 10.7$, $P < 0.005$; Fig. 11). Likewise, the effect of browsing severity during summer on leader growth differed significantly depending on whether or not the leading shoot(s) were browsed ($F_{1,1782} = 5.6$, $P < 0.05$); summer browsing of the lateral shoots, but

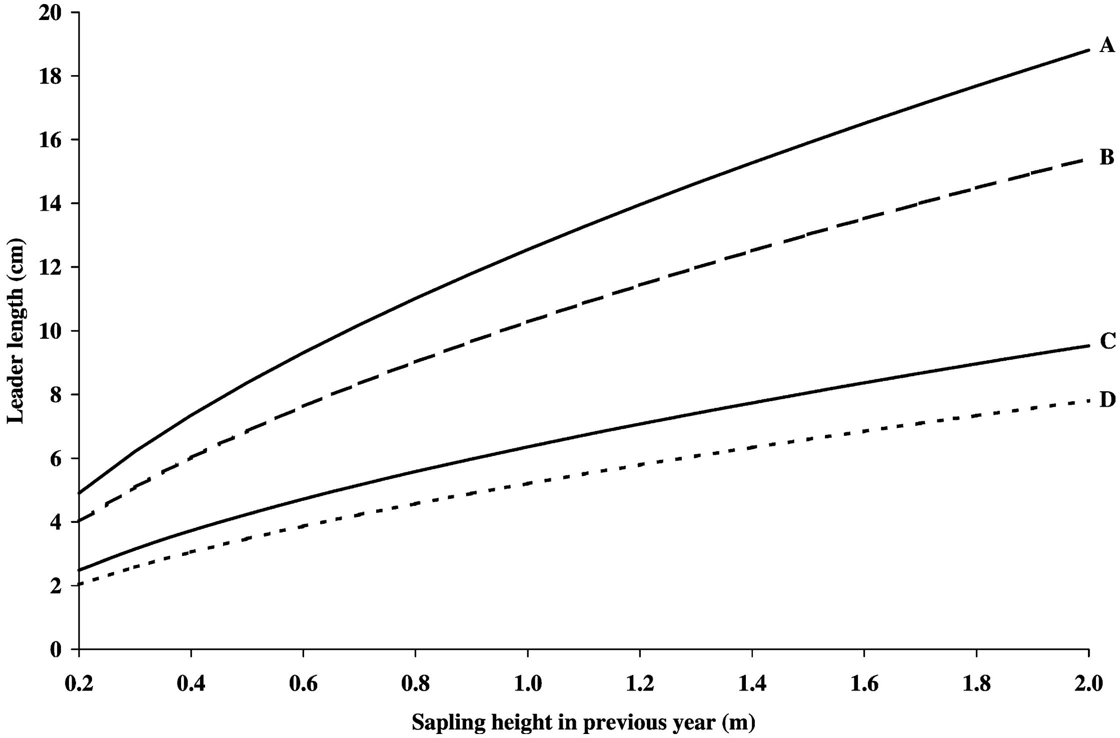


Fig. 8. Predicted effects of soil type, aspect and annual variation on leader growth of unbrowsed Scots pine saplings growing above the ground layer: (A) on a dry mineral soil with a southerly aspect in a good year; (B) as (A) but in a poor year; (C) on a wet peaty soil with a northerly aspect in a good year; (D) as (C) but in a poor year.

not the leading shoot(s), resulted in a slight increase in leading shoot length (Fig. 11). There were significant interactions of sapling height relative to the ground vegetation canopy with both the winter ($F_{1,1795} = 13.4$, $P < 0.001$) and summer ($F_{1,1781} = 6.6, P < 0.05$) percentages of shoots browsed, such that the reduction in leading shoot growth was more marked for a given percentage of shoots browsed on saplings growing above the ground vegetation.

There was no detectable effect of browsing during summer on basal diameter increment. The percentage of shoots browsed during winter had a very limited negative effect on basal diameter increment ($F_{1,1896} = 3.0$, $P < 0.1$).

4. Discussion

In this study, we have attempted to cover a wide range of conditions under which regeneration of Scots pine is occurring, or has the potential to occur, within the Highlands of Scotland. The relationships we have quantified should therefore be generally applicable to other sites within the region, and possibly also to woodlands elsewhere which are dominated by Scots pine and have a similar ground flora. However, as an inevitable consequence of covering such a wide range of sites, there remained much variation in browsing incidence and severity which we could not explain using the variables we measured. In particular, as sites were much smaller (typically the three transects lay within ca. 300 m of each other) than the likely ranges of the deer which used them, the influence of larger-scale factors, such as the forage available in other habitats within the home range, could not be taken into account. In order to predict whether regeneration will occur at a given site and a given level of deer use, the relationships presented here should be regarded together with information from larger spatial scales (e.g. Scott et al., 2000; Palmer and Truscott, 2003).

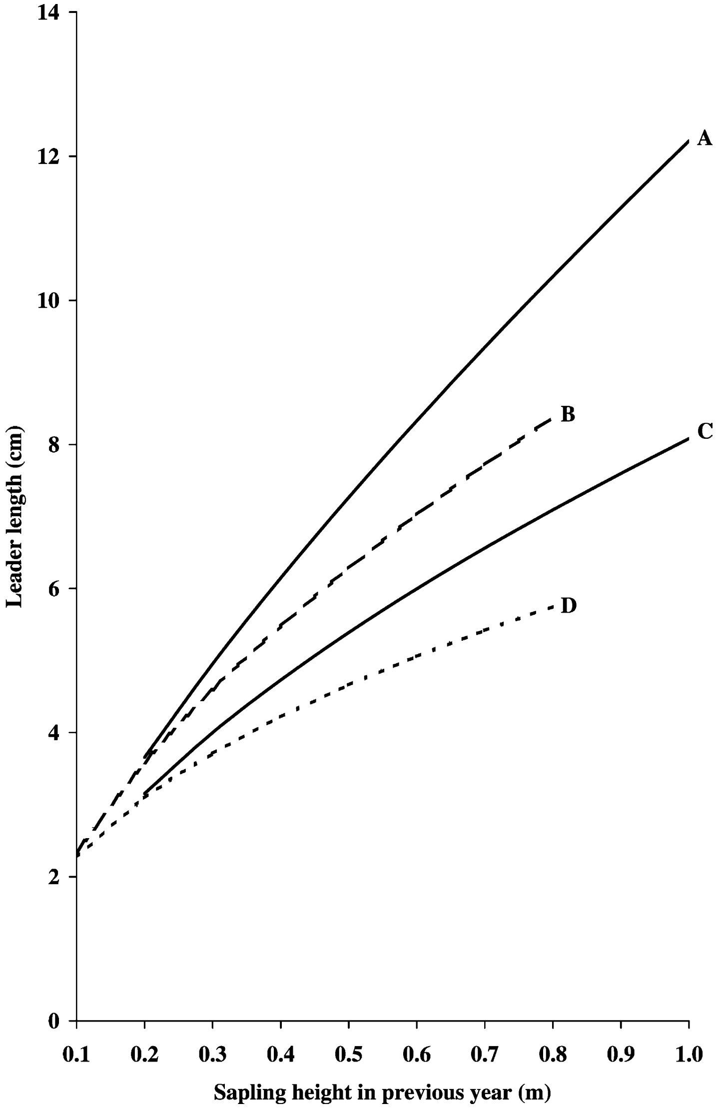


Fig. 9. Predicted effects of height relative to the ground vegetation canopy and growth history index (height to basal diameter log-ratio, Ht:BD) on leader growth of unbrowsed Scots pine saplings: (A) above ground canopy, Ht:BD = 3.0; (B) as (A) but equal to ground canopy; (C) above ground canopy, Ht:BD = 4.0; (D) as (C) but equal to ground canopy.

4.1. Browsing and deer use at the population level (transect scale)

Although winter browsing incidence at the transect scale was related to red deer use over winter, the relationship was substantially improved by the addition of indices of ground vegetation composition and structure along the transects. It was higher for a given dung count in tall heather-dominated vegetation than in shorter vegetation with graminoids or bare ground. There are three possible reasons for this variation between habitats: differences in the selection of trees by deer, differences in dung decay rates and variation in dung visibility to observers. Deer might visit areas with shorter vegetation to graze graminoids, and, because of the higher quality ground forage, ignore

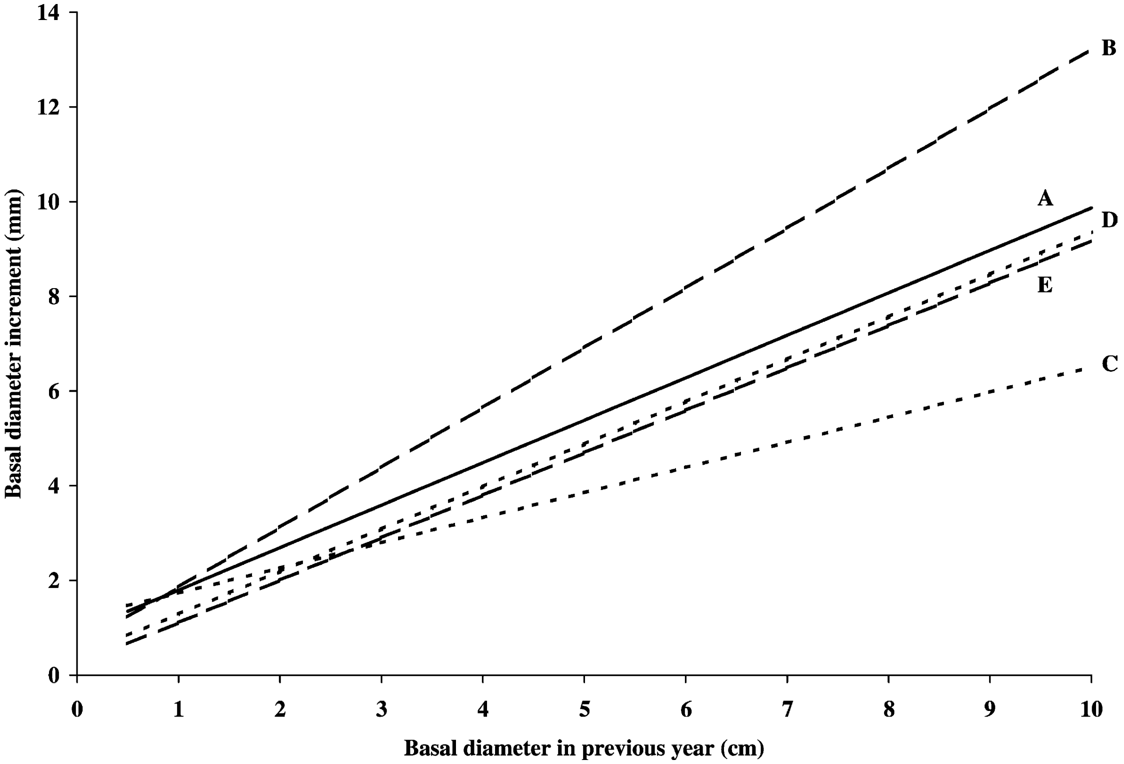


Fig. 10. Predicted basal diameter increment for unbrowsed Scots pine saplings growing on a south-facing site at 300 m: (A) growing above the ground vegetation canopy with intermediate height to basal diameter log-ratio, Ht:BD = 3.5; (B) as (A) but Ht:BD = 4.0; (C) as (A) but Ht:BD = 3.0; (D) as (A) but equal to the canopy; (E) as (A) but below the canopy.

Scots pine saplings. In contrast, in areas with only Scots pine saplings and heather as available forage, both of which are of relatively poor quality, pine shoots may be more attractive, and browsed more frequently for a given length of time spent there by the deer. However, in areas with shorter vegetation, particularly if there is bare ground, freshly deposited dung may dry out quickly and become quite resistant to decay, and it is possible that some dung counted in the spring standing crop might have remained from the previous year. We attempted to classify pellet group as ‘recent’ (since the previous visit, i.e. within roughly 6 months) and ‘older’, but felt that such a highly subjective method was not reliable, and preferred instead to use the standing crop count together with accumulation periods estimated from similar habitats. A more likely problem though, is the rapid disappearance of dung during summer, owing to a more nutritious diet, warmer temperatures and more rapid plant growth (especially in grassy habitats), leading to under-estimation of summer use. Clearing dung on a regular basis would avoid the problem of differential rates of dung disappearance, certainly during the winter months. It may also be possible that pellet groups were missed in tall heather-dominated vegetation if they were well concealed.

Despite the sites originally being selected to cover a range of red deer use, there was no significant relationship between browsing incidence during summer and red deer dung counts. However, summer browsing incidence did increase with roe deer dung counts. Furthermore, for a given density of roe deer dung, the predicted browsing incidence was higher for transects with short, grassy vegetation than for transects with tall heather. This was the converse of the interaction observed between red deer dung counts and vegetation during winter, and might be due to roe deer favouring areas with relatively high cover of

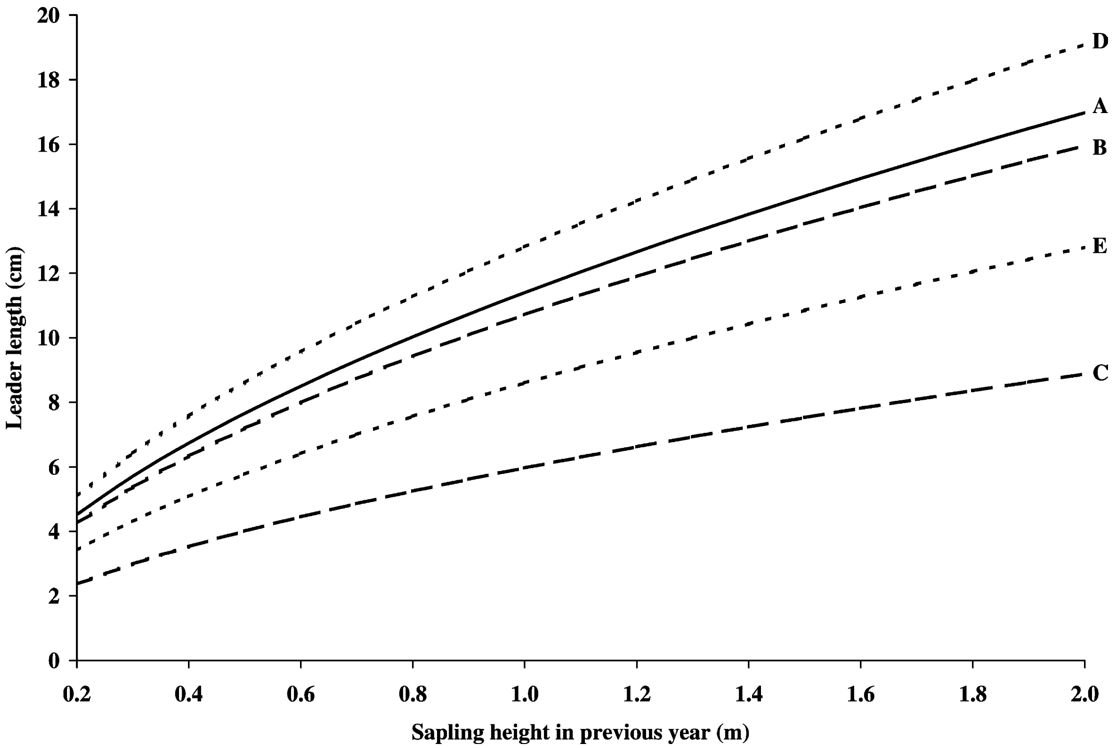


Fig. 11. Predicted effect of browsing on leader growth of Scots pine saplings growing above the ground vegetation canopy on a south-facing dry site: (A) not browsed; (B) 40% of shoots browsed during winter, leading shoot(s) not browsed; (C) as (B) but leading shoot(s) browsed; (D) 10% of shoots browsed during summer, leading shoot(s) not browsed; (E) as (D) but leading shoot(s) browsed.

graminoids and herbs during mid-summer at the time when Scots pine shoots have just commenced growing, and are presumably high in nutrients.

Interactions between dung counts and ground vegetation in the model should, however, be treated with some degree of caution, especially at high levels of deer use, as the variation in ground vegetation was much greater between sites than within sites (by 2.5 times for the first vegetation PCA axis and 6.5 times for the second) and hence deer present at any one site had only a limited range of ground vegetation across which to forage.

4.2. Variation in browsing incidence to individual trees

In addition to increasing with use by red deer, the probability of a Scots pine sapling being browsed during winter increased with its height. This was not simply an artefact of sapling heights being confounded with deer use, as the relationship remained if heights were normalised (as z scores) within site. Saplings above the ground vegetation were more likely to be browsed than those equal to it, apparently indicating that the visibility of a sapling to deer is important. Miller et al. (1982) also found that the likelihood of Scots pine saplings being browsed by red deer depended on the relative heights of the sapling and the ground vegetation, albeit with both being considerably smaller than were typical at our sites. However, in the present study, the probability of the leading shoot(s) being damaged if the sapling were browsed during winter decreased with sapling height. Combining these two relationships at a level of red deer use equivalent to 15 deer/km^2 suggested that, overall, leader damage during winter was most likely for saplings around 50 cm tall. This agrees well with the range of 30–50 cm reported by Welch et al. (1991) for leader browsing of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) saplings in a forestry plantation in

Argyll, where leader browsing incidence was greater during winter than summer.

Many Scots pine saplings, although browsed during winter, had few shoots damaged, and hence the proportion of shoots damaged was greater for small saplings with few shoots than for large ones with many shoots. The proportion of shoots damaged was also greater for saplings with a high height to basal diameter log-ratio, i.e. those which had rarely been browsed before, as they generally had fewer shoots than saplings of similar height with a history of repeated previous browsing.

During summer, saplings of intermediate height, around 1 m, were most likely to be browsed. Summer browsing incidence was related to use by roe deer rather than red deer, in contrast to the winter observations. Saplings with a history of repeated previous browsing were much more likely to be browsed than saplings with no such history. Although the probability of the leading shoot(s) being damaged if the sapling were browsed decreased with sapling height, as it did during winter, the greatest likelihood of leader browsing was for saplings of around 80 cm, somewhat higher than the modal height during winter. The phenomenon of repeated browsing to the leading shoots of particular saplings was particularly prevalent at Glen Tanar, where it was assumed to be occurring when shoots were first elongating in June, but could not be attributed unequivocally to roe deer (Palmer and Truscott, 2003). Similarly, Staines and Welch (1984) recorded the highest levels of leader browsing to Sitka spruce during winter and the May–June period, and Welch et al. (1988) found that browsing of Sitka spruce by roe deer was greatest about 10 days after bud-burst. The significant relationship in the present study between browsing incidence to Scots pine and roe deer dung counts during summer constitutes further evidence that roe deer, the more selective feeder of the two species, were more likely to have caused this particular type of highly seasonal damage.

One factor not examined which could potentially influence the likelihood of browsing is the density of saplings, as transects were not placed at random with respect to sapling density, but where sufficiently large samples of saplings could be obtained. If sapling density is not an important determinant of habitat use, for example if saplings are small or at low density, then we would expect the incidence and/or severity of damage to decline with increasing sapling density. This has been reported for red deer browsing Scots pine (Cummins and Miller, 1982) and for moose (*Alces alces* (L.)) browsing Scots pine (Andrén and Angelstam, 1993) and birch *Betula pubescens* Ehrh. (Vivås and Sæther, 1987). Moreover, saplings at low density may be preferred by browsing ungulates; Thompson et al. (1989) found that thinned stands of balsam fir (*Abies balsamea*) offered better quality browse to moose than denser stands, although whether the same would hold true for naturally occurring low density stands is not clear. However, if deer preferentially use areas of higher than average sapling density, for example when the ground vegetation is covered by snow, then browsing incidence might increase with sapling density. Palmer and Truscott (2003) reported a positive effect on browsing incidence of the interaction between winter red deer dung count and an index of pine shoot availability. Heikkilä and Härkönen (1996) found that leader browsing incidence to young Scots pine saplings by moose was independent of pine sapling density, but the biomass of pine shoots consumed increased with sapling density, although in their study, the availability of deciduous tree saplings was an important factor. Clearly more research is required to determine under what conditions deer are attracted to areas where sapling density is relatively high, and the levels of damage which ensue.

4.3. Growth of pine saplings if not browsed

Slow growth rates similar to those observed in this study have previously been reported for naturally regenerated Scots pine saplings (McVean, 1963; Beaumont et al., 1995; Scott et al., 2000). Successful regeneration has been associated with mineral soils with short vegetation cover (Henman, 1961), and although Scots pine can germinate on poorly drained ground, subsequent survival is usually poor (Carlisle and Brown, 1968). The effect of light, not considered in the present study as most sites were open or had very few mature trees, is also influential in the establishment of Scots pine saplings (Vickers and Palmer, 2000). Although we found some variation in leader length due to static environmental conditions (soil type and aspect), differences between years were substantially greater: the variation in leader length relative to sapling height between years was almost

20 times greater than the largest variation in any of the spatial strata (location, site and transect). Thus, long-term growth predictions cannot be made satisfactorily from data collected from many sites in only 1 year; many years' data are required in order to account for the effects of weather on growth. There was also evidence for increased leader growth following a history of browsing prior to the current year. However, basal diameter increments were reduced in such circumstances. This suggests that Scots pine saplings compensate for a history of repeated browsing by directing resources away from development of girth towards increasing height. Edenius et al. (1993) have shown that Scots pine saplings are able to compensate for moderate levels of browsing in terms of their subsequent shoot biomass, but for saplings which have been repeatedly browsed, the optimum response when released from browsing pressure may be to gain height as quickly as possible to escape future browsing pressure.

4.4. Effects of browsing on sapling growth

If a Scots pine sapling is able to grow free from browsing, it will normally remain as a single-leader tree until much taller than 2 m (provided the leader buds are not damaged by other agents, such as invertebrates, birds or fungal attack), and its growth rate is simply a straightforward function of its height and environmental conditions. Browsing of lateral shoots during winter had a very limited detrimental effect on leader growth and basal diameter increment. Similarly, browsing had little long-term effect on the girth of Sitka spruce (Welch et al., 1992). There was also some evidence that browsing of laterals during summer resulted in increased leader growth, but this finding should be treated with caution, as only 7% of saplings equal to or above the ground vegetation canopy were browsed during the summer. However, when summer browsing did occur, it was often to the leading shoots, and it may therefore constitute a potentially detrimental effect on sapling growth even at low levels of deer use. A single incidence of browsing to the leader normally set growth back just 1 year, but had the additional effect that the replacement leader was not as long as the original would have been, which supports the findings of Beaumont et al. (1995) and Scott et al. (2000). However, as described above, if leader browsing persists, saplings appear to be able to compensate to some extent in the longer term.

4.5. Mortality

Mortality of pine saplings above or equal to the ground vegetation and below 2 m tall at the eight retained sites was generally low. The exception was at the site in Glen Cannich, where a quarter of saplings alive in autumn 1996 were dead a year later, and further lower levels of mortality continued for the next 2 years. The heaviest browsing at the site occurred during winter 1995–1996, and the greatest mortality therefore occurred between 12 and 18 months after the heavy browsing, consistent with the findings of Edenius et al. (1995). Canham et al. (1994) found that probability of survival of three deciduous tree species was least when simulated browsing damage occurred during the growing season, but high levels of browsing during summer are probably rare for evergreen conifers. Survival is also affected by soil fertility, with saplings rooted in relatively fertile soil more liable to browsing but with a higher chance of recovery after damage than nutrient deficient saplings (Danell et al., 1991; Edenius et al., 1995).

5. Conclusions

The likely success of natural regeneration depends critically on the balance between growth and browsing, especially of leading shoots. Together these determine whether a sapling can reach a height at which it should be safe from browsing by deer, although it might still be damaged by bark stripping. The results from this study have shown that if deer use alone is taken into account, then although browsing incidence can be shown to increase as deer use increases, the relationships are influenced by several other factors, which must be taken into account in making quantitative predictions and recommending approaches to management of deer in woodlands. Further research is required to verify the relationships between deer use and browsing rates specified in this study, and to develop more general relationships across a wider range of woodland types. As new data are acquired, browsing and growth relationships need to be combined in a simulation model and run for 20–25 years to determine under what conditions trees can grow above the height at which they are under threat from browsing by deer.

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