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GRAZING IN ATLANTIC OAKWOODS: FINAL REPORT

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SUMMARY

- The relationship between the use of Atlantic oakwood sites by large herbivores (red deer, roe deer and sheep) and browsing of tree saplings was studied at five sites in western Scotland between 1998 and 2000. The principal objective was to establish the threshold densities of large herbivores which will allow regeneration of the Atlantic oakwoods.
- The use of the sites by herbivores was estimated by counting and clearing dung throughout the year. An estimated seasonal offtake, derived from published species-specific seasonal defecation rates and dry matter intake, was used as an index of grazing pressure.
- The incidence of browsing to saplings during summer and winter was estimated by recording damage by ungulates to individually-identified trees on permanently-marked plots throughout the growing season. Changes in height and damage to leaves by invertebrates were also recorded. A supplementary site was established to examine growth of oak saplings under more open conditions than were prevalent at the five main sites.
- Many saplings disappeared without trace, more so the two large-seeded species, oak and hazel, and less frequently the two small-seeded species, birch and rowan. Such losses were proportionally higher over winter than during summer, and were assumed to be principally due to browsing by ungulates, although that could not be proven.
- The incidence of browsing / loss varied considerably according to site, season and tree species from a summer minimum of around 20 % of saplings to a winter maximum of over 70 %.
- The incidence of browsing was not related to the estimated offtake during summer, but during winter, the maximum browsing incidence (assuming all losses were due to browsing) increased significantly with estimated offtake. In contrast, there was a significant difference between tree species in the maximum browsing incidence during summer (highest incidence for rowan, lowest for oak), but not during winter.
- During both seasons, taller saplings were more likely to be browsed than shorter saplings, and saplings surrounded by short ground vegetation were more likely to be lost than those in taller vegetation.
- Newly-germinated oak and hazel seedlings were more likely to be browsed during summer than older saplings of the same species, even after the greater height of first year plants had been taken into account.
- Mean saplings heights did not increase during the study. Oak and hazel saplings typically averaged less than 15 cm. Rowan and birch were generally slightly taller, with birch attaining a mean height of just over 30 cm at one site.
- Browsed saplings lost height on average, but growth of saplings which escaped browsing was also generally poor, with birch showing the best performance at a mean increment of only 2 cm. The majority of unbrowsed saplings (especially oaks) did not increase in height at all. The lack of growth was assumed to be largely because most saplings occurred under the shade of a mature tree canopy. At the supplementary site, mean growth increments of larger oak saplings growing under more open conditions averaged 2 cm in one year.

- Most saplings experienced attack to leaf tissue by invertebrates or fungi during the course of the summer, with up to 20 % or so of leaf area damaged by the end of the growing season.
- It was not possible to establish threshold densities of large herbivores which will allow regeneration of the Atlantic oakwoods. This was because the incidence of browsing did not differ greatly between sites, despite large variation in use of the sites by ungulates. Two suggested reasons for the weak relationships between browsing and dung counts were (1) the use of some sites during the winter by deer for shelter, but not for heavy grazing and (2) targeted browsing of saplings around the time of bud-burst in spring, probably by roe deer.
- Although ungulates undoubtedly browsed many small saplings, it appeared unlikely that even their complete removal would result in widespread regeneration, especially of oak. Not only did saplings located under the mature tree canopy show poor growth, if at all, but there were extremely few young oaks growing in more open areas at any distance from the parent trees, suggesting that a negligible proportion of acorns (produced in abundance during good mast years) were dispersed by animal vectors, such as squirrels and jays. Areas cleared of conifers or *Rhododendron* are therefore likely to develop into birch thicket, with no oak or hazel component, unless these larger-seeded species are deliberately introduced by active management.
- A supplementary experiment was set up to assess methods applicable to the restoration and expansion of oak into areas cleared of conifers. The growth, browsing incidence and survival of planted year-old oak saplings was studied in three habitats: (1) under a birch canopy, (2) under an oak canopy and (3) in an area cleared of Sitka spruce (with additional treatments of fencing and brash removal).
- The browsing incidence was higher for saplings in the clear-felled area than under the oak and birch canopies. In the clear-felled area, lines of brash left after felling protected saplings against browsing by ungulates, and the probability of browsing was inversely related to the depth of brash. However, survivorship and performance was lower for seedlings planted in the brash than for seedlings planted between brash lines.
- Mechanisms that might affect the survival and performance of oak in clear-felled areas, such as the development of the ground flora, are discussed.

INTRODUCTION

The Atlantic oakwoods of the western coastal fringes of Europe have been identified as a habitat of conservation importance under the European Union (EU) Habitats Directive. They are important because of their limited oceanic distribution in Europe, and many of the woods exist as small, isolated fragments. A characteristic of these woods is the presence of holly *Ilex aquifolium*, and they are notable for their rich assemblages of ferns and epiphytic mosses and lichens. From a conservation perspective, the oakwoods face three principal threats: invasion by exotic species, particularly *Rhododendron ponticum*, under-planting with conifer crops and a history of grazing by deer and domestic sheep *Ovis aries*.

In many semi-natural upland oakwoods in the British Isles, there is little or no natural regeneration of oak *Quercus* spp. and other deciduous tree species which may be present as mature trees (Rackham, 1980; Humphrey and Swaine, 1997a). Many factors including ungulate density and habitat use, light conditions, seed sources, soil fertility and ground flora will influence local tree regeneration. Grazing has been shown to have an important impact on regeneration (Peterken and Tubbs 1965; Shaw 1968, 1974). Although the complete absence of large herbivores might secure the most rapid or maximum regeneration, it also results in the ground vegetation growing tall and often changing in composition and becoming less diverse, so some authorities have advocated light or very light use by large herbivores as being desirable for the conservation of oakwoods (Mitchell and Kirby, 1990). Also, it is often impractical to prevent access entirely to woods by large herbivores, especially deer, so knowledge about the maximum densities that can be tolerated without serious damage to young trees is highly desirable. Because herbivores are selective in the browse that they eat (Henry, 1978a,b; Putman, 1988; Gill, 1992; Tixier *et al.*, 1997), it is likely that at densities approaching the threshold levels, they modify the species composition of woodland by preventing the species they select most, e.g. willows *Salix* spp., from growing beyond the sapling stage.

Many of the Atlantic oakwoods were under-planted with conifers, particularly Sitka spruce *Picea sitchensis*, during the second half of the 20^{th} century. This resulted in the reduction of extent and quality of oakwood habitat with the associated loss of species (Kirby and May, 1989). The UK Habitat Action Plan for Upland Oakwoods discourages the restocking of conifer plantations adjacent to or within extant upland oakwoods. In the course of the EU LIFE-97 project 'The Restoration of Atlantic Oakwoods', of which the research presented here forms a part, large areas of conifers have been clear-felled, some to waste. Within the five oakwood candidate Special Areas of Conservation (cSAC) in Scotland, more than 300 ha of conifers have been removed. While the LIFE project is mitigating many of the primary threats to Atlantic oakwoods through restorative management, there is currently an incomplete understanding of the processes and the potential for fully restoring and extending Atlantic oakwood habitat on degraded sites (Humphrey and Nixon, 1999).

The principal aim of this research was to investigate the relationship between ungulate use and browsing incidence of tree saplings in Atlantic oakwoods with the objective of establishing the threshold densities of large herbivores which will allow regeneration of the woods. A secondary aim was to assess methods applicable to the restoration and expansion of Atlantic oakwoods into areas cleared of conifers, and in particular to test the hypothesis that brash left from felling protects seedlings against browsing by ungulates.

METHODS

PRINCIPAL SITES

Five sites were established in May-June 1998: Ariundle National Nature Reserve (Scottish Natural Heritage; O.S grid reference NM8364) and Laudale Wood (private ownership; NM7559) in the Loch Sunart cSAC, Glen Nant Caledonian Forest Reserve (hereafter Nant West) (Forest Enterprise; NN0127) and Glen Nant National Nature Reserve (hereafter Nant East) (Scottish Natural Heritage; NN0129) in the Loch Etive cSAC and Firkin Wood (private ownership; NN3302) in the Loch Lomond cSAC. The sites ranged in size from about 2 to 5 ha and were selected to cover a range of use by red deer *Cervus elaphus*, roe deer *Capreolus capreolus* and domestic sheep, based on information from managers and site inspections made in April-May 1998.

At each site a grid of fifteen plots was set up at a nominal spacing of 50 to 75 m (depending on site size), on which to record ungulate dung and tree saplings. Each plot measured 20 m x 4 m, was aligned with its long axis to the north (east at Nant East) and was permanently marked with wooden stakes at each corner. Attributes of the plots recorded comprised the slope and aspect, the number of mature oak, hazel, birch and rowan on the plot, a visual estimate of the average canopy cover above the plot and the perpendicular distances to the nearest four mature oak trees from each side of the plot (if within 50 m).

Each site was visited three times during the growing-season - spring (May-June), mid-summer (July-August) and early autumn (September-October) - for three years from 1998 to 2000, although visits during 1998 were a month or so later, owing to the time taken to obtain permissions and set up the sites. At each visit, all dung on the plots was identified to species and removed. Additional visits to record and clear dung were made during the intervening two winters: during March 1999, November 1999 and March / early April 2000.

At each visit during the growing-season, the positions of individually-identified saplings[1] were recorded to the nearest 10 cm. Rowan (at all sites) and birch (at all sites except Ariundle and Firkin) were sub-sampled to yield a total of around 50 of each at each site; full counts of the numbers present on each plot were made in 1998 only. Otherwise, all individual saplings on each plot were recorded, with the exception that newly-germinated oak seedlings were sub-sampled at Firkin from 1999 and at Ariundle in 2000, following good mast crops the previous year. Additional saplings were recorded beyond the plot perimeter where present in order to increase the number of saplings of the four commonest species (oak, hazel, birch and rowan) at each site to a minimum of around 50 individuals each if possible. Supplementary plots were set up at Nant East to record additional oak saplings for the same reason.

The height of each sapling was measured at each visit. If the sapling appeared to have been browsed by an ungulate, the proportion of leaf area removed was estimated, and the location of browsing (leading shoot, lateral shoots, leader and laterals) was noted. Each leaf present was assigned to one of five damage categories according to the estimated proportion of its area lost (namely none, 1-10%, 11-25%, 26-50%, over 50%) to caterpillars, other defoliating insects (particularly leaf-miners and, on oak, gall-formers), molluscs, fungi and lagomorphs. An estimate was made (once only upon first recording the sapling) of shading by the tree canopy, as the proportion of the sun's arc between due east and due west which would be obscured by the canopy. The number of bracken *Pteridium aquilinum* stems in a semi-circle

[1] For the purposes of this report, the term 'saplings' is taken to mean all young trees, including newly-germinated seedlings, unless otherwise stated

of 1 m radius from east through south to west was recorded (annually, and normally at the mid-summer visit) as a second index of shading. The ground vegetation surrounding the sapling (within a 20 cm radius) was assigned to one of four height classes (less than 5 cm, 5-10 cm, 10-25 cm, over 25 cm), and one of three moisture classes (dry, intermediate, wet).

Height measurements were not considered to be entirely reliable for two reasons: (1) heights were measured to a resolution of 1 cm, and the likely measurement error of 1-2 cm was large relative to the heights of most saplings and to growth increments, and (2) the growth of moss and/or grass during the summer could make some trees 'shrink' relative to the apparent ground surface. At the mid-summer and early autumn 2000 visits, we therefore also noted explicitly whether the sapling had increased in height since the previous visit, and if so, by how much.

SUPPLEMENTARY SITE

An additional site was set up in 1999 in a large exclosure (installed by Forest Enterprise in 1998) at Aird Trilleachan beside the north end of Loch Etive in the Loch Etive cSAC (NN1044). The purpose of this site was to record growth of oak saplings under more open conditions than prevail at the other sites. A single transect with a sample of about 30 small saplings was set up under a moderate birch canopy, and a further sample of about 30 larger oak saplings (up to 82 cm) was recorded at a number of points within the exclosure.

PERFORMANCE OF OAK IN AREAS CLEARED OF CONIFERS

To examine the performance of oak if it were to colonise areas cleared of conifers or be planted in such habitats, an experiment was established at Nant West in March 2000. Oak saplings which had been raised the previous year from acorns of local provenance were planted into plots set up in each of six habitats:

Cleared conifer area	within exclosure	within brash line
Cleared conifer area	within exclosure	between brash line
Cleared conifer area	outwith exclosure	within brash line
Cleared conifer area	outwith exclosure	between brash line
Under oak canopy ('control' for comparison with naturally germinated saplings)		
Under birch canopy		

The conifers (Sitka spruce *Picea sitchensis*) had been cleared during 1998, and the brash raked into lines roughly 5 m apart. The deer exclosure was constructed during the winter 1999-2000. Ten 2 m x 2 m plots were placed within each habitat (at 5 m intervals along three transects) and ten saplings were planted within each plot (i.e. 100 saplings per habitat). The saplings were between 10 and 15 cm tall at the time of planting.

The growth, browsing incidence and survival of the saplings was assessed during mid-June and mid- September 2000. Data recorded for saplings were the same as for the five principal sites with the following exceptions/additions. The vegetation height was measured at four points in the plot rather than being assigned to height classes for each tree. Estimates were made of litter, bare ground, and brash cover for each plot, and brash depth was measured for each sapling. The percentage cover of the main vegetation components (grasses, mosses, etc.) was recorded at each visit. The number of naturally regenerated tree saplings on each plot was also recorded.

DATA ANALYSIS

Use by ungulates and browsing of saplings

The data were analysed on a seasonal basis: summer, during which saplings were in leaf, and winter, when they were dormant. For 1999 and 2000, summer was taken to be the period between the spring and early autumn visits. For 1998, the third growing-season visit took place in late autumn, by which time leaves were either dead (oak) or dropped (other species) and the seasonal patterns of use by ungulates had changed, in particular there being a substantial influx of red deer into Firkin Wood. Summer 1998 was therefore taken to be the period between the first and second growing-season visits, and consequently winter 1998-99 extended from early autumn 1998 through to May 1999.

Seasonal pellet group counts were aggregated at the site scale for each herbivore species (Table 1), and then converted to animal days per hectare using seasonal daily defecation rates for each species (red deer - Mitchell and McCowan, 1984; roe deer - Mitchell *et al.*, 1985; sheep - Welch, 1982). Species-specific habitat use estimates were then converted to estimates of seasonal dry matter offtake at each site using species-specific daily dry matter (DM) intake requirements (Armstrong, 1996), in order to give a single index of the browsing pressure on saplings at each site in each season (Table 1).

Analysis of browsing incidence and growth of saplings was limited to the four most common species, for which there were sufficient sample sizes, *viz*. oak, hazel, birch and rowan. As many saplings disappeared without trace, a sapling not found on three consecutive growing-season visits was treated as lost. A **minimum browsing incidence** for a species within a site was calculated as the proportion of saplings known to have been browsed (i.e. found and clearly bitten by an ungulate at least once during a season) and a **maximum browsing incidence** as the proportion of saplings known to have been browsed or lost (i.e. assuming all losses were due to ungulate browsing). As saplings were grouped within plots and plots grouped within sites, analyses of growth were performed by fitting linear mixed models[2] to individual tree-level data using the MIXED procedure in SAS version 6.12, with site and plot included as random effects and year, plot sapling density, species and other tree-level explanatory variables as fixed effects. Similarly, analyses of browsing incidence were performed by fitting generalised linear mixed models[3] (GLMM) using the SAS GLIMMIX macro, with site and plot as random effects and year, estimated offtake, species and other tree-level explanatory variables as fixed effects.

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[2] A **linear mixed model** is an extension of analysis of variance and multiple regression. It fits an observed variable to a linear combination of **fixed** explanatory variables which may be either factors (as in ANOVA) or covariates (as in regression). Also included are **random** variables, which account for variation from several sources (error strata) rather than just one. The residual errors at each stratum are assumed to be normally distributed.

[3] A **generalized linear mixed model** is an extension of a linear mixed model which allows residual errors at the lowest stratum (i.e. the individual observations) to have a distribution other than normal (e.g. binomial or Poisson). The dependent variable is related to the linear combination of explanatory variables through a link function. In the case of browsing of individual trees, the error term was binomial (trees were either browsed or not), and the link function was the ‘logit’ transformation.

RESULTS

DUNG COUNTS AND ESTIMATED OFFTAKE

All sites had higher ungulate dung counts during the winter than during the summer (Figure 1). However this pattern masks considerable seasonable variation between the three principal herbivore species: red deer, roe deer and sheep (Table 1). No dung of hares *Lepus* spp. or rabbits *Oryctolagus cuniculus* was found at any of the sites, although there were a very few saplings which appeared to have been browsed by lagomorphs, presumably vagrant rabbits.

Estimated offtake was low throughout the year at Ariundle (below 10 kg DM / ha) and during the summer at Nant East and Nant West. Firkin and Laudale had higher estimated offtake rates during the summer (maximum at Laudale during 2000 of 68 kg DM / ha) (Table 1). The high estimated offtake at Firkin was principally accounted for by sheep using the wood for much of the year, with red deer coming into the wood in the autumn and through the winter. At Laudale the high estimated offtake in summer was solely accounted for by a herd of feeder stags, which divided their time between the wood and semi-improved pasture nearby, on which they were given supplementary feed during winter. A small herd of cattle was introduced to the site in late summer 1999 (but with access to only three of the plots). Winter offtake varied considerably from 6.6 kg DM / ha at Ariundle to 162 kg DM / ha at Firkin. Both deer species and sheep occurred at moderate levels at the two Glen Nant sites during the winter.

BROWSING

For oak, birch and hazel, the incidence of browsing and loss was higher during winter than summer at all sites (Figure 2). Browsing and loss of rowan did not show such seasonal variation, with about 40 % of saplings browsed year round. During the summer, the maximum browsing incidence at all sites was between 20 and 40 %, and generally, proportionally fewer saplings were lost than during winter. Birch had a higher incidence of known browsing than oak and a lower incidence of loss, giving an overall similar pattern of maximum browsing with between 20 and 35 % of saplings browsed during the summer and 35-65 % during the winter. The maximum summer browsing for hazel was about 30 % and winter maximum browsing was about 50 %. Hazel, like oak had a higher rate of loss than the two small-seeded species birch and rowan. The maximum browsing incidence of oak saplings during winter was greatest at Firkin, where 72 % of saplings were browsed/lost, whereas at the other four sites the corresponding figure was about 40-50 %.

Relationship between offtake and browsing

The relationships of winter loss and maximum browsing incidence were not significant if all data were analysed, but became highly significant if data for Laudale were omitted. This was because the estimated offtake (Table 1) was on average the highest of all sites, owing to the presence of feeder stags, but browsing incidence was not particularly high (Figure 2). Analyses of the effect of offtake on winter browsing incidence are therefore presented with Laudale data omitted, and for the sake of consistency, summer data were treated in the same way.

Summer

In summer, there was no significant effect of estimated offtake on minimum browsing incidence, loss or maximum browsing incidence. There was a significant difference between species in the minimum browsing incidence (*P* < 0.001), decreasing in the order rowan > birch >hazel > oak. However, in summer, the low incidence of loss, although also differing significantly between species (*P* < 0.001), failed to compensate fully, and there was a significant effect of species on the maximum browsing incidence (*P* < 0.001), decreasing in the order rowan > birch >hazel > oak. The predicted probabilities of browsing are illustrated for the minimum browsing incidence (Figure 3). There were significant differences between years for both minimum browsing incidence and loss (both *P* < 0.001). They were also to some extent compensatory, but resulted in a significant difference between years in the maximum browsing incidence (*P* < 0.05), with the highest of 32 % in 2000 being significantly greater than the lowest of 26 % in 1998.

Winter

In winter, there was a highly significant positive relationship between the maximum browsing incidence and estimated offtake (*P* < 0.001), largely due to the relationship between loss and offtake (*P* < 0.001), as offtake had no significant effect on the minimum browsing incidence. There was a significant difference between species in the minimum browsing incidence (*P* < 0.05) with probability of browsing decreasing in the order rowan > birch >hazel > oak, but also a compensatory significant effect on loss (*P* < 0.001), with hazel > oak > birch > rowan. Thus, the small-seeded species (birch and rowan) were more likely to be found at the start of spring with signs of browsing, whereas the large-seeded species (oak and hazel) were more likely to disappear without trace (Figure 2). The net result was that there was no significant difference between species in maximum winter browsing incidence given the same estimated offtake, although the predicted incidence for rowan was somewhat lower than for the other three species (Figure 4).

The effects of sapling characteristics and environment on browsing of saplings

Analysis of browsing in relation to sapling height was limited to saplings under 30 cm tall, as saplings heights were positively skewed, with 95 % of saplings below that height.

Summer

In summer the probability of minimum browsing in summer increased significantly (*P* < 0.001) with sapling height (Figure 5). In contrast, the probability of loss during summer decreased with sapling height (*P* < 0.001), but was insufficient to compensate for known browsing, and the maximum browsing incidence also increased significantly with height (*P* < 0.001). The ground vegetation height class had a highly significant effect (*P* < 0.001) on loss during the summer, with saplings most likely to be lost from the shortest vegetation less than 5 cm tall, and this was reflected in the maximum browsing incidence, albeit less strongly (*P* < 0.05). There was no significant effect of moisture class on any measure of browsing in summer. Having accounted for the effects of sapling height and ground vegetation, the significant differences between species were broadly as reported above for minimum browsing incidence (*P* < 0.05) and loss (*P* < 0.001), but there was no difference between species in maximum browsing incidence.

The possible influence of sapling age could be tested for oak and hazel only, as only these large-seeded species could be aged reliably. Newly germinated seedlings were more likely to be browsed or lost during summer than saplings that were a year or more old (minimum browsing incidence *P* < 0.05, loss *P* < 0.05, maximum browsing incidence *P* < 0.01).

Winter

The minimum browsing incidence increased with sapling height ($P < 0.001$) and, as in summer, the probability of loss decreased with height ($P < 0.001$), but did not compensate fully, and the maximum browsing incidence (Figure 6) increased significantly with height ($P < 0.001$). The ground vegetation had no effect on either minimum or maximum browsing incidence, although there was a significant effect of ground vegetation height on loss of saplings in winter ($P < 0.01$), with saplings in shorter vegetation were more likely to be lost than saplings in taller vegetation.

Browsing in relation to sapling density

Indices of sapling density were calculated for each plot by taking the total number of saplings counted on the plot in 1998, and normalising within site[4]. The minimum browsing incidence increased with the plot sapling density index in both summer ($P < 0.01$) and winter ($P < 0.05$), but there was no significant effect on either loss or maximum browsing incidence in either season.

HEIGHTS AND ANNUAL GROWTH OF SAPLINGS

Mean height

Mean sapling heights at the five principal sites did not alter during the three years of the study (Figure 7). The average oak sapling height was between 12 and 14 cm, with saplings as small as 4 cm recorded. Hazel saplings ranged in average height from 13 cm to 17 cm. Birch saplings were on average taller, ranging up to 31 cm at Nant West. Rowan heights also varied between sites, from around 12 cm at Firkin and Laudale to 23 cm at Ariundle. Thus there was very little evidence of saplings, especially oak and hazel, growing above the field layer on any of the sites, regardless of the levels of ungulate use.

The larger oak saplings at Aird Trilleachan in the more open areas were on average 33 cm tall, whereas those growing under the birch canopy averaged 16 cm.

The effects of browsing on height

The change in height of a sapling during the summer was defined as the difference between its height at the spring visit and the greater height at the two later summer visits. This summer height change differed significantly between years, between species and between saplings known to have been browsed during the summer and those not browsed ($P < 0.001$ for each effect). There were also significant interactions between these three effects. On average, browsed saplings of all species lost height during the summer (Figure 8), although the mean differed significantly from zero for oak and rowan only. Despite the mean increase in height of unbrowsed saplings being significantly greater than zero for all species, the actual average increments during the growing-season were small, with birch being the greatest at 2 cm (Figure 8). Changes in height were significantly less during the wet summer of 1998 than during 1999 or 2000.

The change in height of a sapling between years was defined as the difference between its greatest height at any visit in one summer and the next. For the purposes of this analysis, a

[4] This procedure was required because the counts differed considerably between sites, owing to some species being poorly represented. It involved centring the data for the site by subtracting the site mean count and standardising by dividing by the site standard deviation count to yield z-scores for each plot, which were comparable between sites.

sapling was treated as browsed if it was known to have been browsed during either of the two successive summers or the winter between. There were significant effects of year ($P < 0.01$), species ($P < 0.05$) and browsing ($P < 0.001$) on the change in height, and a significant interaction of species with browsing ($P < 0.01$). Browsed saplings of all species showed a significant reduction in height (Figure 9). Of the four species, only birch had a significant increase in height between years if unbrowsed, and that was only an increment of 2 cm on average.

There were no significant effects of shading by the tree canopy, ground vegetation height class or ground vegetation moisture class on height increments of unbrowsed saplings during the growing-season. However, if not browsed during the summer, newly-germinated oak and hazel seedlings grew on average 0.8 cm, significantly more ($P < 0.01$) than the mean increment of 0.3 cm for saplings that were a year old or older

However, mean height increments can be somewhat misleading, as many unbrowsed trees did not increase in height at all during the summer. The growth of unbrowsed saplings was therefore examined further by defining growth as "increasing in height by more than 2 cm between the spring visit and either of the two later visits, or an increase in height of 1 cm plus the addition of 2 or more new leaves"[5]. On this basis the mean proportions of unbrowsed saplings which grew were roughly 20-35 % of oak, 25-40 % of hazel, 45-75 % of birch and 30-50 % of rowan (Figure 10). Overall, only about a third of unbrowsed saplings grew during the course of the summer, and their mean height increments were 3.0 cm for oak, 4.3 cm for hazel, 5.4 cm for birch and 3.9 cm for rowan. The explicit recording of growth during summer 2000 gave broadly similar results (Figure 11), although rather more saplings at Firkin were recorded as growing by this method. Mean height increments of unbrowsed saplings were also similar at 2.8 cm for oak, 2.7 cm for hazel and 4.1 cm for birch, but rather less at 2.4 cm for rowan.

Growth of oak under more open conditions

At Aird Trilleachan, the small saplings underneath the birch canopy grew on average by 1.0 cm between 1999 and 2000 (0.4 cm between late May 2000 and late September 2000), whereas the larger saplings in fairly open conditions grew by 2.0 cm (1.4 cm ditto). There was some browsing to saplings during the winter months (presumably by a break-in to the exclosure or possibly by a small number of roe deer that were probably resident), but browsing had no significant effect on the change in height of saplings between 1999 and 2000.

The small oak saplings underneath the birch canopy at Aird Trilleachan which grew during 2000 were compared with unbrowsed oaks at the five principal sites which grew and had not germinated in spring 2000 (as all Aird Trilleachan oaks were older). There was no significant difference in height increment during summer 2000 between the sites. However, the Aird Trilleachan oaks had a significantly higher maximum leaf count of 20 leaves than at all the other sites, which ranged from 3 to 10 ($P < 0.001$). The mean increase in leaf count also differed significantly between sites ($P < 0.01$), with the highest mean increase of 10.6 leaves at Aird Trilleachan, but the proportional increase in leaf number did not differ significantly between sites.

[5] This definition was applied to allow for variation due to measurement error or changes in moss depth. Saplings apparently growing by just 1 cm but not putting out new leaves were omitted as uncertain growth.

DAMAGE BY INVERTEBRATES AND FUNGI

The general pattern was of a high incidence of leaf damage and an increasing trend during the course of the summer (Figure 12). By the end of the summer, it was usual for upwards of 80 % of saplings to show some form of invertebrate or fungal damage. The third visit in 1998 was too late for the data to be meaningful, as many sapling had dropped their leaves.

Although the incidence of leaf damage was very high, the mean proportion of leaf tissue damaged or removed from saplings which were attacked was generally between about 10 and 20 % by the end of the summer (Figure 13), having showed a similar pattern of increase during the season. The mean leaf area damaged was highest for oak saplings with on average 19 % of the leaf area damaged by early autumn, but the highest rate of increase in damage severity was shown by rowan.

PERFORMANCE OF OAK IN AREAS CLEARED OF CONIFERS

Sapling survivorship

Significant differences were detected in sapling survivorship rates between plots with brash and plots without brash ($P < 0.05$). In the unfenced plots with brash, only 50 % of the saplings had survived by June (only three months after planting) compared to 86 % of saplings in the plots without brash (Figure 14). Similarly in the fenced area, there was 100 % survivorship of saplings in the plots without brash compared to only 53 % of saplings planted in the brash plots surviving by September.

In June, sapling survival was greater for the fenced brash plots then the unfenced brash plots, but by September only around 50 % of the saplings had survived in both the fenced and unfenced brash plots. However, the difference in June may have arisen if some saplings in the unfenced brash plots had already had all their leaves removed by browsing, and could not be located amongst the dense tangle of brash. As only 53 of the saplings were located in the fenced brash plots in September and only 11 out of the 53 saplings were browsed (predominantly by voles), it seems unlikely that browsing was the only factor responsible for poor survivorship.

Browsing incidence

The browsing incidence in the unfenced clear-felled habitats was substantially higher than under the oak and birch canopies (Figure 15). The browsing incidence for the saplings planted under the oak and birch canopies were very close to the 17 % summer browsing incidence for naturally germinated oak saplings on the principal Nant West site. By September in the unfenced clear-felled habitats, the 86 % browsing incidence on saplings planted within the no brash plots was significantly higher than the 42 % incidence on saplings planted in the plots with brash ($P < 0.01$). By September, 10 % of saplings were browsed in both the brash and non-brash plots within the exclosure. A roe deer pellet group was found within the exclosure in September, indicating that at least one animal had broken into the exclosure. Lagomorph browsing was also observed, and there was evidence of vole damage to six oak saplings in the brash plots within the exclosure.

Further evidence that brash was giving the saplings protection against ungulates came from the unfenced plots with brash. Saplings were significantly more likely to be browsed with decreasing brash depth ($P < 0.05$). The mean brash depth where saplings were browsed was 23 cm, whereas for saplings that were not browsed it was 30 cm.

Oak sapling leaf number

Significant differences in the mean number of leaves per sapling were detected between brash plots and plots without brash, and between fenced and unfenced plots (Figure 16). The average leaf number for unbrowsed saplings in September was 8 in fenced brash plots compared to 15 in fenced plots without brash ($P < 0.05$). The opposite pattern was observed for unfenced plots with more leaves per sapling in the brash plots (mean 10 leaves) than in the plots with no brash (mean 4 leaves). There was a significant difference between clear-felled habitats in the increase in leaves between June and September ($P < 0.05$), with a mean increase of 5.5 for fenced plots without brash compared to 0.9 for fenced plots with brash.

Sapling height and growth

Growth of the saplings was negligible in terms of height increments, with even some unbrowsed saplings apparently decreasing in height during the growing-season. When the growth criteria used for the principal sites were applied to unbrowsed saplings, only 12 % of oak saplings planted under the birch canopy grew between June and September and 20-30 % of the oak saplings in the other treatments grew. For all saplings irrespective of whether they were browsed or not, 36 % of oak saplings planted under the oak canopy were classed as having grown compared to only 18 % of saplings planted under the birch canopy.

Incidence of invertebrate damage

The incidence of invertebrate damage in June was greater for saplings planted under an oak canopy than in the clear-felled areas or under a birch canopy (Figure 17). This suggests a degree of host specificity under an oak canopy. The general pattern was of a high incidence of leaf damage by the end of the summer, especially on oak where 80 % of saplings were damaged by invertebrates.

Although the incidence of leaf damage was very high, the mean percentage of leaf tissue removed was generally between 10 and 25 % (Figure 18). Saplings planted under the oak canopy were more heavily defoliated than saplings in the clear-felled areas or under the birch canopy. In the clear-felled areas, the percentage of leaf damage showed an increase during the summer.

Ground vegetation and natural regeneration

Changes in the ground flora occurred in the clear-felled areas. Prolific regeneration of early successional species such as birch was already taking place by the time of experimental planting in response to the disturbance initiated by conifer removal. The birch established rapidly on the plots with up to 76 seedlings recorded on a 2 m x 2 m plot. The nearest oak tree to the plots was only 30 m away, but no naturally regenerated oak seedlings were found, despite the favourable light and open conditions. This may be because the wood experienced a particularly poor mast year in 1999.

Further recolonisation of the ground flora occurred rapidly between June and September 2000. In the clear-felled areas, species such as rosebay willow-herb *Chamaenerion angustifolium*, foxglove *Digitalis purpurea*, soft rush *Juncus effusus* and sedges *Carex* spp. were locally abundant. In the unfenced area the ground vegetation was very short (mean 4 cm) and dominated by mosses, indicating the locally heavy grazing pressure exerted by a group of up to eight sheep which made use of the coupe throughout the summer. In contrast, the ground vegetation within the exclosure was considerably taller (mean 10 cm) and had a very different species composition.

DISCUSSION

BROWSING

The five principal sites studied covered a wide range of summer and winter use by ungulates, yet the relationships established between estimated ungulate use and browsing of saplings were weak, with the predicted browsing incidence at high use being not much more than that at low use. There are a number of possible reasons why this should be so.

Many saplings disappeared without trace in the two months between one summer visit and the next, or during the winter period of dormancy. The two larger-seeded species, oak and hazel, were more likely to disappear than birch and rowan. Undoubtedly some of the missing saplings were browsed, as saplings often 'reappeared' during the summer following browsing, when new leaves were grown from the bitten stem. Some saplings were browsed down almost to ground level, making the stem practically impossible to find, unless new leaves were grown. There is also the possibility of small saplings being uprooted and removed entirely from the plot, even if not completely consumed. A few uprooted saplings were found, but very close to the position at which they had been growing. High loss rates of around 10 % were recorded for summer 2000, but presumably many of these saplings would have been relocated the following year, had the study continued. We attempted to allow for this problem by analysing the minimum browsing incidence (the browsed sapling was located), the incidence of loss, and the maximum browsing incidence (assuming all losses were due to browsing). However, the assumption that all losses were due to browsing may not be justified, as Langbein (1997) found similar summer mortality of oak seedlings in fenced and unfenced plots within the same site, suggesting that summer mortality occurred for the most part independent of grazing by deer and sheep. The true incidence of browsing therefore probably lay somewhere between our minimum and maximum values, although our data suggest that the assumption is more likely to be valid for winter than for summer.

It was regrettable that we felt it necessary to omit data from one of the five sites when relating browsing to use by ungulates. It was clear that although large amounts of red deer dung were found on the plots at Laudale, limited grazing occurred within the wood itself, where the ground flora was dominated by purple moor-grass *Molinia caerulea*, which is dead and unpalatable during winter. A herd of around 40 stags was given supplementary feed during the winter, and during the summer the same animals grazed on pastures adjacent to the wood, moving into the wood if disturbed. However, such behaviour may also hint at the general problem of weak relationships between browsing and dung, namely deer entering woods to shelter for short periods during winter, and possibly leaving considerable amounts of dung but browsing very few saplings. This phenomenon was especially likely at the other site with high dung counts, Firkin Wood, which formed a narrow band of woodland between the open hill and a main road. If this were so, and we were able to estimate the proportions of time spent feeding in the wood and sheltering / resting without feeding or with minimal feeding, then we would expect to obtain a closer relationship between the use made of the site for feeding and the incidence of browsing.

The derivation of a single estimated offtake for each site in each season was also not ideal, as it may have masked differences in browsing patterns between the two deer species and sheep. However, preliminary analyses aimed at relating seasonal browsing incidence to species-specific habitat use estimates proved problematic, partly because of the (apparent) absence of some species from some sites (Table 1).

Although there were difficulties in interpreting analyses of browsing incidence and use of the sites by the three ungulate species, there was a significant positive relationship between minimum browsing incidence in summer and use by roe deer, suggesting that this species might be the principal browser of small tree saplings. Indeed, roe deer are generally regarded as a browsing ungulate, whereas red deer and sheep are regarded as grazers. Furthermore, it is possible that browsing by roe deer might actually contribute to the poor relationships between browsing incidence and estimated offtake. If roe deer were concentrating their foraging on saplings, particularly around bud-burst in spring, when the young tree leaves would be rich in nutrients, then they would damage a large number of saplings per pellet group deposited. Fresh sapling leaves might well be the most attractive forage available, as the ground flora of the sites was dominated by grasses (typically bents *Agrostis* spp., wavy hair-grass *Deschampsia flexuosa*, etc.) and, especially at Ariundle, bluebell *Hyacinthoides non-scripta*. Such monocotyledons have basal meristems, and thus the most nutritious growing parts of the plant would be difficult for ungulates to reach. The correlations in both summer and winter between known browsing and the density of saplings on the plot also suggest that saplings were being particularly sought for browsing by at least one of the ungulate species for at least some part of the year. Browsing during early spring by roe deer could become even more important if red deer numbers in the cSAC areas are reduced, as there is some evidence that roe deer numbers might be limited in some areas by competition with red deer (e.g. Latham *et al.*, 1996), and may increase following a red deer cull.

Taller saplings were more likely to be browsed than shorter saplings, and this height effect was slightly more pronounced during summer than during winter. Furthermore, although saplings were more likely to disappear completely from short vegetation than from taller vegetation during both seasons, vegetation height had a significant effect on maximum browsing incidence during summer only. Even when height had been taken into account, newly germinated oak and hazel seedlings were more likely to be browsed than older saplings, possibly because they had larger leaves or the leaves were richer in nutrients. These findings offer further evidence that ungulates deliberately search for saplings to browse during the summer and damage the most apparent saplings, but during the winter browse them at random whilst grazing the ground vegetation sward. Although extrapolation should be treated with considerable caution, the relationship between known browsing incidence in summer and sapling height up to 30 cm suggests that once a sapling were to attain a height of about 70 cm, it would almost certainly to be browsed at least once during summer given the conditions prevailing at the sites studied.

GROWTH OF SAPLINGS

Saplings were not able to compensate in terms of height within one season for material lost to browsing, as was also observed in other studies of grazing in upland woodlands (Hester *et al.*, 1996; Nolan *et al.*, 1998). However, even saplings which were not browsed grew very little, if at all, on the five principal sites. In most cases, fewer than half of unbrowsed saplings gained in height during the summer, and mean sapling heights failed to reach 20 cm for most species on most of the sites. Birch was the only species to show a significant increase in height between years if not browsed. Although there was no significant effect of shading by the tree canopy on growth across all species and sites, the larger birch saplings tended to be clustered on the more open plots. Newly germinated oak and hazel saplings grew well for one season, but once the initial seed reserves were exhausted, they performed less well in subsequent years. Oak saplings at Aird Trilleachan, growing under a birch canopy, had more leaves than oak saplings growing in their parents' shade, and also managed a very modest 1 cm mean growth over the course of a year. Oak saplings planted into the experimental areas cleared of conifers did not gain in height during the subsequent summer, but that is to be expected following transplanting. When protected from grazing and free from shading by brash, though, they grew substantial numbers of new leaves, and were presumably therefore well-prepared to increase in height during subsequent summers. The largest oak saplings studied were in the most open conditions at Aird Trilleachan, and they grew on average 2 cm in one year.

This lack of satisfactory growth of oak saplings has been found in previous studies. Shaw (1968) found that growth of oak saplings in an oakwood in Wales was generally poor, with the height increment often being negative. 50 % of saplings that were aged from stem sectioning were only in their first or second year with few surviving over four years. The oldest sapling sampled was in its eighth year but the tallest sapling (16.5 cm) was in its first year. Langbein (1997) found that many oak saplings at or below the height of the surrounding field vegetation were already several years old, but remained at heights less than 35 cm and often less than 20 cm due to persistent browsing over the years. The mean height increments for unbrowsed birch and rowan saplings in this study were rather less than half of those reported by Hester *et al.* (1996) for unbrowsed saplings of the same species in an upland woodland in Cumbria.

A further limitation on the potential growth of saplings in Atlantic oakwoods is the presence of bracken. Within the principal sites, dense bracken was generally confined to the more open areas; under a dense canopy it was generally much thinner. Areas beyond the main oak canopy that would otherwise be suitable sites for oak regeneration were generally dominated by dense and very tall stands of bracken. Bracken has been shown to affect oak sapling growth by shading (Jarvis, 1964), and competition from bracken in the summer months has been shown to have a significant effect on accumulated sapling biomass and net leaf area (Humphrey and Swaine, 1997a) partly as a result of reduced light availability. The dying back of bracken fronds at the end of the summer was proposed by Watt (1919) to cause mechanical damage to oak saplings such as stem breakage. No such damage was observed by Humphrey and Swaine (1997a), although sapling biomass and net leaf area were significantly reduced by smothering of bracken fronds in winter, and it was suggested that initiation of growth at the start of the growing-season might be delayed through shading by the dead bracken fronds.

DAMAGE BY INVERTEBRATES AND FUNGI

A further limitation on the growth of seedlings and small saplings, particularly of oak, is defoliation by invertebrates. The great majority of saplings had been attacked to some extent by the end of the summer, with damaged oaks on average losing almost 20 % of their leaf area to insects or fungi. Higher levels of insect damage to saplings planted under an oak canopy were recorded at Ariundle by Humphrey and Swaine (1997b), with 54 % of leaves suffering between up to a quarter of leaf area lost and 24 % of leaves losing more than half their photosynthetic surface. It has previously been shown that oak rarely regenerates under its own shade, or even in small gaps (less than 0.1 ha) owing to the impacts of defoliating insects (Shaw, 1974; Humphrey and Swaine, 1997b). Larger gaps are normally needed (upwards of 0.4 ha) to ensure regeneration. Also, at low light levels, Jarvis (1964) found that mildew *Microsphaera alphitoides* was an important limiting factor for one year old seedlings.

Thus the incidence of invertebrate damage on saplings under an oak canopy may seriously affect their growth. Low photosynthetically active radiation under a mature oak canopy will act synergistically with sapling leaf area losses to reduce photosynthetic potential. However, there was evidence that the severity of damage to oak sapling is likely to be rather lower on oak saplings growing away from the oak canopy compared to those growing underneath it.

THE POTENTIAL SPREAD OF OAKWOOD

The potential exists within some Atlantic oakwoods for fragmented oak-birch stands to become connected by the colonisation, either naturally or by planting, of areas cleared of exotic species, including commercial conifers and *Rhododendron*. In this study, we investigated the potential for protection by fencing and by brash on oak saplings planted in one such area recently cleared of conifers. However, the data from only one year's observations at a single site merely provide an indication of the initial responses; a longer series of observations from a fully-replicated experiment would be required in order to predict how rapidly regeneration might proceed in such conditions.

Ad hoc surveys conducted around the periphery of the principal sites revealed that there were extremely few, if any, oak seedlings beyond the canopy of parent trees. It would appear that acorns are not being dispersed in any appreciable numbers, and that oak may not therefore be able to colonise cleared areas, or any other more open areas with sufficient light for growth, in the foreseeable future, unless given assistance by man. The most effective dispersers of acorns, jays *Garrulus glandarius* and red squirrels *Sciurus vulgaris* were rare or absent from the fragmented study sites.

Large number of birch seedlings had established in the clear-felled areas, but no naturally regenerating oak seedlings were found. It is likely, therefore, that without planting of oak seedlings, birch would dominate clear-felled areas until the slower growing oak reached the canopy layer. The erection of fencing to exclude both domestic and wild herbivores may aid already established tree saplings, if such 'advance regeneration' is present. However, as seen in this study, less than a year after exclosure there was rapid development of tall ruderal species, which may limit natural tree colonisation and shade already established tree seedlings.

The browsing incidence during the first summer after planting was higher on saplings in clear-felled areas than under adjacent oak and birch canopies. In the clear-felled areas, lines of brash left after felling protected saplings against browsing by ungulates. Browsing rates in the clear-felled areas were twice as high for saplings planted between lines of brash than for saplings planted within the brash lines, with the depth of brash also affecting the probability of browsing. However, survivorship and performance was lower for saplings planted in the brash than for saplings planted in the plots with no brash presumably because the latter experienced higher light levels, and moreover, six saplings planted within brash were apparently browsed by rodents. It therefore seems likely that the best results would be obtained by planting between lines of brash, but only if grazers were at very low density or absent completely. In this case, the problem was one of high local grazing pressure by a few sheep. It is not clear how natural but low numbers of red deer or roe deer might impact upon regeneration in clear-felled areas.

GENERAL CONCLUSIONS

General predictions of the relationships between ungulate density and oak regeneration are complex and cannot really be made with any degree of certainty. The incidence of browsing and disappearance of saplings in the study sites was fairly high, and higher in winter than summer, but it could not readily be predicted from dung counts, which provide the best index of herbivore use over time (Putman, 1984). However, it is most unlikely that browsing alone is preventing regeneration of the woods, except perhaps of a few saplings growing in gaps in the canopy, as saplings which escaped browsing showed poor growth performance. The levels of light under the canopy of mature oaks are insufficient to allow saplings to survive repeated browsing or grow sufficiently to compensate for it. In more open areas oak saplings that have survived for longer periods do manage to show a satisfactory growth rate following the exclusion of grazing.

Our results also indicate that the use made of the woods by ungulates varies on a seasonal basis, in some places quite dramatically, and that therefore blanket recommendations based upon a 'threshold density which will allow regeneration' are likely to be grossly over-simplistic. Even at the least used site, Ariundle, with estimated herbivore use of around 1 roe deer day / ha (nominally equivalent to about 1.2 animals / km^2 if all habitats were used homogeneously) during summer and 3 roe deer days / ha and 5 red deer days / ha during winter (likewise equivalent to about 3.3 animals / km^2), there was no increase in tree sapling heights and on average roughly 25 % were browsed each summer and 40 % each winter. We suggest that roe deer, and possibly sheep, may actively select hardwood saplings as browse during the growing-season, especially during spring, but that during winter, the greatest threat to saplings comes from the larger red deer which enter the woods, probably principally to obtain shelter during periods of bad weather, and damage saplings incidentally as they graze the ground vegetation. In order to separate these effects fully, and experimental programme of seasonal protection of saplings would be required.

There is no doubt that the Atlantic oakwoods have the potential to regenerate. Newly established oak seedlings were abundant, with some of the highest sapling densities recorded in some of the more heavily grazed woods. As oaks are long-lived, the number of saplings within all the oakwoods sites is more than adequate for replacing existing mature oaks, if opportunities for regeneration were to be created, for example under the long-rotation or standard rotation high forest management models proposed by Peterken and Worrall (2001).

We suggest that the small and fragmented nature of these oakwoods means they are not able to support many squirrels and jays. As a result there is little dispersal of acorns, and oak saplings are confined to growing under the shade of mature trees. However, even if there were greater natural dispersal of acorns or planting within more open areas and grazing were excluded, there is an additional problem of bracken dominance of many open areas. Effective control of dense bracken stands would therefore be necessary to promote successful regeneration.

Atlantic oakwoods have a long history of management and utilisation by local communities, but by the beginning of the 20th century this traditional management had largely ceased. As a consequence of light limitation, browsing, insect defoliation and lack of dispersal, active management of these oakwoods is essential. The reintroduction of active management of these woodlands, including practices such as coppicing, would promote their continued viability, and general management guidelines for upland semi-natural oakwoods recommend that felling coupes of at least 0.3 to 1 ha are necessary to promote successful natural regeneration of oak. Several factors need to be addressed before these oakwoods can regenerate successfully. In order to promote the expansion of oakwoods (especially into novel habitats from which exotic species have been cleared) and increase connectivity between woodland fragments, a programme of oak sapling planting should be considered.

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Table 1 Seasonal estimates of ungulate use and offtake at principal sites 1998 - 2000.

Site	**Estimated ungulate use (animal days / ha)**						**Estimated offtake**	
	Red deer		**Roe deer**		**Sheep**		**kg DM / ha**	
	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter
Ariundle 1998 1999 2000	0 1.2 0.3	6.7 3.6	0 0.8 0.8	2.4 2.9	0 0 0	0 1.5	0 3.2 1.3	9.3 6.6
Firkin 1998 1999 2000	0.3 4.6 13.6	78.5 109	0 0 1.6	14.0 10.6	0.5 23.5 10.8	21.6 30.9	1.3 43.3 46.8	119 162
Laudale 1998 1999 2000	5.8 20.8 26.2	112 99.3	0 0 0	0 0	0 0 0	0 0	15.0 54.0 68.2	157 139
Nant East 1998 1999 2000	0 0 0.6	5.3 8.0	0 0 0	17.8 7.7	0 0 1.5	9.3 9.3	0 0 3.4	20.3 19.6
Nant West 1998 1999 2000	0 0 0	6.2 8.0	1.2 0 0	26.5 8.7	0.5 0 0	15.7 26.5	1.6 0 0	29.3 32.0

Conversion rates for intake (kg DM / day) adapted from Armstrong (1996):
Summer : red deer 2.6 (Laudale), 2.25 (other sites); roe deer 0.75; sheep 1.4.
Winter : red deer 1.4 (Laudale), 1.25 (other sites); roe deer 0.4; sheep 0.7.

Figure 1. Mean seasonal dung counts (total of red deer, roe deer and sheep) per 100 days at each site. Error bars show 1 standard error.

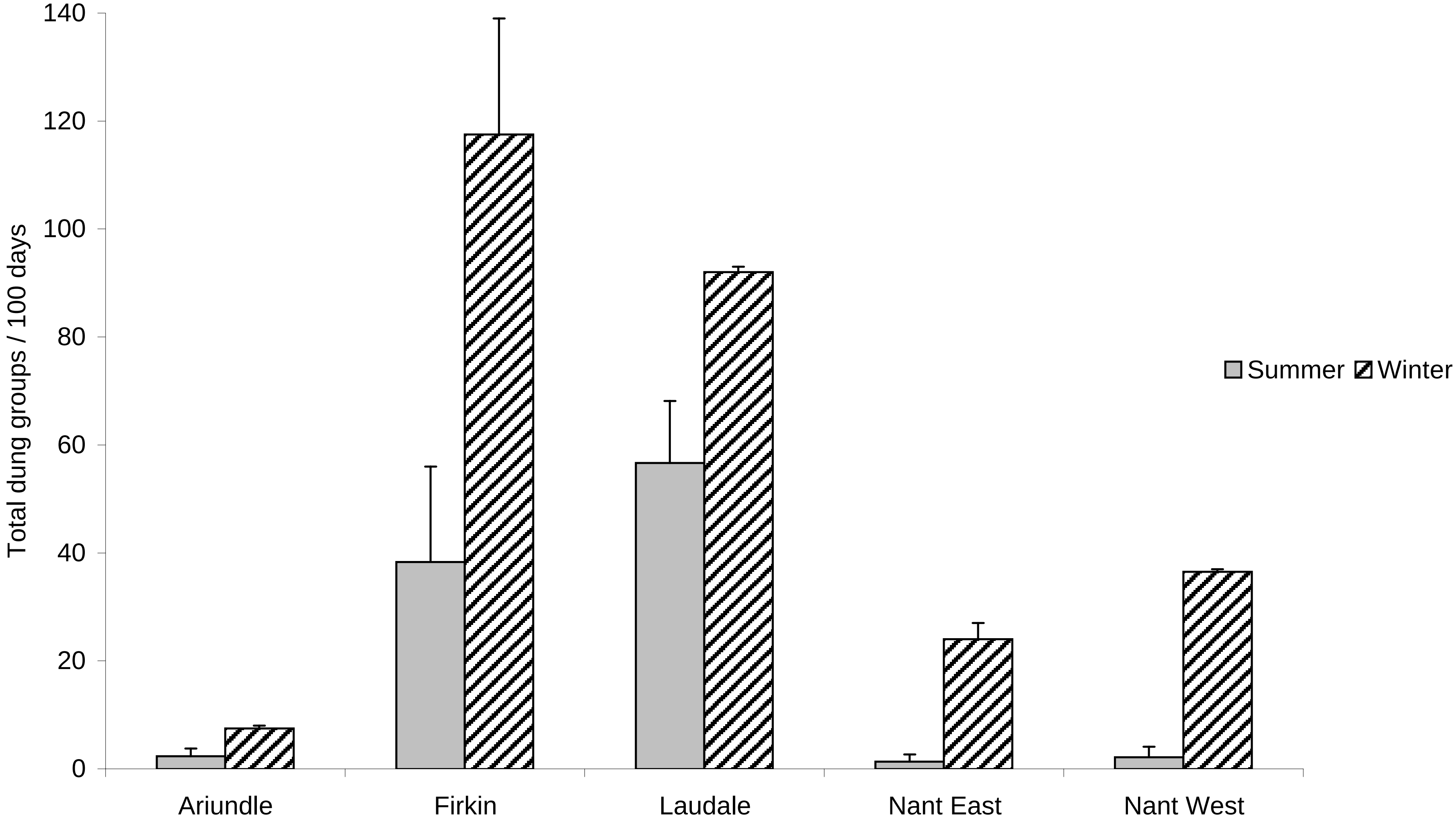


Figure 2. Mean seasonal incidence of known browsing and loss for oak, hazel, birch and rowan saplings (minimum 15 per species)

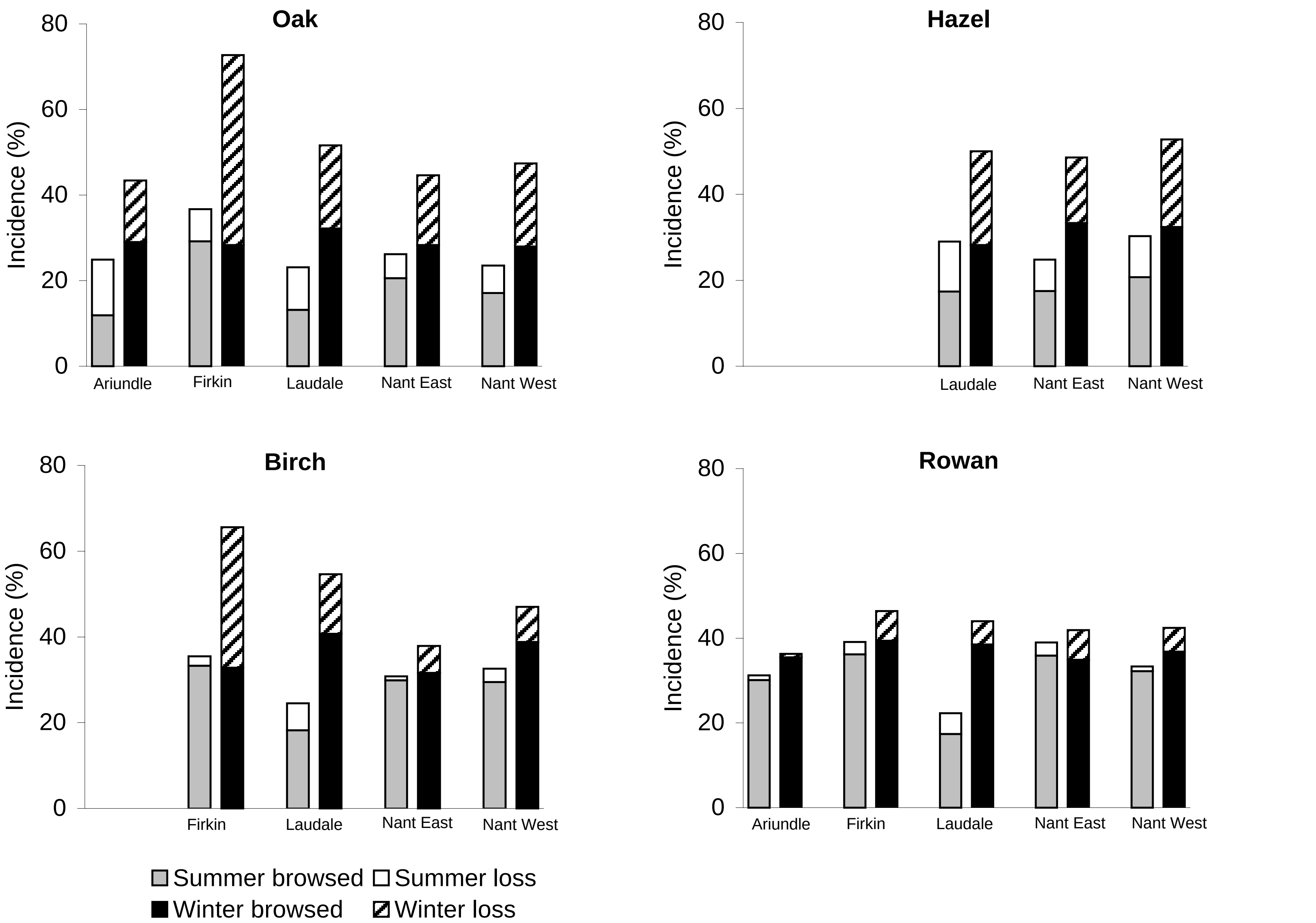
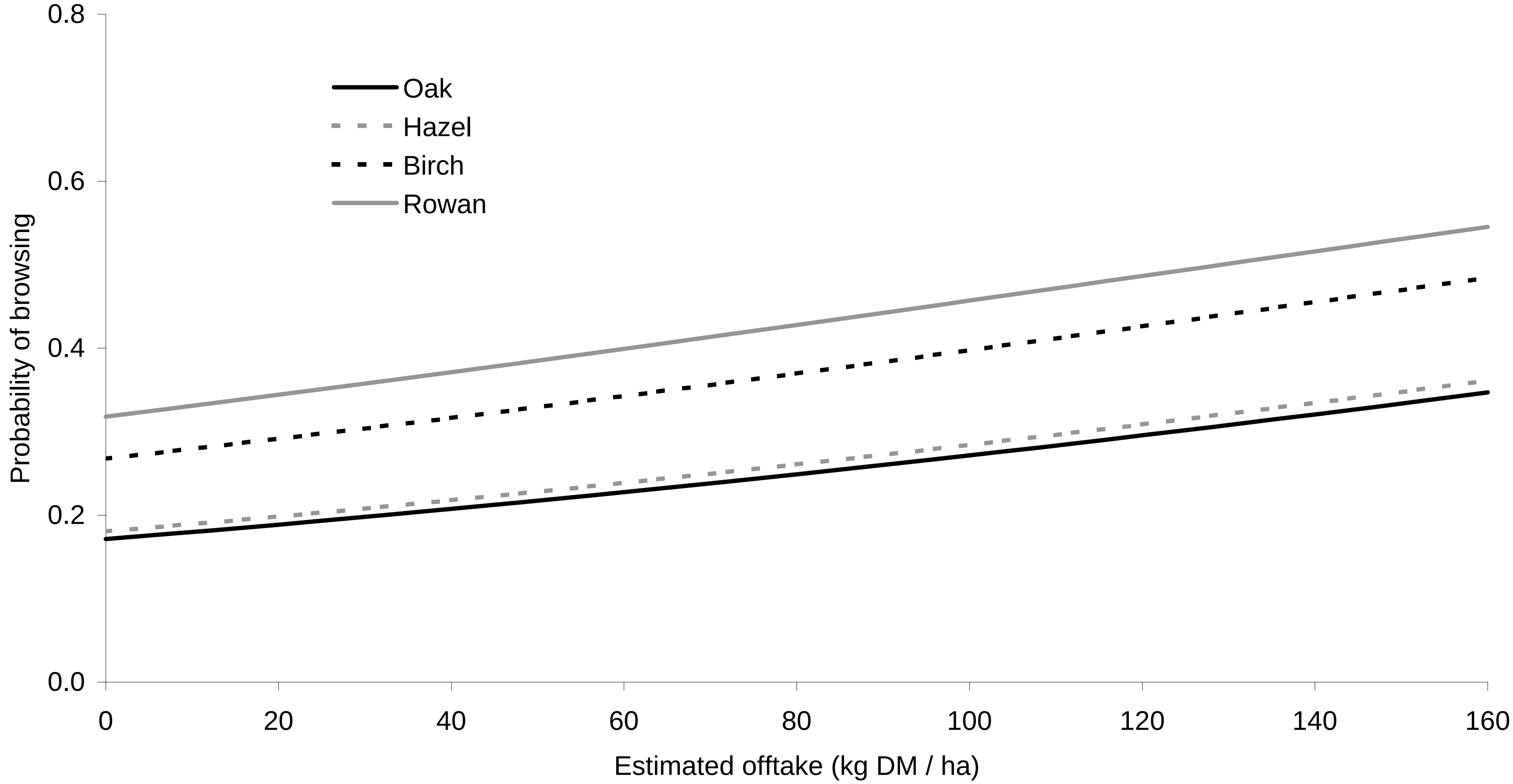


Figure 3



Oak
Hazel
Birch
Rowan
0.8
0.6
0.4
0.2
0.0
Probability of browsing
0
20
40
60
80
100
120
140
160
Estimated offtake (kg DM / ha)

Figure 4. Predicted probability of browsing or loss of saplings during winter in relation to estimated offtake by ungulates.

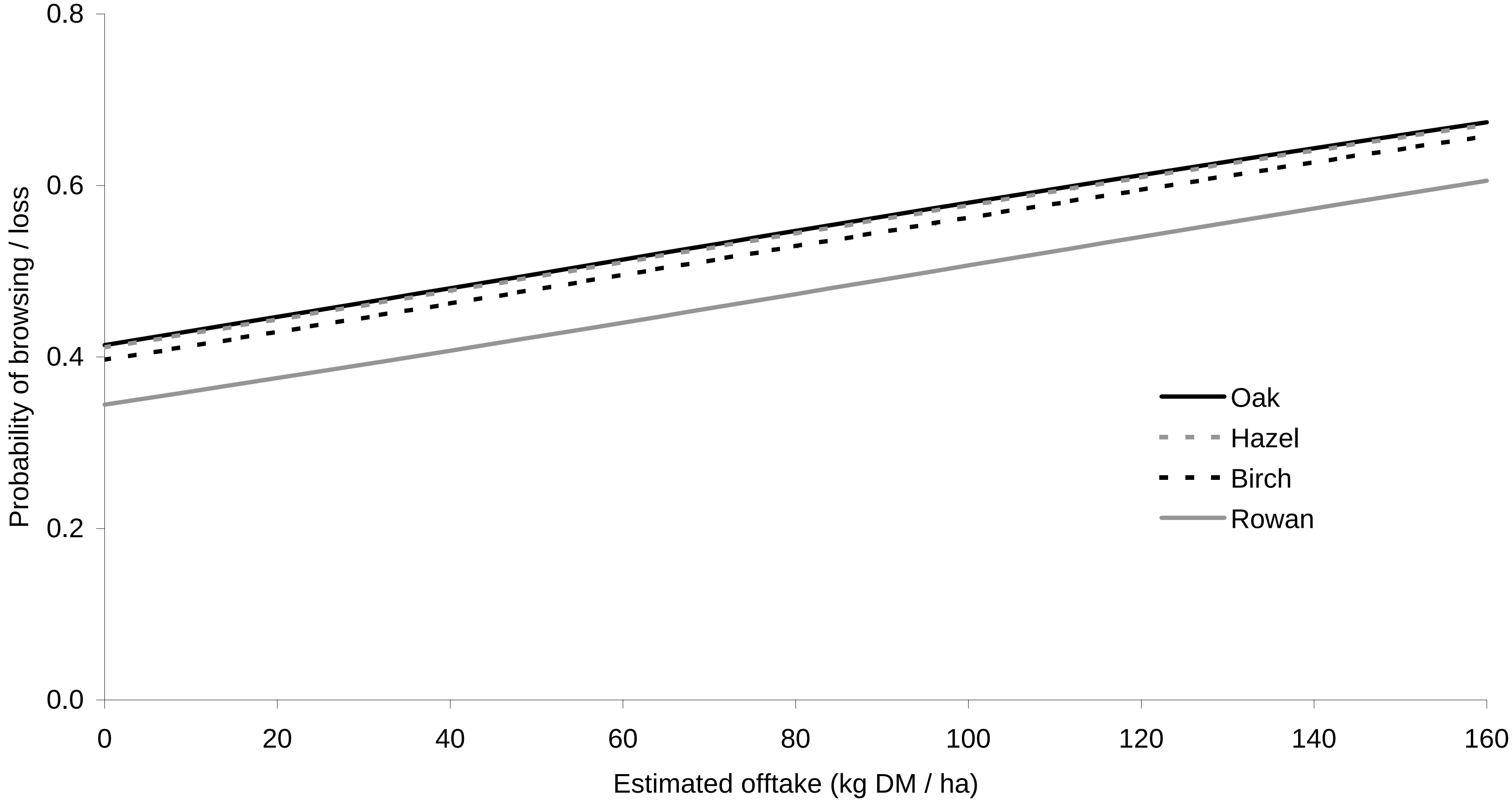


Figure 5. Predicted probability of minimum browsing incidence during summer in relation to sapling height.

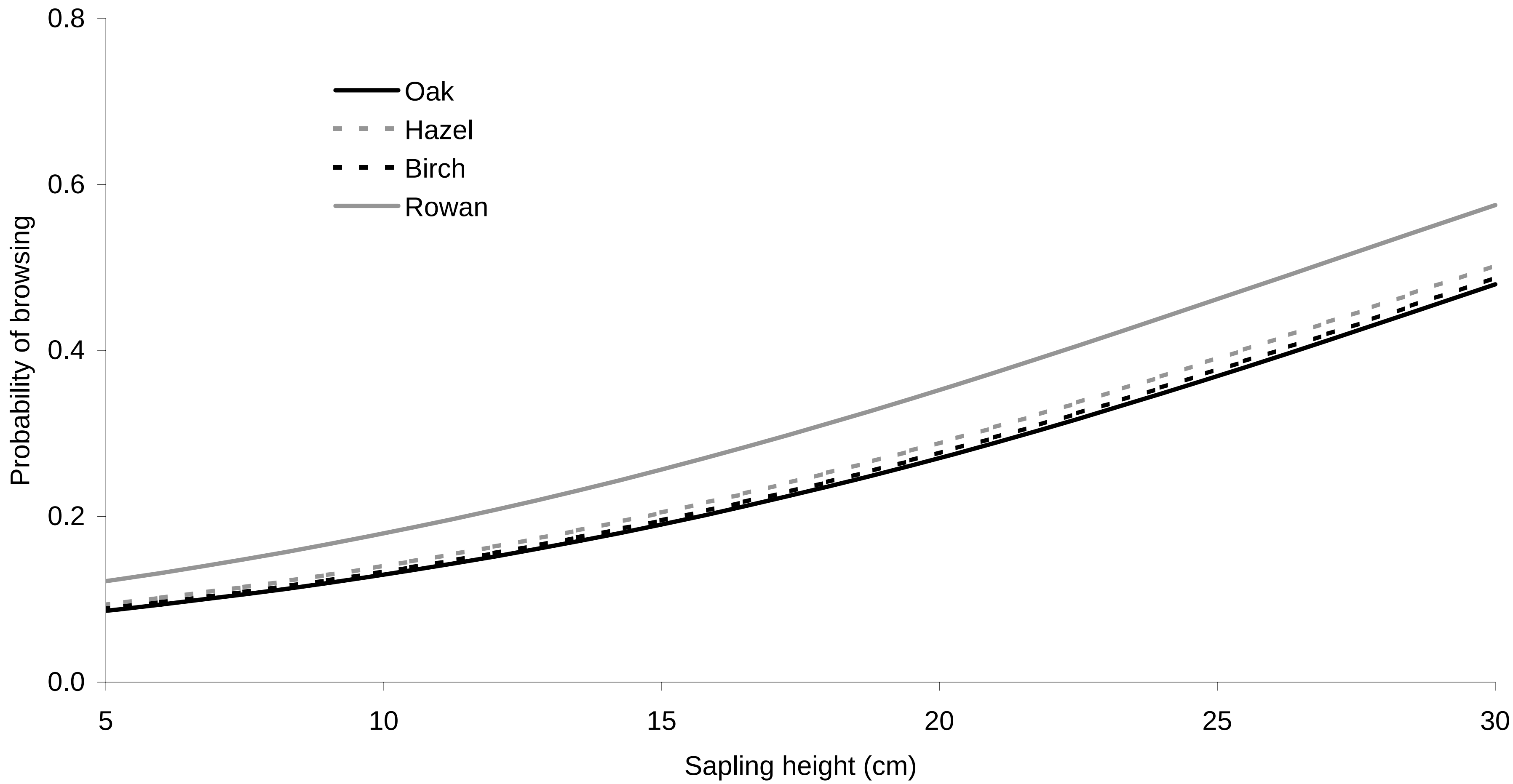


Figure 6. Predicted probability of maximum browsing incidence during winter in relation to sapling height.

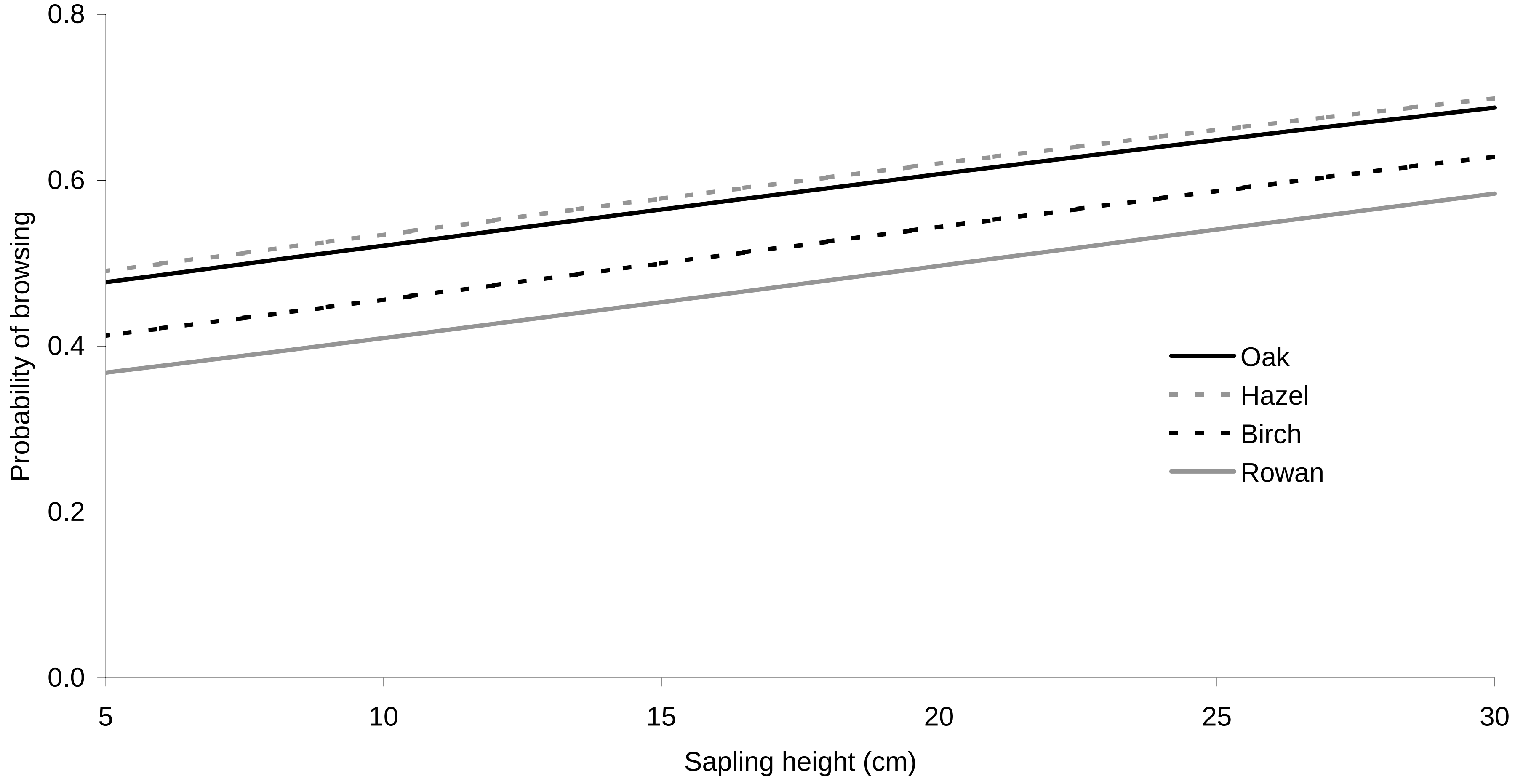


Figure 7. Mean height of oak (O), hazel (H), birch (B) and rowan (R) saplings in three successive summers 1998 to 2000.

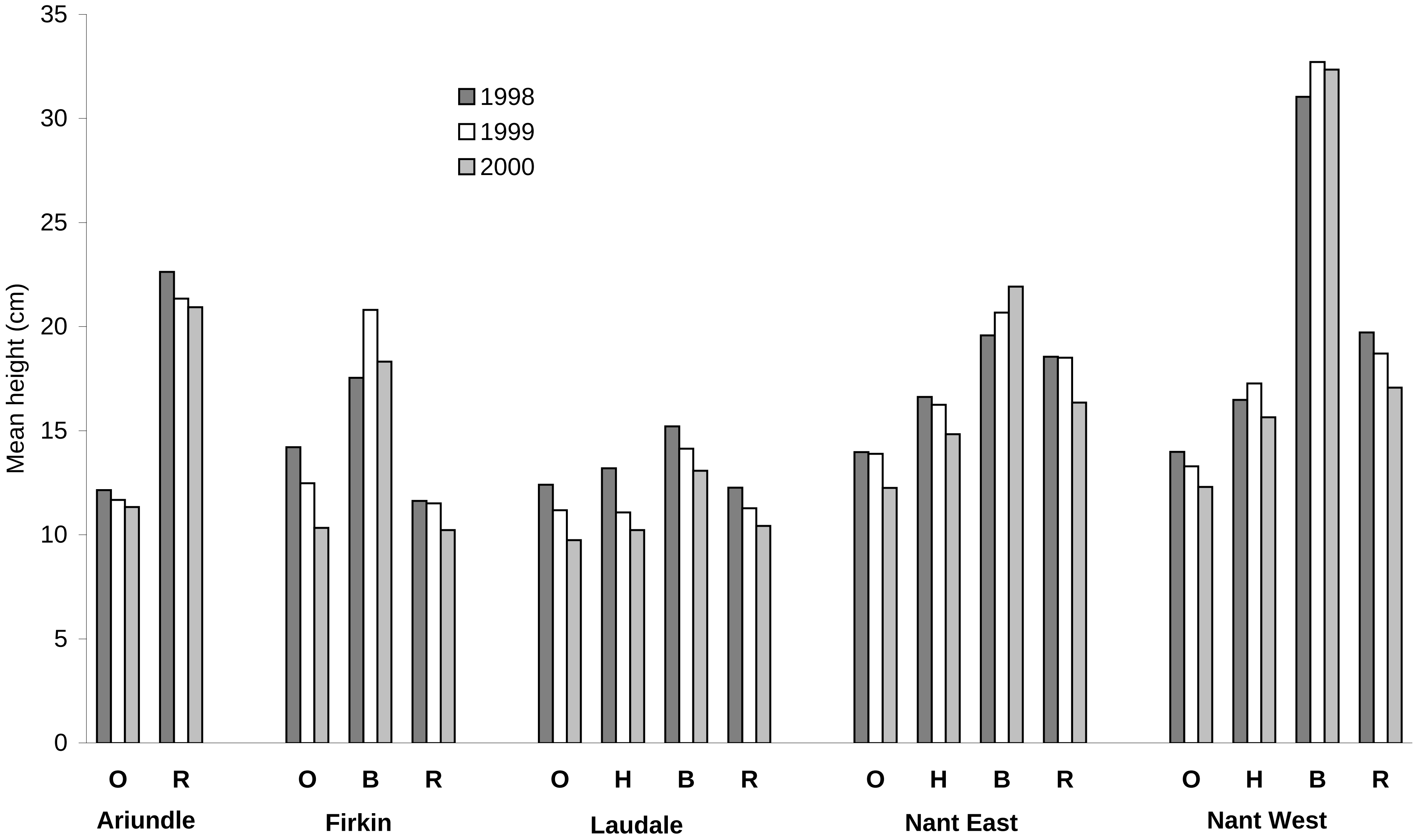


Figure 8. Mean change in height during the summer of browsed and unbrowsed saplings (averaged across years and sites).

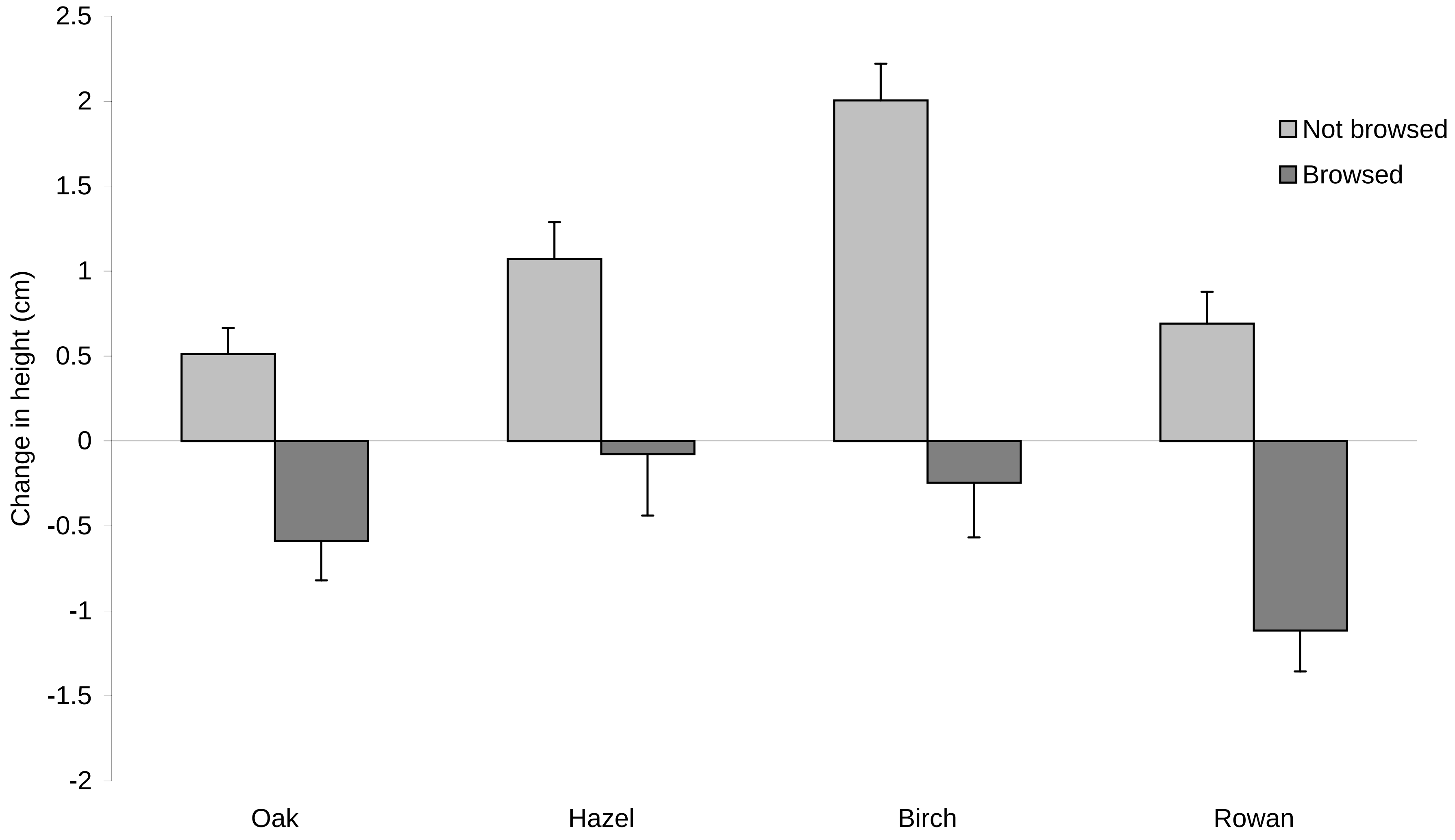


Figure 9. Mean change in height between years of browsed and unbrowsed saplings (averaged across years and sites).

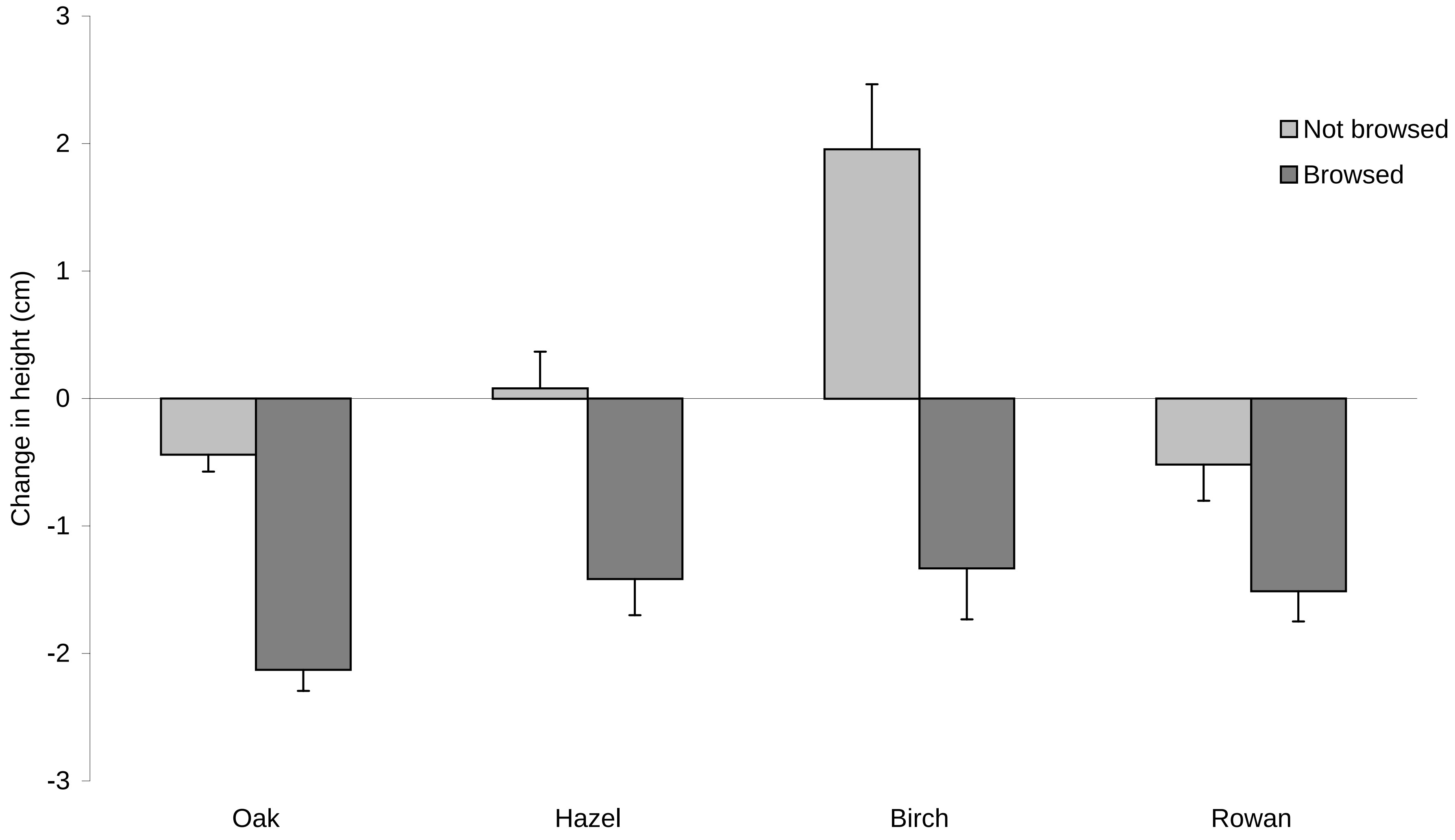


Figure 10. Proportions of unbrowsed saplings growing during the summer (averaged across years).

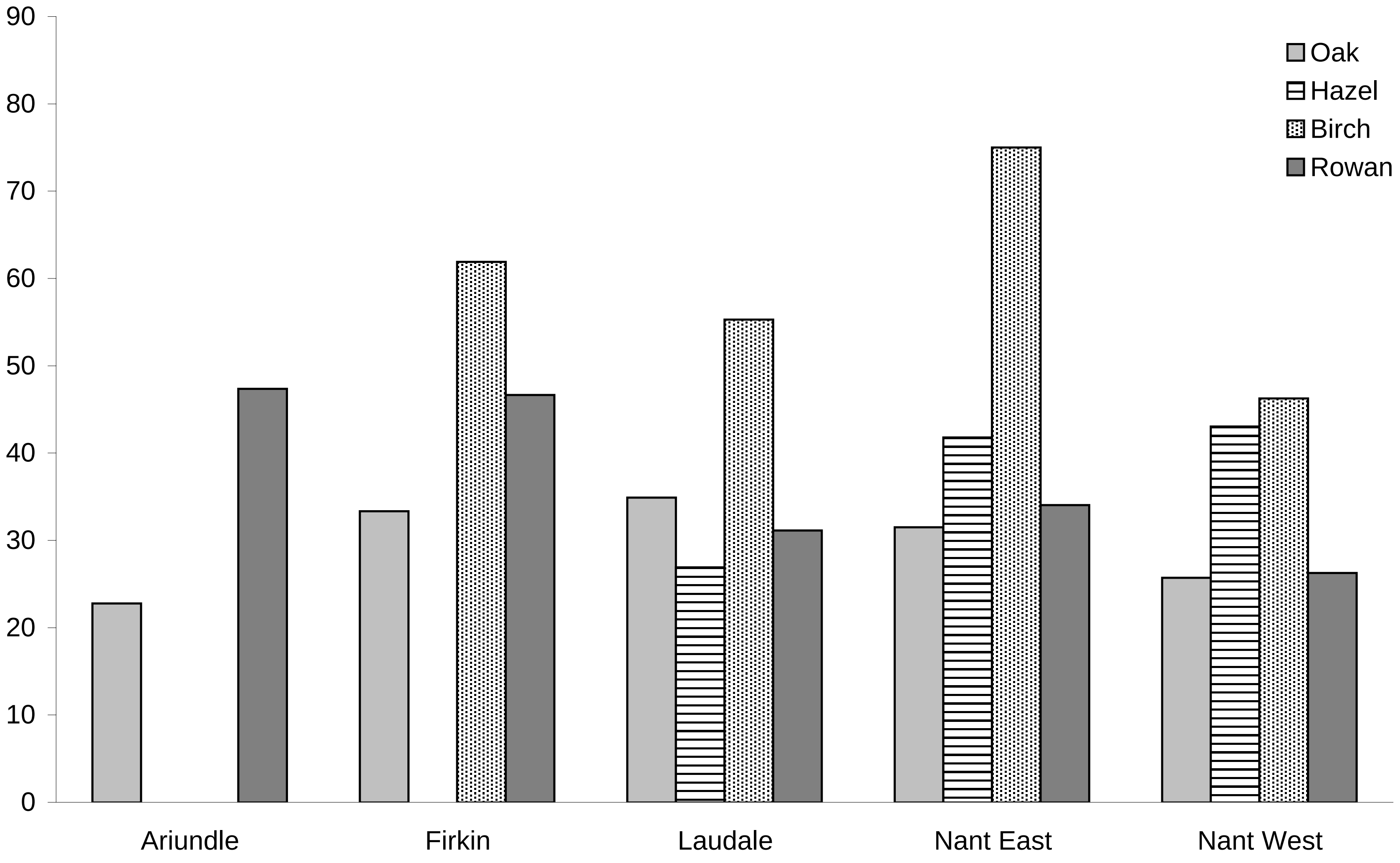


Figure 11. Proportions of unbrowsed saplings growing during summer 2000 (explicitly recorded).

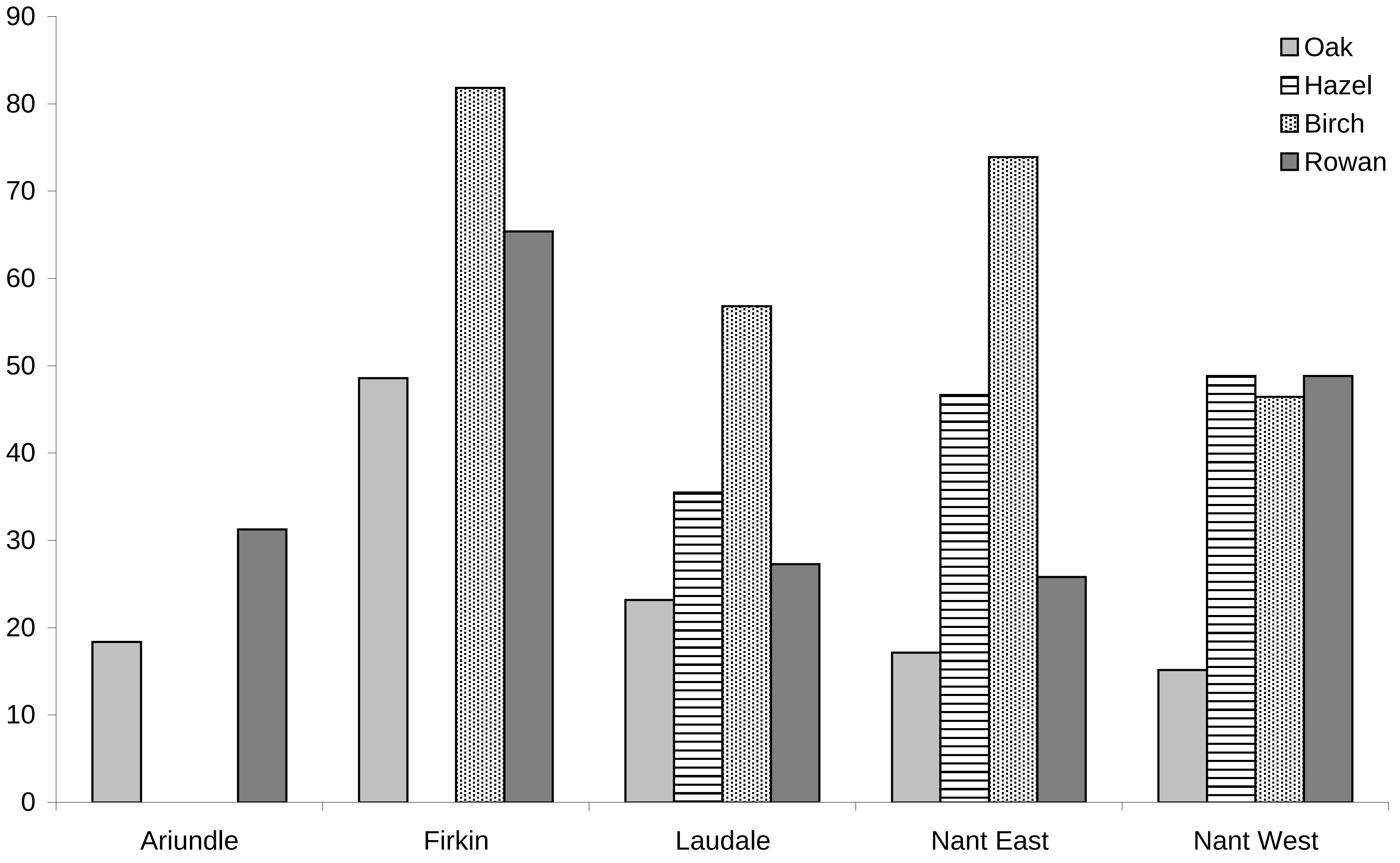


Figure 12. Incidence of damage to leaves by invertebrates, fungi, etc. A, B, and C are spring, mid-summer and autumn visits respectively.

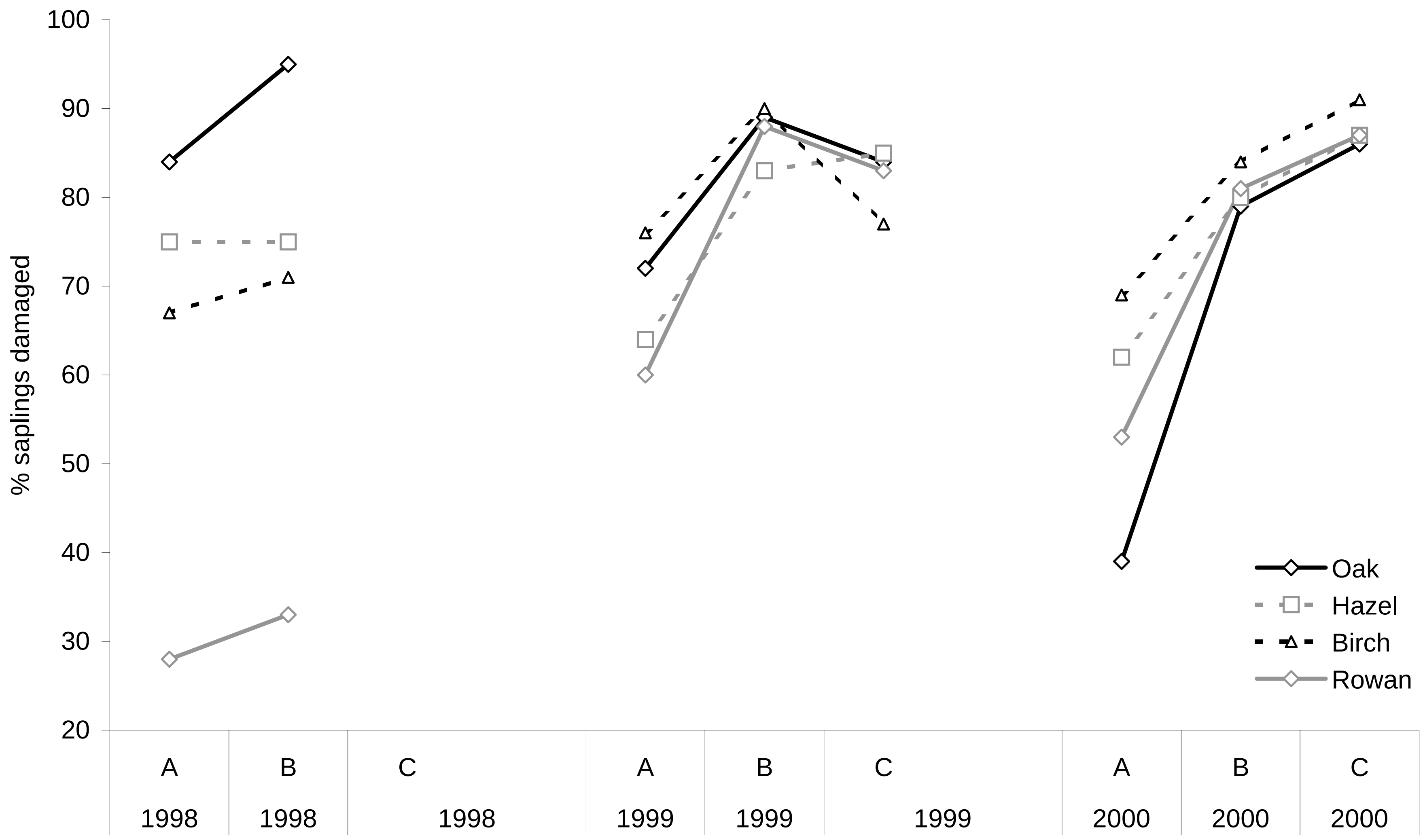
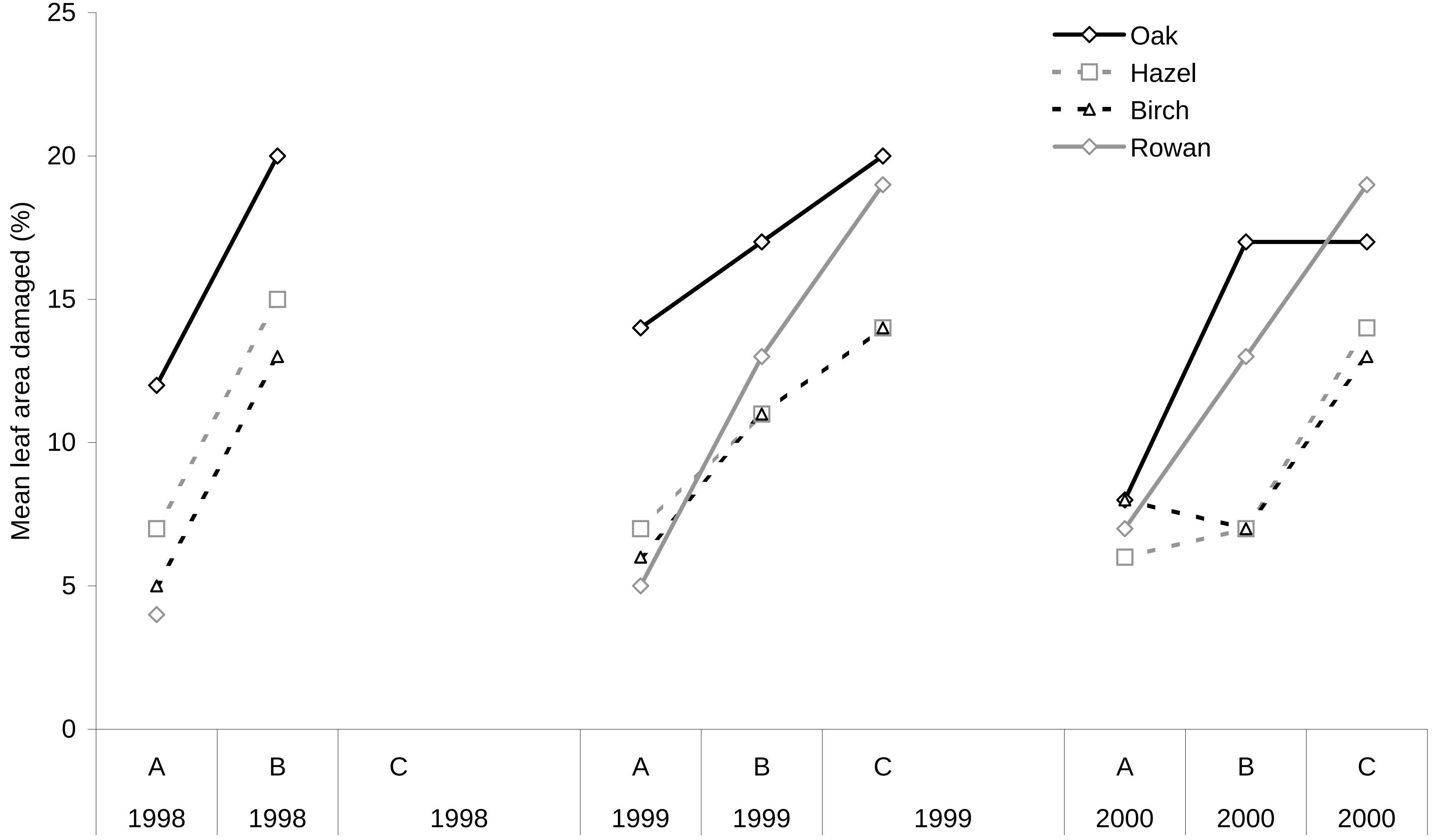


Figure 13



25
20
15
10
5
0
Mean leaf area damaged (%)
Oak
Hazel
Birch
Rowan
A
B
C
A
B
C
A
B
C
1998
1998
1998
1999
1999
1999
2000
2000
2000

Figure 14. Survival of oak saplings planted into six habitats at Nant West duting summer 2000.

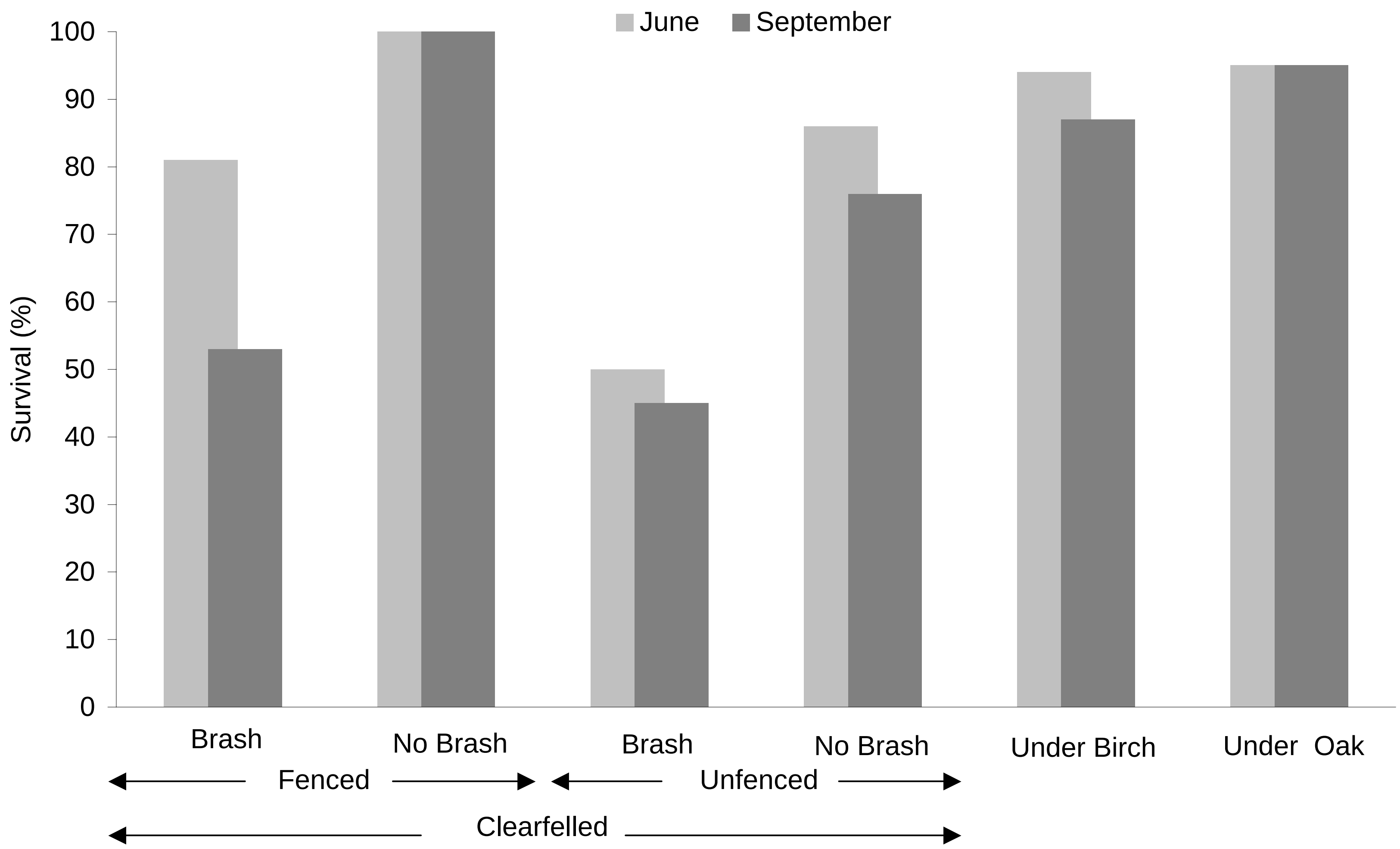


Figure 15. Incidence of known browsing on surviving oak saplings planted into six habitats at Nant West duting summer 2000.

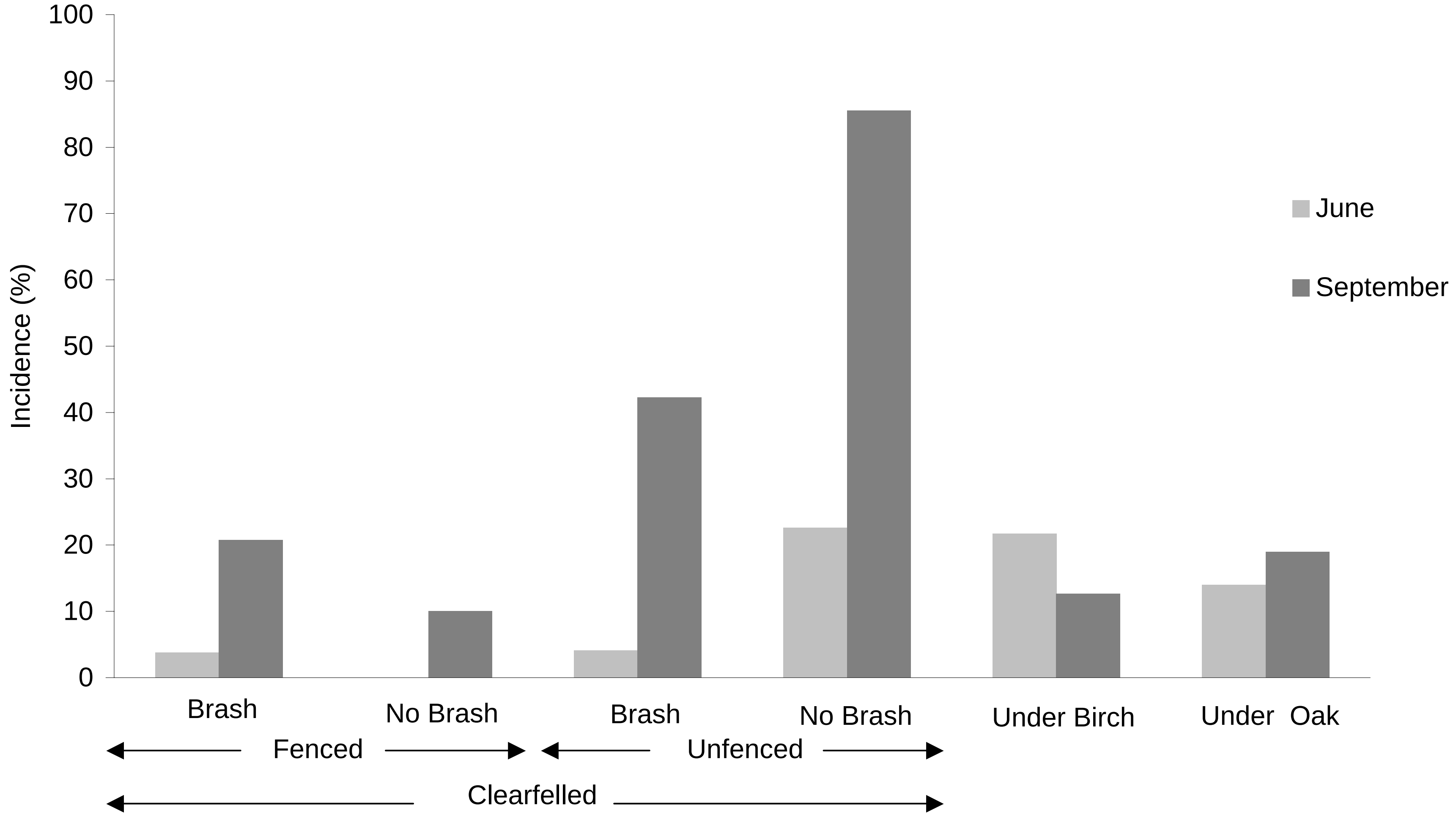


Figure 16. Survival of oak saplings planted into six habitats at Nant West duting summer 2000. Error bars show 1 standard error.

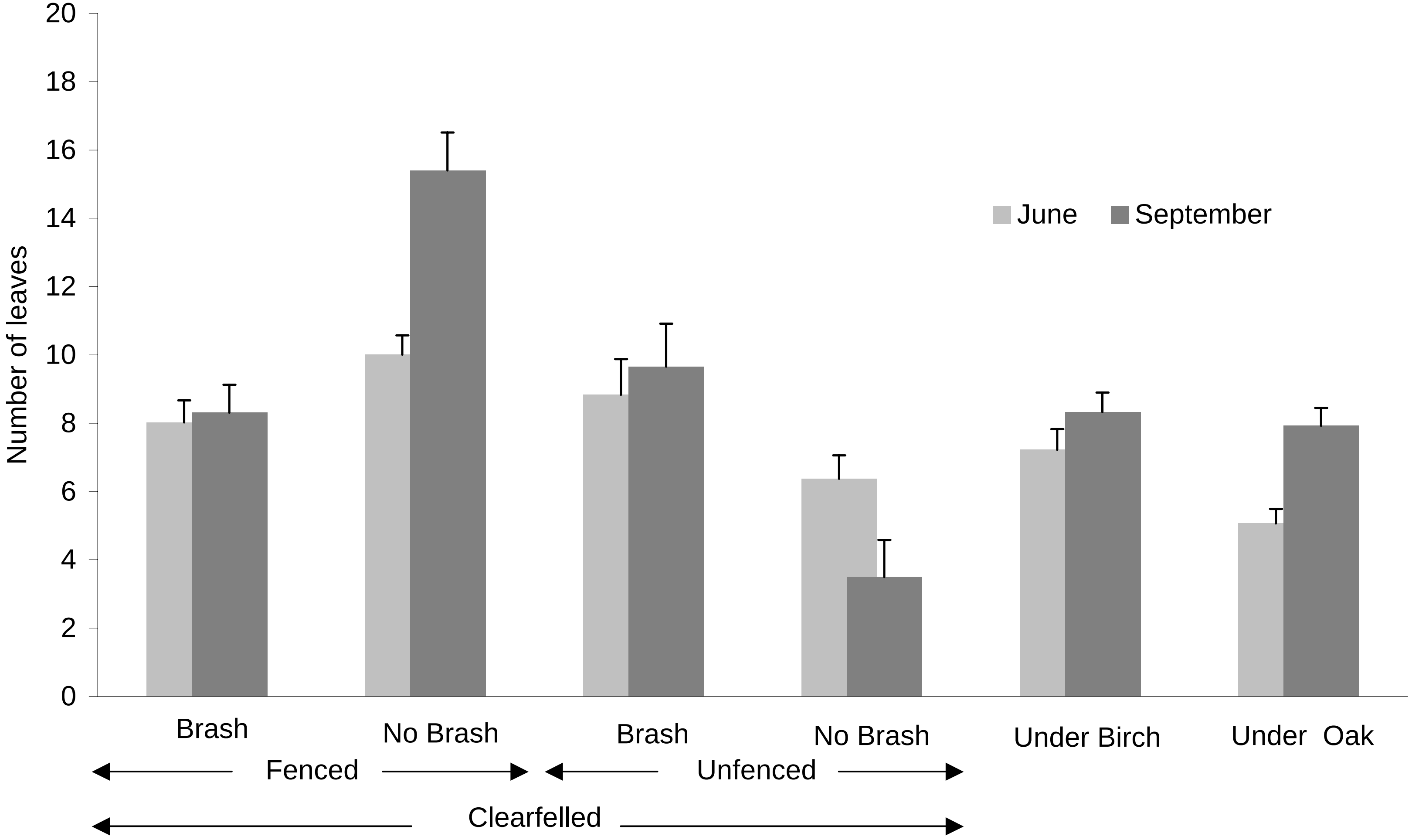


Figure 17. Incidence of invertebrate damage to oak saplings planted into six habitats at Nant West duting summer 2000. Error bars show 1 std. error.

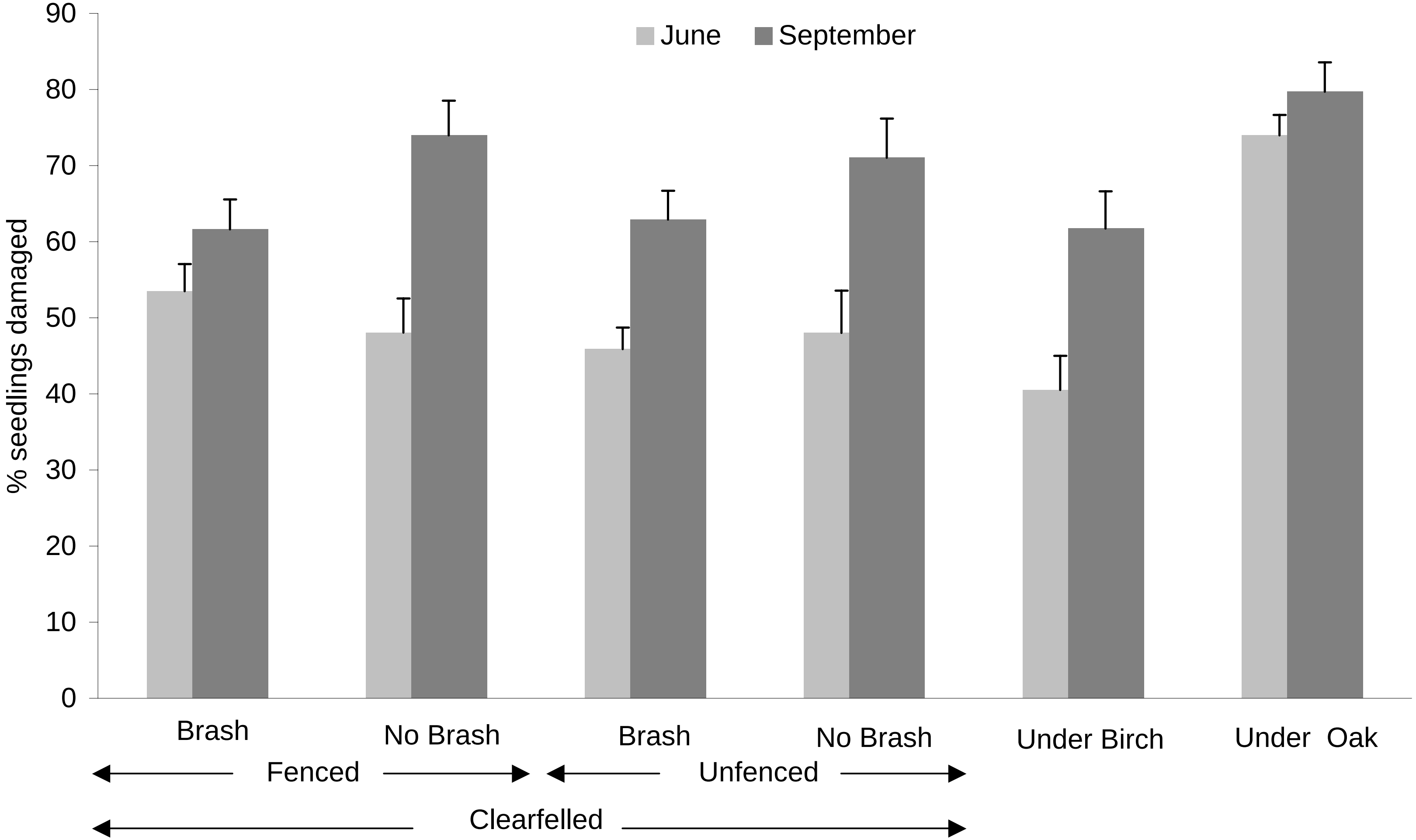
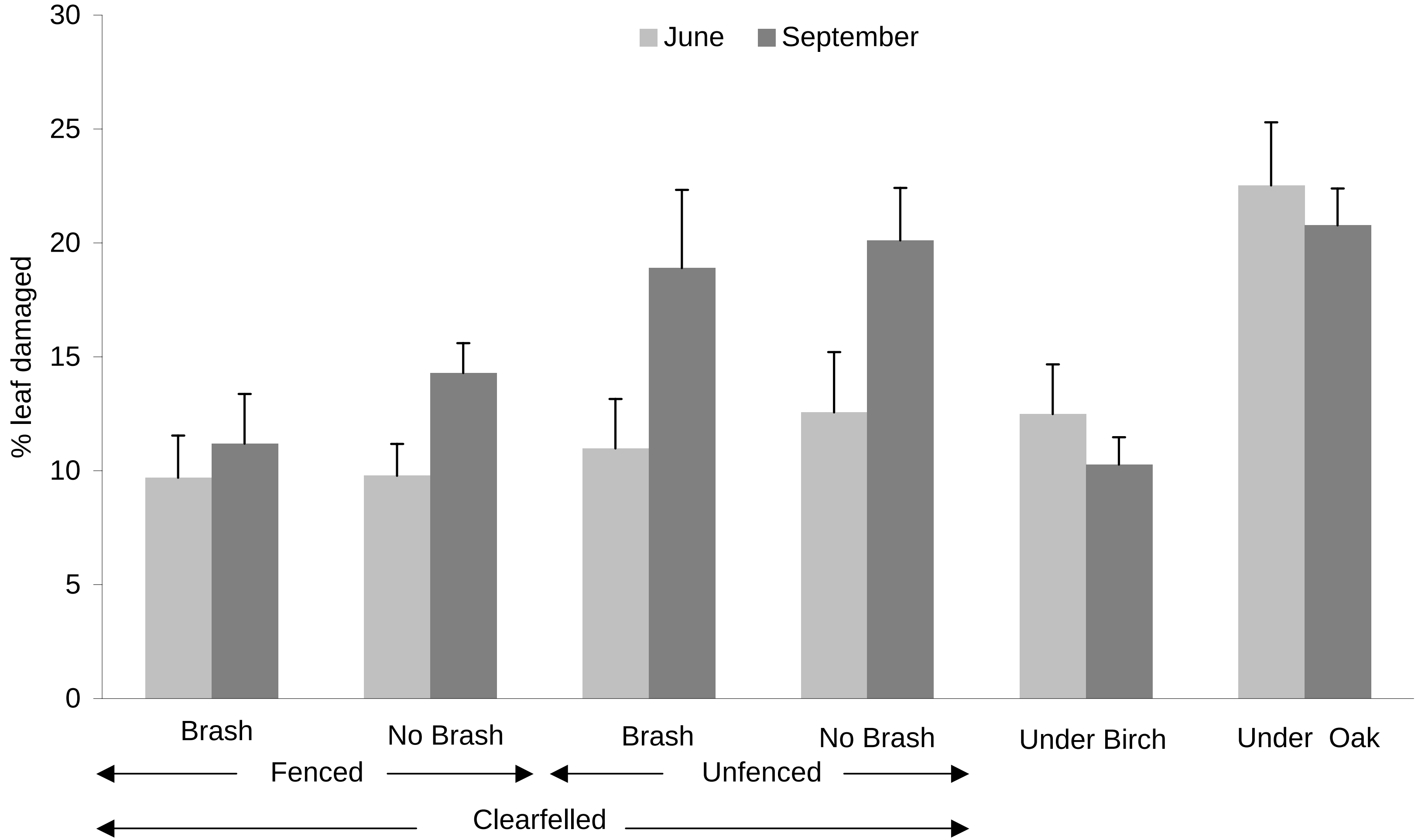


Figure 18. Severity of invertebrate damage to oak saplings planted into six habitats at Nant West duting summer 2000. Error bars show 1 std. error.



Year	**Season**	**Ariundle**	**Firkin**	**Laudale**	**Nant East**	**Nant West**
1998	Summer	0.5	3	35	0.5	6
1998/1999	Winter	7	96	93	27	37
1999	Summer	5	55	61	0.5	0.5
1999/2000	Winter	7	139	91	21	36
2000	Summer	2	57	74	4	0.5

	Ariundle	**Firkin**	**Laudale**	**Nant East**	**Nant West**
Summer	2.333333	38.333	56.6667	1.3333333	2.16666667
Winter	7.5	117.5	92	24	36.5
summer se	1.452966	17.676	11.4649	1.3333333	1.92209377
winter se	0.5	21.5	1	3	0.5

Site	Sp	Summer browsed	Summer loss	max	Winter browsed	Winter loss	max
Ariundle	B						
	B						
Firkin	B	33.3	2.2	35.8			
	B				32.8	32.8	65.6
Laudale	B	18.2	6.3	23.9			
	B				40.7	13.9	54.6
Nant East	B	29.9	0.9	30.8			
	B				31.6	6.3	38
Nant West	B	29.5	3.1	31.8			
	B				38.8	8.2	47.1
AR	O	11.9	13	24.8			
					29	14.4	43.3
FH	O	29.2	7.5	36			
					28.3	44.4	71.7
LH	O	13.2	9.9	22.8			
					32.2	19.4	51.1
NE	O	20.6	5.6	26.3			
					28.3	16.3	44.6
NW	O	17.1	6.4	23.6			
					28	19.4	47.3
AR	R	30.1	1.1	31.1			
					35.5	0.8	36.4
FH	R	36.2	2.9	38.1			
					39.4	7	46.5
LH	R	17.4	4.9	22.2			
					38.5	5.5	44
NE	R	35.9	3.1	38.2			
					34.9	7	41.9
NW	R	32.2	1.1	33.3			
					36.8	5.6	42.4
AR	Z						
FH	Z						
LH	Z	17.4	11.6	27.5			
					28.2	21.8	48.7
NE	Z	17.5	7.3	24.9			
					33.3	15.3	45.9
NW	Z	20.7	9.6	30.3			
					32.4	20.4	52.8

Effect of species on minimum summer browsing incidence (LH omitted)

Parameters

Intercept	-1.6942		-1.6942		-1.6942		-1.6942		55		-55	
1998	0.1011	0.333333	0.1011	0.333333	0.1011	0.333333	0.1011	0.333333	0	0	0	0
1999	0.4396	0.333333	0.4396	0.333333	0.4396	0.333333	0.4396	0.333333		0		0
Offtake	0.0059		0.0059		0.0059		0.0059		0		0	
Birch	0.508	0	0.508	0	0.508	1	0.508	0	0	0	0	0
Oak	-0.0624	1	-0.0624	0	-0.0624	0	-0.0624	0	0	1	0	1
Rowan	0.7514	0	0.7514	0	0.7514	0	0.7514	1	0	0	0	0
Hazel	0	0	0	0	0	0	0	0	0	0	0	0

Offtake		**Oak**		**Hazel**		**Birch**		**Rowan**				
0	-1.58	0.171	-1.51	0.180	-1.01	0.268	-0.76	0.318	55.00	1.000	-55.00	0.000
8	-1.53	0.178	-1.47	0.187	-0.96	0.277	-0.72	0.328	55.00	1.000	-55.00	0.000
16	-1.48	0.185	-1.42	0.195	-0.91	0.287	-0.67	0.339	55.00	1.000	-55.00	0.000
24	-1.43	0.192	-1.37	0.202	-0.86	0.296	-0.62	0.350	55.00	1.000	-55.00	0.000
32	-1.39	0.200	-1.33	0.210	-0.82	0.306	-0.57	0.360	55.00	1.000	-55.00	0.000
40	-1.34	0.207	-1.28	0.218	-0.77	0.316	-0.53	0.371	55.00	1.000	-55.00	0.000
48	-1.29	0.215	-1.23	0.226	-0.72	0.327	-0.48	0.382	55.00	1.000	-55.00	0.000
56	-1.25	0.223	-1.18	0.234	-0.68	0.337	-0.43	0.394	55.00	1.000	-55.00	0.000
64	-1.20	0.232	-1.14	0.243	-0.63	0.348	-0.38	0.405	55.00	1.000	-55.00	0.000
72	-1.15	0.240	-1.09	0.252	-0.58	0.359	-0.34	0.416	55.00	1.000	-55.00	0.000
80	-1.10	0.249	-1.04	0.261	-0.53	0.370	-0.29	0.428	55.00	1.000	-55.00	0.000
88	-1.06	0.258	-0.99	0.270	-0.49	0.381	-0.24	0.439	55.00	1.000	-55.00	0.000
96	-1.01	0.267	-0.95	0.279	-0.44	0.392	-0.20	0.451	55.00	1.000	-55.00	0.000
104	-0.96	0.276	-0.90	0.289	-0.39	0.403	-0.15	0.463	55.00	1.000	-55.00	0.000
112	-0.92	0.286	-0.85	0.299	-0.35	0.415	-0.10	0.475	55.00	1.000	-55.00	0.000
120	-0.87	0.296	-0.81	0.309	-0.30	0.426	-0.05	0.486	55.00	1.000	-55.00	0.000
128	-0.82	0.306	-0.76	0.319	-0.25	0.438	-0.01	0.498	55.00	1.000	-55.00	0.000
136	-0.77	0.316	-0.71	0.329	-0.20	0.449	0.04	0.510	55.00	1.000	-55.00	0.000
144	-0.73	0.326	-0.66	0.340	-0.16	0.461	0.09	0.522	55.00	1.000	-55.00	0.000
152	-0.68	0.336	-0.62	0.350	-0.11	0.473	0.13	0.534	55.00	1.000	-55.00	0.000
160	-0.63	0.347	-0.57	0.361	-0.06	0.485	0.18	0.545	55.00	1.000	-55.00	0.000

Effect of species on maximum winter browsing incidence (LH omitted)

Parameters											
Intercept	-0.3174		-0.3174		-0.3174		-0.3174		55		-55	
1998	-0.0859	0.5	-0.0859	0.5	-0.0859	0.5	-0.0859	0.5	0	0	0	0
Offtake	0.0067		0.0067		0.0067		0.0067		0		0	
Birch	-0.0591	0	-0.0591	0	-0.0591	1	-0.0591	0	0	0	0	0
Oak	0.0126	1	0.0126	0	0.0126	0	0.0126	0	0	1	0	1
Rowan	-0.2828	0	-0.2828	0	-0.2828	0	-0.2828	1	0	0	0	0
Hazel	0	0	0	0	0	0	0	0	0	0	0	0

Offtake			**Oak**		**Hazel**		**Birch**		**Rowan**				
	0	-0.35	0.414	-0.36	0.411	-0.42	0.397	-0.64	0.345	55.00	1.000	-55.00	0.000
	8	-0.29	0.427	-0.31	0.424	-0.37	0.410	-0.59	0.357	55.00	1.000	-55.00	0.000
	16	-0.24	0.440	-0.25	0.437	-0.31	0.423	-0.54	0.369	55.00	1.000	-55.00	0.000
	24	-0.19	0.453	-0.20	0.450	-0.26	0.436	-0.48	0.382	55.00	1.000	-55.00	0.000
	32	-0.13	0.467	-0.15	0.464	-0.21	0.449	-0.43	0.394	55.00	1.000	-55.00	0.000
	40	-0.08	0.480	-0.09	0.477	-0.15	0.462	-0.38	0.407	55.00	1.000	-55.00	0.000
	48	-0.03	0.493	-0.04	0.490	-0.10	0.476	-0.32	0.420	55.00	1.000	-55.00	0.000
	56	0.03	0.507	0.01	0.504	-0.04	0.489	-0.27	0.433	55.00	1.000	-55.00	0.000
	64	0.08	0.520	0.07	0.517	0.01	0.502	-0.21	0.447	55.00	1.000	-55.00	0.000
	72	0.13	0.534	0.12	0.530	0.06	0.516	-0.16	0.460	55.00	1.000	-55.00	0.000
	80	0.19	0.547	0.18	0.544	0.12	0.529	-0.11	0.473	55.00	1.000	-55.00	0.000
	88	0.24	0.560	0.23	0.557	0.17	0.542	-0.05	0.487	55.00	1.000	-55.00	0.000
	96	0.30	0.573	0.28	0.570	0.22	0.556	0.00	0.500	55.00	1.000	-55.00	0.000
	104	0.35	0.586	0.34	0.583	0.28	0.569	0.05	0.513	55.00	1.000	-55.00	0.000
	112	0.40	0.599	0.39	0.596	0.33	0.582	0.11	0.527	55.00	1.000	-55.00	0.000
	120	0.46	0.612	0.44	0.609	0.38	0.595	0.16	0.540	55.00	1.000	-55.00	0.000
	128	0.51	0.625	0.50	0.622	0.44	0.608	0.21	0.553	55.00	1.000	-55.00	0.000
	136	0.56	0.637	0.55	0.634	0.49	0.621	0.27	0.567	55.00	1.000	-55.00	0.000
	144	0.62	0.650	0.60	0.647	0.55	0.633	0.32	0.580	55.00	1.000	-55.00	0.000
	152	0.67	0.662	0.66	0.659	0.60	0.645	0.38	0.593	55.00	1.000	-55.00	0.000
	160	0.72	0.674	0.71	0.671	0.65	0.658	0.43	0.606	55.00	1.000	-55.00	0.000

Effect of height (<30cm) and species on minimum summer browsing incidence

Parameters												
Intercept	-3.4816		-3.4816		-3.4816		-3.4816		55		-55	
1998	-0.916	0.333333	-0.916	0.333333	-0.916	0.333333	-0.916	0.333333	0	0	0	0
1999	0.4175	0.333333	0.4175	0.333333	0.4175	0.333333	0.4175	0.333333		0		0
Birch	-0.0586	0	-0.0586	0	-0.0586	1	-0.0586	0	0	0	0	0
Oak	-0.0902	1	-0.0902	0	-0.0902	0	-0.0902	0	0	1	0	1
Rowan	0.2941	0	0.2941	0	0.2941	0	0.2941	1	0	0	0	0
Hazel	0	0	0	1	0	0	0	0	0	0	0	0
Ht	0.0912		0.0912		0.0912		0.0912		0		0	
Veg ht 1	0.0565	0	0.0565	0	0.0565	0	0.0565	0				
Veg ht 2	0.3463	1	0.3463	1	0.3463	1	0.3463	1				
Veg ht 3	0.2166	0	0.2166	0	0.2166	0	0.2166	0				
Veg ht 4	0	0	0	0	0	0	0	0				
Dry	0.5744	1	0.5744	1	0.5744	1	0.5744	1				
Intermediate	0.5292	0	0.5292	0	0.5292	0	0.5292	0				
Wet	0	0	0	0	0	0	0	0				

Height		Oak		Hazel		Birch		Rowan				
0	-2.82	0.056	-2.73	0.061	-2.79	0.058	-2.43	0.081	55.00	1.000	-55.00	0.000
1.5	-2.68	0.064	-2.59	0.070	-2.65	0.066	-2.30	0.091	55.00	1.000	-55.00	0.000
3	-2.54	0.073	-2.45	0.079	-2.51	0.075	-2.16	0.103	55.00	1.000	-55.00	0.000
4.5	-2.41	0.083	-2.32	0.090	-2.38	0.085	-2.02	0.117	55.00	1.000	-55.00	0.000
6	-2.27	0.094	-2.18	0.102	-2.24	0.096	-1.89	0.132	55.00	1.000	-55.00	0.000
7.5	-2.13	0.106	-2.04	0.115	-2.10	0.109	-1.75	0.148	55.00	1.000	-55.00	0.000
9	-2.00	0.120	-1.91	0.129	-1.96	0.123	-1.61	0.166	55.00	1.000	-55.00	0.000
10.5	-1.86	0.135	-1.77	0.146	-1.83	0.138	-1.48	0.186	55.00	1.000	-55.00	0.000
12	-1.72	0.152	-1.63	0.163	-1.69	0.156	-1.34	0.208	55.00	1.000	-55.00	0.000
13.5	-1.59	0.170	-1.50	0.183	-1.55	0.174	-1.20	0.231	55.00	1.000	-55.00	0.000
15	-1.45	0.190	-1.36	0.204	-1.42	0.195	-1.06	0.256	55.00	1.000	-55.00	0.000
16.5	-1.31	0.212	-1.22	0.228	-1.28	0.217	-0.93	0.283	55.00	1.000	-55.00	0.000
18	-1.18	0.236	-1.09	0.252	-1.14	0.242	-0.79	0.312	55.00	1.000	-55.00	0.000
19.5	-1.04	0.261	-0.95	0.279	-1.01	0.268	-0.65	0.342	55.00	1.000	-55.00	0.000
21	-0.90	0.289	-0.81	0.307	-0.87	0.295	-0.52	0.373	55.00	1.000	-55.00	0.000
22.5	-0.77	0.318	-0.68	0.337	-0.73	0.324	-0.38	0.406	55.00	1.000	-55.00	0.000
24	-0.63	0.348	-0.54	0.369	-0.60	0.355	-0.24	0.439	55.00	1.000	-55.00	0.000
25.5	-0.49	0.380	-0.40	0.401	-0.46	0.387	-0.11	0.473	55.00	1.000	-55.00	0.000
27	-0.35	0.412	-0.26	0.434	-0.32	0.420	0.03	0.507	55.00	1.000	-55.00	0.000
28.5	-0.22	0.446	-0.13	0.468	-0.19	0.454	0.17	0.541	55.00	1.000	-55.00	0.000
30	-0.08	0.480	0.01	0.502	-0.05	0.488	0.30	0.575	55.00	1.000	-55.00	0.000

Effect of height (<30cm) and species on maximum winter browsing incidence

Parameters												
Intercept	-0.3783		-0.3783		-0.3783		-0.3783		55		-55	
1998	-0.1286	0.5	-0.1286	0.5	-0.1286	0.5	-0.1286	0.5	0	0	0	0
1999	0	0.5	0	0.5	0	0.5	0	0.5		0		0
Birch	-0.3145	0	-0.3145	0	-0.3145	1	-0.3145	0	0	0	0	0
Oak	-0.0536	1	-0.0536	0	-0.0536	0	-0.0536	0	0	1	0	1
Rowan	-0.503	0	-0.503	0	-0.503	0	-0.503	1	0	0	0	0
Hazel	0	0	0	0	0	0	0	0	0	0	0	0
Ht	0.0352		0.0352		0.0352		0.0352		0		0	
Veg ht 1	0.3323	0	0.3323	0	0.3323	0	0.3323	0				
Veg ht 2	0.2425	1	0.2425	1	0.2425	1	0.2425	1				
Veg ht 3	0.0917	0	0.0917	0	0.0917	0	0.0917	0				
Veg ht 4	0	0	0	0	0	0	0	0				
Dry	-0.014	1	-0.014	1	-0.014	1	-0.014	1				
Intermediate	-0.006	0	-0.006	0	-0.006	0	-0.006	0				
Wet	0	0	0	0	0	0	0	0				

Height		**Oak**		**Hazel**		**Birch**		**Rowan**				
0	-0.27	0.433	-0.21	0.447	-0.53	0.371	-0.72	0.328	55.00	1.000	-55.00	0.000
1.5	-0.21	0.446	-0.16	0.460	-0.48	0.383	-0.66	0.340	55.00	1.000	-55.00	0.000
3	-0.16	0.460	-0.11	0.473	-0.42	0.396	-0.61	0.352	55.00	1.000	-55.00	0.000
4.5	-0.11	0.473	-0.06	0.486	-0.37	0.408	-0.56	0.364	55.00	1.000	-55.00	0.000
6	-0.06	0.486	0.00	0.499	-0.32	0.421	-0.51	0.376	55.00	1.000	-55.00	0.000
7.5	0.00	0.499	0.05	0.512	-0.26	0.434	-0.45	0.389	55.00	1.000	-55.00	0.000
9	0.05	0.512	0.10	0.526	-0.21	0.447	-0.40	0.401	55.00	1.000	-55.00	0.000
10.5	0.10	0.525	0.16	0.539	-0.16	0.460	-0.35	0.414	55.00	1.000	-55.00	0.000
12	0.15	0.539	0.21	0.552	-0.11	0.473	-0.29	0.427	55.00	1.000	-55.00	0.000
13.5	0.21	0.552	0.26	0.565	-0.05	0.487	-0.24	0.440	55.00	1.000	-55.00	0.000
15	0.26	0.565	0.31	0.578	0.00	0.500	-0.19	0.453	55.00	1.000	-55.00	0.000
16.5	0.31	0.578	0.37	0.591	0.05	0.513	-0.14	0.466	55.00	1.000	-55.00	0.000
18	0.37	0.590	0.42	0.603	0.11	0.526	-0.08	0.479	55.00	1.000	-55.00	0.000
19.5	0.42	0.603	0.47	0.616	0.16	0.539	-0.03	0.492	55.00	1.000	-55.00	0.000
21	0.47	0.616	0.53	0.628	0.21	0.552	0.02	0.506	55.00	1.000	-55.00	0.000
22.5	0.52	0.628	0.58	0.641	0.26	0.565	0.07	0.519	55.00	1.000	-55.00	0.000
24	0.58	0.640	0.63	0.653	0.32	0.578	0.13	0.532	55.00	1.000	-55.00	0.000
25.5	0.63	0.652	0.68	0.665	0.37	0.591	0.18	0.545	55.00	1.000	-55.00	0.000
27	0.68	0.664	0.74	0.676	0.42	0.604	0.23	0.558	55.00	1.000	-55.00	0.000
28.5	0.74	0.676	0.79	0.688	0.47	0.616	0.29	0.571	55.00	1.000	-55.00	0.000
30	0.79	0.687	0.84	0.699	0.53	0.629	0.34	0.584	55.00	1.000	-55.00	0.000

Site	Species	Level	n	1998	1999	2000	se98	se99	se00	Max98	Max99	Max00
		0	1914	16.04	15.32	14.41	0.29	0.26	0.27	101	101	99
	B	1	229	21.7	21.81	21.72	1.16	1.08	1.27	100	83	97
	O	1	1126	13.08	13.35	12.49	0.19	0.26	0.29	28	82	99
	R	1	276	17.77	16.73	15.68	0.66	0.6	0.6	101	101	90
	Z	1	283	15.4	14.85	13.71	0.5	0.54	0.52	61	56	47
AR		2	536	16.45	14.09	13.52	0.87	0.52	0.47	101	101	97
AT		2	72	.	24.82	26.7	.	1.8	1.98	.	82	99
FH		2	369	14.37	13.16	11.23	0.48	0.39	0.47	62	60	63
LH		2	396	13.01	11.87	10.69	0.33	0.29	0.29	48	37	36
NE		2	263	17.31	16.81	15.63	0.5	0.46	0.49	40	40	42
NW		2	278	19.78	19.83	18.66	0.83	0.86	0.94	70	75	80
AR	O	3	449	12.15	11.67	11.33	0.28	0.2	0.18	22	24	24
AR	R	3	63	22.63	21.35	20.93	1.9	1.84	1.72	101	101	90
FH	O	3	280	14.21	12.48	10.33	0.38	0.26	0.37	28	26	26
FH	B	3	44	17.54	20.81	18.32	1.87	2.62	2.83	62	60	63
FH	R	3	40	11.63	11.51	10.22	0.89	0.66	0.76	25	22	24
LH	O	3	179	12.4	11.18	9.74	0.35	0.33	0.32	27	28	27
LH	H	3	77	13.19	11.07	10.22	0.52	0.38	0.48	25	18	23
LH	B	3	82	15.21	14.14	13.08	1.25	0.8	0.84	48	37	36
LH	R	3	58	12.26	11.27	10.43	0.83	0.78	0.76	31	29	31
NE	O	3	82	13.97	13.89	12.25	0.79	0.78	0.76	28	38	36
NE	H	3	89	16.62	16.24	14.83	0.55	0.59	0.61	29	33	27
NE	B	3	42	19.58	20.67	21.92	1.16	1.02	1.25	37	36	42
NE	R	3	50	18.55	18.51	16.35	1.23	1.13	0.98	40	40	29
NW	O	3	64	13.98	13.29	12.3	0.61	0.7	0.8	28	29	30
NW	H	3	101	16.48	17.27	15.65	1.21	1.29	1.19	61	56	47
NW	B	3	48	31.04	32.71	32.35	2.84	2.84	3.31	70	75	80
NW	R	3	65	19.72	18.71	17.07	0.94	0.85	0.9	45	45	43
FH	H	3	5	12	8.75	8	.	1.8	.	12	14	8
AR	B	3	13	32.58	31.08	37.09	8.76	6.94	9.27	100	83	97
AR	H	3	11	11.71	10.78	11.57	0.64	1.19	0.78	14	18	14
AT	O	3	72	.	24.82	26.7	.	1.8	1.98	.	82	99

Effect of annual browsing on change in height between years - Fig 9

Species	Browsed	Not browsed	se browsed	se not browsed
Oak	-2.12587	-0.43976	0.16889	-0.13402
Hazel	-1.4152	0.07955	0.28574	0.28742
Birch	-1.33028	1.95455	0.40235	0.51134
Rowan	-1.51014	-0.51724	0.23965	-0.28545

Effect of summer browsing on change in height within years- using LS means Fig 8

Species	Browsed	Not browsed	se browsed	se not browsed
Oak	-0.58684	0.51114	0.23379	0.1535
Hazel	-0.07582	1.0709	0.3631	0.21678
Birch	-0.24515	2.00416	0.32271	0.21539
Rowan	-1.11356	0.69093	0.24278	0.18685

	Ariundle	Firkin	Laudale	Nant East	Nant West
Birch		61.90476	55.29412	75	46.26866
Oak	22.76119	33.33333	34.91124	31.50685	25.71429
Rowan	47.36842	46.66667	31.14754	34.04255	26.26263
Hazel			26.92308	41.79104	43.03797

SITE	SPECIES	N not grow	N growing	% growing	Dht not gro	Dht growing
AR	B	6	10	62.5	-1.66667	7.9
AR	O	207	61	22.76119	-0.59903	2.78689
AR	R	50	45	47.36842	-1.4	4.4
AR	Z	5	1	16.66667	-0.4	3
AT	O	45	14	23.72881	-0.31111	3.64286
FH	B	8	13	61.90476	-1.625	5.69231
FH	O	76	38	33.33333	-1.11842	3.34211
FH	R	16	14	46.66667	-0.8125	3.35714
LH	B	38	47	55.29412	-1.34211	4.2766
LH	O	110	59	34.91124	-1.07273	2.88136
LH	R	42	19	31.14754	-0.78571	2.89474
LH	Z	38	14	26.92308	-0.92105	2.14286
NE	B	9	27	75	-1.44444	5.92593
NE	O	50	23	31.50685	-0.52	3.04348
NE	R	31	16	34.04255	-0.58065	3.4375
NE	Z	39	28	41.79104	-1.05128	4.07143
NW	B	36	31	46.26866	-1.41667	5.58065
NW	O	52	18	25.71429	-0.78846	2.88889
NW	R	73	26	26.26263	-1.35616	4.23077
NW	Z	45	34	43.03797	-0.88889	5.5

Purely for seedlings recorded as specifically grown in 2000

	Ariundle	Firkin	Laudale	Nant East	Nant West	
Birch		82	57	74	46	**60**
Oak	18	49	23	17	15	**16**
Rowan	31	65	27	26	49	**37**
Hazel			35	47	49	**48**

SITE	SPECIES	N not grow	N growing	% growing	Dht not gro	Dht growing
AR	O	169	38	18	0	1.92
AR	R	22	10	31	0	1.8
FH	B	2	9	82	0	4.444
FH	O	36	34	49	0	4.23529
FH	R	9	17	65	0	3.05882
LH	B	19	25	57	0	3.8
LH	O	53	16	23	0	1.9375
LH	R	24	9	27	0	2.44444
LH	Z	20	11	35	0	1.81818
NE	B	6	17	74	0	4.176
NE	O	29	6	17	0	3.04348
NE	R	23	8	26	0	1.75
NE	Z	24	21	47	0	2.47619
NW	B	15	13	46	0	4.23077
NW	O	28	5	15	0	2.88889
NW	R	22	21	49	0	2.28571
NW	Z	22	21	49	0	3.66667

	1998	1998	1998	1999	1999	1999	2000	2000	2000	
Species	**A**	**B**	**C**	**A**	**B**	**C**	**A**	**B**	**C**	
	Incidence of damage									
Oak	84	95		72	89	84	39	79	86	
Hazel	75	75		64	83	85	62	80	87	
Birch	67	71		76	90	77	69	84	91	
Rowan	28	33		60	88	83	53	81	87	
	Severity of damage									
Oak	12	20		14	17	20	8	17	17	19
Hazel	7	15		7	11	14	6	7	14	14.33
Birch	5	13		6	11	14	8	7	13	13.33
Rowan	4			5	13	19	7	13	19	19

Proportion of Seedlings Browsed in Different Habitat Types

			June	September		Bch
Fenced	Brash	Clearfell	3.7975	20.755		CEB
Fenced	No brash	Clearfell	0	10		CEC
Unfenced	Brash	Clearfell	4.0816	42.222		COB
Unfenced	No brash	Clearfell	22.619	85.526		COC
		Birch	21.7391	12.6444		Oak
		Oak	13.9785	18.947		

Proportion of seedlings browsed in vsb in different habitat types
This is looking at seedlings that were found in vsa (ie btype 0,1,2,3) and then btype (0,1,2,3,7,8,12) in vsb
to try and get an idea of those seedlings that were known to be established in vsa but were subsequently
browsed or not found in vsb. This is to show browsing and known loss bewteen vsa and vsb
however the loss may not be because of browsing but because the seedlings have just died between vsa and vsb

			Numbers kr	Nos. lost
Fenced	Brash	Clearfell	5	29
Fenced	No brash	Clearfell	10	0
Unfenced	Brash	Clearfell	19	5
Unfenced	No brash	Clearfell	65	9
		Birch	10	6
		Oak	18	2

Depth of brash and browsing incidence

	Browsed						
			0	**1**		Mean	Std Err
Browsed Type	**Not Browsed**	**Browsed**	Sterr	Sterr	CEB	34.84	1.10414
Brash depth (cm)	30.08	22.95	2.20484	1.96976	COB	30.46	1.22478

Survivorship rates

			June	September
Fenced	Brash	Clearfell	81	53
Fenced	No brash	Clearfell	100	100
Unfenced	Brash	Clearfell	50	45

Unfenced	No brash	Clearfell	86	76
		Birch	94	87
		Oak	95	95

Mean total number of leaves when not browsed vsa or vsb

			June	September	SEtotlvs	SEtotlvs
Fenced	Brash	Clearfell	8.0263	8.3095	0.64427	0.8197
Fenced	No brash	Clearfell	10.01	15.4	0.55786	1.1133
Unfenced	Brash	Clearfell	8.8298	9.6538	1.05067	1.2598
Unfenced	No brash	Clearfell	6.3692	3.5	0.69114	1.0856
		Birch	7.2222	8.3226	0.60683	0.5753
		Oak	5.0625	7.9254	0.42929	0.5224

					Standard Errors	
Incidence of Leaf damage			June	September	**June**	**Sept**
Fenced	Brash	Clearfell	53	62	3.5847	3.93294
Fenced	No brash	Clearfell	48	74	4.4923	4.57473
Unfenced	Brash	Clearfell	46	63	2.8161	3.76517
Unfenced	No brash	Clearfell	48	71	5.5593	5.14109
		Birch	41	62	4.4750	4.90915
		Oak	74	80	2.68645	3.86105

% damage

			June	September	June SEDp	Sept SEDpct
Fenced	Brash	Clearfell	9.6885	11.193	1.85989	2.17991
Fenced	No brash	Clearfell	9.7765	14.2887	1.397	1.31416
Unfenced	Brash	Clearfell	10.9783	18.8969	2.17275	3.43695
Unfenced	No brash	Clearfell	12.5585	20.1149	2.65	2.30322
		Birch	12.4888	10.2682	2.1765	1.2
		Oak	22.5257	20.775	2.76666	1.61439