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How do different competing species influence the response of *Betula pubescens* Ehrh. to browsing?

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Abstract

When attempting to expand existing woodland through natural regeneration, herbivory and competition from the existing vegetation may impede the regenerating saplings. This work addresses how browsing and competition with other vegetation interact to drive sapling growth and morphology of the widespread tree species *B. pubescens*.

We took above-ground morphological measurements of *B. pubescens* saplings within an intimate mosaic of *Calluna vulgaris* and *Molinia caerulea*, comparing saplings growing with each of the two plant species under three different red deer (*Cervus elaphus*) densities, allowing comparison of different levels of both past and present levels of browsing damage.

Saplings growing in *M. caerulea* dominated vegetation responded to reduced browsing with faster growth than those growing in *C. vulgaris* dominated vegetation. However, we found that when natural browsing levels were high, browsing masked any differences in inter-specific interactions between plant species. We propose that, in regeneration schemes where deer densities are reduced, these differences should confer a competitive advantage to saplings growing with *M. caerulea* over those growing with *C. vulgaris*. Additionally, our results highlight the importance of browsing history, rather than just current browsing levels, in determining sapling growth responses under different herbivore management regimes.

This study highlights the importance of multi-factor interactions in determining plant growth and morphology under different conditions. In particular we identify the prevalence of interactions between competition, herbivory and time, as determining the potential growth and morphology of *B. pubescens* saplings in regeneration areas. This has important implications for the management of sites where browsing impedes the natural

regeneration of trees and shrubs, or where herbivore densities have been reduced to encourage woodland regeneration.

Key Words: above-ground plant interactions; *Betula pubescens*; browsing; competition; forest regeneration; herbivory; semi-natural woodland

Introduction

In heavily grazed systems successful tree establishment is a rare occurrence (Hester, Mitchell & Kirby 1996; Pigott 1983). Direct and indirect effects of browsing can result in morphological (Bergström & Danell 1987; Hester et al. 1996; Van Hees, Kuiters & Slim 1996), physiological (Millard, Hester, Wendler, & Baillie 2001), and induced chemical (Hol et al. 2004, Bryant, Danell, Provenza, Reichardt, Clausen et al. 1991a; Bryant, Provenza, Pastor, Reichardt, Clausen et al. 1991b; Bryant, Kuropat, Reichardt & Clausen 1991c; Tallamy & Raup 1991) sapling responses. Inter- and intra-specific plant associations also influence tree sapling establishment success (Berkowitz, Canham & Kelly 1995; Gordon & Rice 2000). In forest systems, competition with surrounding vegetation, as well as other trees, has been shown to be important at all stages of woodland development (Goldberg & Barton 1991; Steven 1991; Mallik 2003; Scott, Welch, Thurlow & Elston 2000). While the responses of plants to herbivory or competition have been widely studied, the interactions between browsing impacts and competitive associations have been little studied, yet this is highly relevant for forest management as the combined effects on sapling growth and establishment success are not always predictable (Crawley 1997; Augustine & McNaughton 1998; Olofsson, Moen & Oksanen 2002).

From the few studies carried out to date, it appears that interactions with other plants can alter the effect of browsing on tree sapling survival and development (Edenius, Danell & Bergström 1993; Hjältén, Danell & Ericson 1993). The relationships are not linear and may

depend on the stage of development (Meiners & Handel 2000) or the relative influence of the forest canopy (Harmer 2001). Hjältén et al. (1993), for example, found that the ability of *B. pubescens* to compensate after different types of browsing damage (leader removal and defoliation) decreased with increasing competition. However, in *Acer rubrum* and *Quercus palustris* seedlings, Meiners et al. (2000) found an interaction between competition and herbivory for seedling mortality, but not for growth. Harmer (2001) also reported no effect of competition removal on the growth of broadleaved species (*Acer pseudoplatanus*, *Fraxinus excelsior*, *Fagus sylvatica* and *Quercus robur*) under an existing woodland canopy. What these studies do not address, however, is possible species-specific differences in the effect of competition and the interactive effect of browsing damage on such differences.

The aim of this field study was to address how browsing and competition interact to drive growth and morphology of the tree species *Betula pubescens* growing with two contrasting competing plant species (*Calluna vulgaris* (L.) Hull and *Molinia caerulea* (L.) Moench), under differing levels of browsing damage. *Betula pubescens* is widely distributed in Europe and is the dominant component of many semi-natural forest systems and a co-occurring species in many other semi-natural woodland systems (Atkinson 1992). *M. caerulea* and *C. vulgaris* are both widespread through Northern Europe, and are dominant in many of the upland areas in which regeneration of semi-natural woodland occurs. They have contrasting growth habits; *C. vulgaris* is an evergreen ericaceous shrub whereas *M. caerulea* is a deciduous tussock grass (Gimingham 1960; Taylor, Rowland & Jones 2001). Therefore, it is hypothesised that their influences on the above-ground environment of regenerating *B. pubescens* saplings will be different, with *Calluna* providing a greater barrier to growth than *Molinia* due to its increased interference with the light environment. Below-ground interactions are also hypothesised to be different (Heil & Bruggink 1987), but this was not part of this study. We took above-ground morphological measurements of *B. pubescens*

saplings growing in *C. vulgaris* or *M. caerulea*, under different levels of browsing damage, to test the hypothesis that the response of *B. pubescens* saplings to browsing is influenced by the species of competing vegetation.

Materials and methods

Site descriptions

This study was conducted within an upland area in the Scottish Highlands (UK grid reference: NN479875). This area was selected due to its abundance of *Betula pubescens* saplings (hereafter *Betula*) which were regenerating in *Molinia caerulea* (hereafter *Molinia*) and *Calluna vulgaris* (hereafter *Calluna*) dominated vegetation, and the availability of information on present and past grazing pressure (NCC 1989). The main vegetation type in this area is *Calluna* and *Molinia* dominated heath, with very little remaining semi-natural woodland, due to a long history of heavy browsing by high densities of deer and sheep (NCC 1989). This study was conducted within two adjacent land management units (Creag Meagaidh and Ardverikie), with contrasting deer management strategies but similar vegetation, topography and soils. At both sites the soils are predominantly humic podzols overlaying acidic schists and granulites (NCC 1989). The main deer species in the area is the red deer (*Cervus elaphus*), but roe deer (*Capreolus capreolus*) are also present in small numbers. Creag Meagaidh has been managed since 1985 for regeneration of woodland via reduction in deer numbers and removal of sheep (NCC 1989). Ardverikie is a traditionally managed sporting estate, with relatively high deer densities which are maintained through winter-feeding. The boundary with Creag Meagaidh is fenced with an open-ended fence, which allows limited movement of deer between the estates. The Ardverikie estate supports distinctly higher densities of deer than Creag Meagaidh, giving a deer density gradient both within and between these two adjacent land management units.

Site/plot choice

The strong gradient of herbivore densities present in the area enabled us to compare the effect of different levels of browsing damage on naturally regenerating *Betula pubescens* saplings. Saplings were sampled from three sites chosen for their contrasting levels of deer usage; two in Creag Meagaidh: Choire Chomharsain (low deer densities: <1 deer km^{-2}) and Coire Chrannaig (intermediate deer densities: approximately 6 deer km^{-2}) (deer densities based on data in Putman (2003)) and one in Ardverikie (high deer densities: approx. 20 deer km^{-2} (P.Duncan, pers. comm.)). Accordingly, throughout this paper ‘site’ and ‘deer density’ are analogous. Within each site, saplings were sampled from three replicate 100 m^2 plots. The criterion for selection of plots was the presence of *Betula* regeneration at or below browsing height (<2 m) growing within an area where *Calluna* and *Molinia* coexist in small (approximately 1-4 m^2) discrete patches, rather than in continuous stands. Equal numbers of saplings were sampled from each of these two vegetation types within each plot.

We measured local soil moisture and light environment, as part of site characterisation, to assess whether there were any consistent differences between the two vegetation types in terms of these two key physical characteristics. Soil cores (10 cm in diameter) were taken at random from each vegetation type at each plot (one per vegetation type per plot (total of 18)). Each core was placed within the vegetation type using random methods. Soil was taken to a depth of 15cm. Percentage moisture was calculated as the difference in soil weight before and after drying (72 hours at 28 °C). Light measurements were taken at two different times of the year (25th April and 15th August). Measurements of photosynthetic photon flux density (400-700 nm) (PPFD) and red to far-red (660/730 nm) photon flux ratio (r:fr) were taken above and within the canopy of *Molinia* and *Calluna* at ten randomly assigned points within plot 1 in Choire Chomharsain (i.e. ten measurements for each vegetation type), using a PAR Quantum sensor (SKP 210, Skye Instruments Ltd.) and 660/730 sensor (SKR 110, Skye Instruments Ltd.).

Sapling sampling procedure

Saplings were measured between 1st and 31st August 2002 (end of summer growing season); the same plots were re-sampled between 1st and 14th May 2003 (at bud-burst and before new shoot growth for 2003). This was to allow for any differential effects due to seasonality of deer use. Within each 100 m² plot, 15 trees from each vegetation type were selected, using randomly generated grid coordinates and carefully searching for the closest sapling to that point, giving 45 trees per site. The following morphological measurements were taken in 2002: height of sapling; length; number of main stems; stem diameter; number of branches; leader length (current years growth from the apex of the main stem); distance to lowest branch; number of terminal long shoots; number of lateral long shoots; number of short shoots; number of leaves and canopy cover (canopy cover = area of ellipse = $\pi ab/4$, where a = distance between the edges of the widest part of the canopy and b = the distance between the edges perpendicular to a). A sub-sample of 16 sapling trees (eight from each vegetation type) per plot was removed and aged using growth ring counts, to give a mean sapling age per vegetation type per plot. In spring 2003 sampling period, the following measurements were made: height of sapling; length; number of main stems; stem diameter; number of branches; leader length; distance from the ground to the lowest branch; number of terminal long shoots; number of lateral long shoots; number of short shoots; number of leaves and canopy cover. The percentage of shoots browsed/unbrowsed was also recorded for each sapling. In 2002, previous and current years browsing were recorded. In May 2003, only browsing of 2002 growth was recorded (this represented a full year of browsing of 2002 shoots). The two measurements analysed here are pre-2002 browsing (from 2002 recording) and 2002 browsing (from May 2003 recording). The severity of browsing was calculated as a percentage of all the shoots present in that year.

Data analysis

Data were analysed using ANOVA in Genstat 6th Edition (Lawes Agricultural Trust 2002).

For sapling morphology, treatments were site x surrounding vegetation species x year.

Blocking was applied using 'plot'; for light measurements treatments were vegetation species x measurement location (above- or within vegetation) x time (spring or autumn). Where data did not meet the assumptions required for the use of ANOVA they were transformed using a Log or angular transformation as appropriate (Table 1). R:fr ratio data were antilog transformed before analysis.

Results

Effects of competing plant species

There were significant differences in the majority of the measurements, between saplings growing in the two vegetation types (Table 1). Values were consistently higher for saplings growing in *Molinia* dominated vegetation; saplings had larger stem diameters, more leaves, more terminal and lateral long shoots, more short shoots; larger canopy cover, more branches/cm of length and a larger proportion of lateral long shoots (Fig. 1, Fig. 2 and Fig. 3). Additionally, sapling ages did not differ significantly between *Calluna* and *Molinia* dominated areas at the high deer density site. However, there were significant differences between sites. Saplings were oldest in Ardverikie, but only by a mean of 2.5 years ($x \pm SE$: low density 6.6 ± 0.36 ; intermediate 7.4 ± 0.43 ; high density 9.9 ± 0.49 years). The height and length of saplings was slightly lower in spring 2003 than autumn 2002, after winter browsing (Fig. 1). However, in 2003, saplings had a larger canopy cover (Fig. 1), more branches (Fig. 3), and more long and short shoots (Fig. 2).

Calluna and *Molinia* both reduced the PPFD and r:fr ratio, but to different extents (Table 2).

There were also differences in the extent that PPFD and r:fr ratio were reduced, between spring and late summer, with differences between species in this extent. Measurement of soil

moisture (percent weight) between the two vegetation types showed no significant differences between *Molinia* dominated and *Calluna* dominated areas ($x \pm SE$: *Molinia* $26\% \pm 2.42$; *Calluna* $34\% \pm 6.31$; t-test, $P = 0.13$ ($n = 10$ per vegetation type)).

There was no significant effect of vegetation type on the proportion of shoots browsed at each site (ANOVA, $F_{(1,520)} = 0.49$, $P = 0.942$).

Effects of deer density

There were significant differences between sites in all *B. pubescens* morphological measurements except the number of branches/cm and the total number of long shoots (Table 1). Measurements that relate to the size of the saplings were consistently highest for saplings at the low deer density site and lowest at the high deer density site (Fig. 1). The same differences applied to the number of short shoots (Fig. 2). However, the trend was reversed for leader length (Fig. 3) and the number of long shoots (Fig. 2); with the high density site > intermediate site > low deer density site.

There was a significant effect of site on the proportion of shoots browsed (Fig. 4). Pre-2002 browsing was highest for saplings at the high deer density site, intermediate at the intermediate deer density site and lowest for saplings at the low deer density site, which also received the least browsing in 2002. However, the highest levels of 2002 browsing were at the intermediate deer density site.

There was a significant difference between years, in the amount of browsing damage recorded. Pre-2002 browsing was lower than the browsing that occurred during 2002 (Fig. 4).

There were significant site x vegetation type interactions for the following measurements: number of leaves; branches; terminal long shoots; total long shoots; short shoots and branches per cm of length (Table 1). The difference between saplings in *Calluna* dominated and *Molinia* dominated vegetation consistently increased from high deer density < intermediate <

low density sites, with the highest values occurring in saplings growing in *Molinia* dominated vegetation in the low deer density site (Fig. 1, Fig. 2, and Fig. 3).

Discussion

Complex multi-factor interaction effects are common in natural systems (Storch & Gaston 2004), yet the majority of sapling growth studies to date have concentrated on the main effects or, at most, two-way interactions. In this study we investigated interaction effects between three drivers of plant morphology: herbivore density x vegetation (competition) x year, with the aim of providing a more integrative perspective on how the system functions. We found many strong, significant interactions between the measured factors, illustrating the importance of interactions between herbivory, vegetation type and time on *B. pubescens* growth and morphology. This highlights the importance of explicitly considering multi-way interaction effects in natural systems before designing potentially over-simplistic management regimes.

While the *level* of herbivore pressure dominates development from heath to woodland, inter-specific competition can have a significant influence on tree sapling growth and morphological development. The response of *Betula* saplings to browsing was clearly modified by the species of surrounding vegetation, with *Calluna* appearing to inhibit sapling re-growth to a greater extent than *Molinia*. However, we propose that species-specific competitive differences between *C. vulgaris* and *M. caerulea* are only important after herbivore damage is reduced to a sufficient extent. This is an important finding in relation to predicting the impacts of reducing herbivore numbers on sapling growth within different vegetation types. For example, when managing to regenerate areas of semi-natural woodland, the extent to which saplings should be protected from herbivory may be dependent on the vegetation into which they are growing. From our results, once established, saplings growing

within *Calluna* dominated vegetation will need to be protected from heavy browsing for significantly longer than those growing within *Molinia*, to allow them to grow above the reach of browsing animals.

The non-manipulative nature of this study gives the benefit of recording saplings growing *in-situ* in an undisturbed natural system, but this can also be criticised in terms of control of between-site variability. Our three sites were relatively close to each other (within 3 km) and had previously been managed in the same way. With the exception of deer densities the characteristics of the sites were similar (e.g. elevation, soils, climate) (NCC 1989, Stewart 1996). Additionally, the differences in deer density were due to anthropogenic causes and not due to any other differences between sites. Therefore, it seems likely that the measured sapling differences between the three selected sites were primarily driven by deer density and were not confounded by any other major site-related factors.

Although the mechanisms of competition and reasons for differences between plants cannot be reliably determined from this field study alone, our data point to one key mechanism: light. The different growth strategies of *Molinia* and *Calluna* resulted in measured differences in the light environment, which is likely to cause differences in sapling morphology due to light quality (r:fr ratio) or differences due to differential resource restriction (PPFD). Additionally, although below-ground variables and interactions were not measured in this study, they undoubtedly also influence above-ground responses and vice-versa (Casper & Jackson 1997; Tilman 1997; Millard et al. 2000; Hester, Millard, Baillie & Wendler 2004). From previous work on ericaceous species, we propose that below-ground inhibition of growth through allelopathy is also likely to have contributed to the poorer sapling growth within this vegetation type as compared to within *Molinia* (Mallik 2003). Furthermore, the strength of below-ground competition may also change with differences in resource availability (Casper

et al. 1997) which again has been hypothesised to interact with herbivore browsing, for example by reducing soil N availability (Harrison & Bardgett 2003).

Although our results indicate reduced competition from *Molinia* as compared to *Calluna* for established birch saplings, it is important to note that this may differ for the early seedling establishment phase. Bokdam & Gleichman (2000) found greater *Betula* seedling establishment in *Calluna*-dominated than *Molinia*-dominated vegetation. Kinnaird (1974) also found lower densities of *Betula* seedlings in grass (species not specified) communities than heather communities. If we consider the scales at which these two different stages of tree growth operate, it is possible that *Molinia* may provide greater resistance to seed germination and seedling establishment due to the relatively impenetrable 'mat' of dead leaves, a result of the senescence of previous years' growth. This may impede seeds from reaching the ground and, for any that do, will greatly reduce light (and possibly moisture) reaching the small seeds/seedlings. This is supported by results of germination trials by Stewart (1996) who found that *Betula pubescens* seed germination was restricted to a greater degree by *Molinia* than by *Calluna*, although germination success appeared to be most dependent on the creation of gaps (by deer).

In conclusion, management prescriptions often concentrate on single drivers of ecosystem processes (for example: herbivory, competition (weeds), eutrophication). When regenerating woodland in areas with a history of high levels of herbivore densities it is browsing that is normally identified as the largest hindrance to successful tree establishment. However, our study shows that the growth and morphology of regenerating tree saplings is also dependent on interaction effects with surrounding vegetation when herbivore numbers are reduced and this is highly relevant for choice of sites and predictions about the likely consequences of herbivore management options.

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Table 1. Results of the full factorial univariate analysis on 10 response variables. Source of variation: S = site (three levels); C = competing plant species (2 levels); Y = year (2 levels).

Significance values NS = not significant; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$. n = 45 per surrounding vegetation species.

		Height ¹	Stem Diameter ¹	Canopy Cover ¹	No. Leaves ¹	Total Shoots ¹
Source	d.f.	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>
S	2,6	187.53***	25.82**	168.29***	42.58***	66.15***
C	1,522	3.24 ^{NS}	17.26***	8.34**	19.43***	22.42***
Y	1,522	5.07*	1.87 ^{NS}	5.38*	0.19 ^{NS}	26.22***
S x C	2,522	7.45***	15.98***	2.24 ^{NS}	6.20**	8.28***
S x Y	2,522	8.01***	1.91 ^{NS}	3.98*	8.66***	20.28***
C x Y	1,522	10.43***	0.32 ^{NS}	0.02 ^{NS}	0.27 ^{NS}	0.81 ^{NS}
S x C x Y	2,522	15.73***	8.75***	2.08 ^{NS}	2.17 ^{NS}	1.43 ^{NS}

		No. Short Shoots ¹	Total Long Shoots	No. Terminal Long Shoots ¹	No. Branches ¹	Leader Length ¹
Source	d.f.	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>
S	2,6	107.58***	0.50 ^{NS}	0.032*	37.46***	53.92***
C	1,522	15.28***	26.38***	19.88***	7.59**	0.34 ^{NS}
Y	1,522	27.57***	26.89***	12.32***	4.07*	82.85***
S x C	2,522	7.68***	9.89***	10.54***	5.59**	5.06**
S x Y	2,522	38.08***	3.56*	3.76*	5.83**	2.37 ^{NS}
C x Y	1,522	2.44 ^{NS}	0.00 ^{NS}	2.58 ^{NS}	0.85 ^{NS}	5.58*
S x C x Y	2,522	0.13 ^{NS}	2.53 ^{NS}	0.56 ^{NS}	1.19 ^{NS}	3.22*

¹Data log₁₀ transformed before analysis

Table 2. Results of the analysis of measurements of the light environment taken in *M.*

caerulea or *C. vulgaris* dominated vegetation. Presented are: (A), mean±standard error of photosynthetic photon flux density (400-700nm) (PPFD) and red to far-red (660/730) photon flux ratio (R:FR) of measurements taken above and within the vegetation at two different times in the year (25th April (spring) or 15th August (autumn); and (B), result of the full factorial univariate analysis. Source of variation: L = location of measurement (above or within vegetation), S = species (*C. vulgaris* or *M. caerulea*); T = time of measurement (spring or autumn). Significance values: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. r:fr data were antilog transformed before analysis.

(A)

	PPFD				r:fr ratio			
	<i>Calluna</i>		<i>Molinia</i>		<i>Calluna</i>		<i>Molinia</i>	
	above	within	above	within	above	within	above	within
Spring	576±1.3	170±2.7	616±2.6	457±2.8	1.12±0	0.96±0.01	1.13±0	1.08±0
Autumn	572±1.2	164±1.8	620±2.3	265±1.5	1.12±0	0.61±0.02	1.13±0	0.61±0.02

(B)

	d.f.	<i>F</i>	
		PPFD	R:FR
Location of measurement (above- or within vegetation) (L)	1,72	492.08***	4391.52***
Vegetation species (S)	1,72	63.7***	84.89***
Time of Year (T)	1,72	10.90**	1271.57***
L x S	1,72	25.23***	58.92***
L x T	1,72	10.95**	1283.79***
S x T	1,72	8.83**	66.16***
L x S x T	1,72	10.47**	63.41***

Figure legends

Figure 1. Effect of competing species on height, length, stem diameter and number of leaves on *B. pubescens* saplings growing at three different sites (Mean $\pm$ SEM, n = 45). Data presented are means of measurements taken from the same plots in August 2002 and May 2003. As indicated in Table 2, analysis of some variables was on log₁₀ transformed data. The significance of the effects are shown in Table 2. Bars with different letters above them indicate significant differences between means (Fisher's LSD, $P < 0.05$) (where appropriate LSDs were based on transformed data, as per Table 2). Values for *Calluna* are represented by white bars, those for *Molinia* are represented by grey bars.

Figure 2. Effect of competing species on numbers of shoots on *B. pubescens* saplings growing at three sites (Mean $\pm$ SEM, n = 45). Data presented are means of measurements taken from the same plots in August 2002 and May 2003. As indicated in Table 2, analysis of some variables was on log₁₀, transformed data. The significance of the effects are shown in table 2. Bars with different letters above them indicate significant differences between means (Fisher's LSD, $P < 0.05$) (where appropriate, LSDs were based on transformed data, as per Table 2). Values for *Calluna* are represented by white bars, those for *Molinia* are represented by grey bars.

Figure 3. Effect of competing species on morphological measurements of *B. pubescens* saplings growing at three sites (Mean $\pm$ SEM, n = 45). Data presented for number of branches are means of measurements taken from the same plots in August 2002 and May 2003, data presented for leader length are from 2002 measurements. As indicated in Table 2, analysis of some variables was on log₁₀ transformed data. The significance of the effects are shown in Table 2. Bars with different letters above them indicate significant differences between means (Fisher's LSD, $P < 0.05$) (where appropriate LSDs are based on transformed data, as per Table 2). Values for *Calluna* are represented by white bars, those for *Molinia* are represented by grey bars.

Figure 4. Percentage of shoots browsed of *B. pubescens* saplings growing at three sites.

Values are presented for two different time periods. Pre-2002 values were recorded in August 2002; 2002 values were recorded in May 2003. Means $\pm$ SE, $n = 30$. ANOVA : Site effect: (d.f. 2,6) $P = 0.005$, Year: (d.f. 1,520) $P < 0.001$, Site x Year: (d.f. 2,520) $P < 0.001$; all other effects and interactions NS. Bars with different letters above them indicate significant differences between means (Fisher's LSD, $P < 0.05$)

Figure 1

Figure 2

Figure 3

Figure 4