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Competitive interactions between *Nardus stricta* L. and *Calluna vulgaris* (L.) Hull: the effect of fertilizer and defoliation on above- and below-ground performance

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Summary

1 The role of nutrient supply and defoliation on the competitive interactions between pot-grown *Calluna vulgaris* and *Nardus stricta* plants was investigated.

2 Young plants were grown alone and together in pots under a combination of fertilizer and defoliation treatments. After 18 months, parameters reflecting both above- and below-ground performance were measured, namely: total above-ground biomass, shoot nitrogen and phosphorus content, root length and the extent of mycorrhizal infection of the roots.

3 In the pots that received fertilizer, the shoot nutrient content and above-ground biomass of *Nardus* plants increased to a greater extent than those of *Calluna* plants; this effect was more marked for *Nardus* plants growing with *Calluna* plants than for those growing with other *Nardus* plants. In contrast, *Calluna* plants growing in competition with *Nardus* failed to respond to the addition of nutrients. However, in unfertilized pots, *Calluna* gained more above-ground biomass during the experimental period than *Nardus*.

4 *Calluna* had greater root length than *Nardus*, but *Nardus* had a higher proportion of its root length infected by mycorrhizal fungi. In both plants, the addition of fertilizer reduced the mycorrhizal infection and increased the root length. *Nardus* root length was decreased when grown in competition with *Calluna* only in pots where no nutrients were added. Defoliation decreased the extent of mycorrhizal infection in *Calluna* roots but not in those of *Nardus*; defoliation decreased the shoot nutrient content in *Calluna* plants, but not in *Nardus* plants.

5 These results suggest that the competitive balance between *Nardus* and *Calluna* may be altered by the addition of nutrients, and by defoliation, which may have serious implications for the future dominance of *Calluna* in heathland ecosystems, particularly those where nutrient inputs are increasing significantly or where grazing pressures are high.

Keywords: above-ground biomass, competition, mycorrhizal infection, nutrient uptake, root length

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Introduction

Resource-based competition can be a major structuring force in plant communities (Berendse & Elberse 1990; Goldberg 1990; Tilman 1997) but its effects on plant community structure may be modified by other processes, particularly herbivory, which may shift the competitive balance between species if they differ in their palatability or in their regrowth capacity (Berendse 1985; Louda *et al.* 1990; Crawley 1997). Relatively few studies have attempted to quantify the interacting effects of herbivory and resource availability on the competitive balance between plant species in terms of below-ground growth parameters as well as above-ground ones, but knowledge of the differential effects of herbivory and nutrient availability on plant performance is important in understanding the mechanisms by which one species replaces another.

Calluna vulgaris (L.) Hull-dominated moorland is

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in decline in many areas of Scotland (Sydes 1988; Marrs 1993; Welch & Scott 1995). Overgrazing by sheep and deer is thought to be a major cause of the loss of *Calluna* cover to grass species, particularly to *Nardus stricta* L., a species which is relatively unpalatable to sheep (Welch 1986; Marrs & Welch 1991; Welch & Scott 1995). The decrease in *Calluna* cover is more rapid in some places than in others. This may simply reflect uneven grazing pressures, but it is also possible that herbivory has a more adverse effect on *Calluna* where the soils have a relatively high nutrient value, because this may further favour grasses (Heil & Bruggink 1987; Aerts & Berendse 1988; Berendse *et al.* 1994; Bobbink *et al.* 1998). To understand more about the mechanisms by which *Calluna* is being replaced by *Nardus*, the factors affecting their competitive interactions above- and below-ground need to be examined.

Calluna and *Nardus* have different growth strategies. *Calluna* is a slow-growing evergreen dwarf shrub (Gimingham 1972) and, typical of woody plants with long-lived leaves that are adapted to growing in low nutrient environments (Coley *et al.* 1985), it contains high levels of carbon-based secondary metabolites such as phenolics and tannins (Iason *et al.* 1993). If *Calluna* is grazed, the meristems at the tip of the shoots are lost, and recovery from browsing is therefore slow. In contrast, *Nardus* seedlings have a slightly faster relative growth rate than those of *Calluna* (Grime *et al.* 1988), and *Nardus* is better able to regrow after browsing because its meristems are found at the bases of the leaves. It has lower levels of tannins and lignin than *Calluna*, but the mature leaves are unpalatable to sheep due to high levels of silica (Welch 1986).

In addition to these different above-ground strategies of growth and defence, *Nardus* and *Calluna* have different below-ground growth forms and mycorrhizal associations. *Calluna* roots grow mainly in a dense mat in the upper organic layer of soil (Gimingham 1960). The bulk of the nutrient absorption by *Calluna* takes place via fine hair roots that are always infected with the ericoid mycorrhizal fungus *Hymenoscyphus ericae* (Gimingham 1972; Read & Stribley 1973). This mycorrhizal association may confer an advantage to the host-plant by improving access to nutrients held in forms unobtainable to other plants, e.g. proteins and amino acids (Read & Stribley 1973; Read & Bajwa 1985), and by improved tolerance of low pH and toxic elements in the soil, such as phenolic acids and heavy metals (Leake *et al.* 1989; Hashem 1995). In contrast to ericoid species, *Nardus* has an association with two types of arbuscular mycorrhizae (AM) (Ali 1996). These are thought to increase nutrient absorption area (and thus uptake), particularly for phosphorus (Read *et al.* 1976; Abbot & Robson 1985), and to improve both resistance to pathogens (Fitter 1985; Sharma *et al.* 1992) and drought tolerance (Allen & Allen 1986). The dominance of *Calluna* in low nutrient soils may owe much to the mycorrhizal association it holds, but there have been few studies on the effects of grazing and increased nutrient availability on the relationship between *Calluna* and its mycorrhizal fungus, and none which addresses the effects of these factors on this association relative to the mycorrhizal association of competing grass species.

In this study we examined potential competitive interactions between *Nardus* and *Calluna*, specifically the effects of nutrient addition and defoliation upon this interaction, both above- and below-ground. In order to assess the relative abilities of each species to utilize additional nutrients, we measured changes in above-ground biomass and shoot nutrient content, as well as changes in below-ground factors, namely mycorrhizal infection levels and root length, in response to fertilizer. We also investigated how these parameters were modified by defoliation.

Methods

TREATMENTS

Nardus stricta tussocks and small *C. vulgaris* plants, approximately 3–5 years old, were collected from a recently burned area on the Cairn o' Mount, Kincardineshire (grid reference NO648805) and potted into a mixture (4 : 1) of peat and sand in March 1994. The plants were grown either with the same species or mixed with the other species at densities of four plants (four *Calluna* plants, four *Nardus* tussocks, or two of each) to a pot 25 cm in diameter by 22 cm deep. At the start of the experiment, the plants were sufficiently small (*c.* 3 cm diameter and 5 cm tall) that they could be spaced far enough apart to ensure minimum competition for light. They were allowed to establish for 3 months prior to each pot receiving one of four treatments: control (no treatment), fertilized with NPK, defoliated, or both fertilized and defoliated. NPK was applied as ammonium nitrate (1.1 g pot^{-1} year^{-1}), as superphosphate (0.6 g pot^{-1} year^{-1}) and as sulphate of potash (0.6 g pot^{-1} year^{-1}). This fertilizer application is approximately equivalent to 75 kg N, 25 kg P and 50 kg K ha^{-2} year^{-1}. Fertilizer was applied in three doses during the growing season and watered in. The defoliation treatment removed approximately half of the current year's growth by clipping at three times during the growing season. There were 12 species × treatment combinations (*Calluna*, *Nardus*, or both, × four fertilizer/defoliation treatments) in each of seven replicate blocks, each block consisting of 12 pots and 48 plants (24 *Nardus* and 24 *Calluna*), four pots containing *Nardus* plants only, four containing *Calluna* plants only, and four containing both species. All pots were kept in a hard standing at ITE Banchory (grid reference NO677984) and were regularly watered and weeded.

HARVESTING

All plants were destructively harvested in August 1995. The above-ground growth of each plant was dried in an oven at 80 °C for 48 h and weighed. The dry plant material was milled and analysed for total nitrogen and phosphorus content using a continuous flow colorimetric autoanalyser (Segmented Flow Autoanalyser, Burkard Scientific, Uxbridge, UK), following wet acid digestion (Allen 1989). The nitrogen content was measured as ammonium by a modified Bertholet reaction (Hinds & Lowe 1980; Rowland 1983), and phosphorus was measured as phosphate by the 'Molybdenum blue' method (Burkard Scientific, personal communication; Allen 1989).

A root core (*c.* 15 cm deep by 5 cm diameter) was taken from the centre of each pot and frozen prior to analysis. For analysis of root length, the soil from each core was defrosted overnight and allowed to dry until friable, then two 5-g subsamples (*c.* 5 cm deep by 2 cm diameter) were removed. The roots were removed from the soil by washing in a 1-mm mesh sieve, then cleared in 2–5% potassium hydroxide at 90 °C for 30 min. The roots were washed thoroughly in several changes of deionized water, bleached in hydrogen peroxide for 10 min, then acidified in 1% hydrochloric acid for a further 10 min. They were stained for mycorrhizal infection using 0.05% trypan blue in acidic glycerol for 15 min at 90 °C, then destained overnight in acidic glycerol. Both the root length and percentage mycorrhizal infection were assessed by a modified line intersect method (Brundrett *et al.* 1975; Tennant 1975) using a ×40 magnification under a dissecting microscope (Leica Wild M3Z Type-S, Leica UK Ltd, Milton Keynes, UK).

STATISTICAL ANALYSIS

The results were analysed using the GLM procedure in Minitab. All the results were expressed as mean values of all plants per species per pot. All seven blocks were harvested and analysed for the above-ground measurements (apart from a small number of pots with insufficient material for shoot analyses), giving up to 56 replicates per species (7 blocks × 8 pots per block which contained that species). Due to the labour-intensive nature of the below-ground measurements, only five randomly selected replicate blocks were sampled, giving 40 replicates per species.

Results

ABOVE-GROUND MEASUREMENTS

The addition of fertilizer significantly increased the above-ground biomass of both *Calluna* and *Nardus*, with the exception of *Calluna* plants growing in competition with *Nardus* (Table 1 and Fig. 1). The response of the two species to fertilizer differed according to whether they were grown in competition with each other or with conspecifics. Fertilizer increased biomass to a greater extent in those *Nardus* plants grown with *Calluna* than in those grown with other *Nardus* plants. The effect of the type of competition was in the reverse direction in *Calluna*: fertilizer had an effect only when the competitors were conspecifics (i.e. the pots did not contain *Nardus* plants). There was therefore a significant pot type (i.e. mixed vs. alone)–fertilizer interaction for both species (Table 1). *Calluna* plants growing in the absence of fertilizer were slightly larger in the mixed species pots than when growing with conspecifics, but this was not statistically significant. Fertilizer increased the shoot nitrogen and phosphorus content of both *Calluna* and *Nardus* plants (Table 1 and Fig. 2a,b) but, as with above-ground biomass, the relative size of the increase depended on whether the plants were grown with conspecifics or in mixtures. *Nardus* plants had a greater increase in tissue nitrogen and phosphorus content when growing in competition with *Calluna* plants than with other *Nardus* plants (Fig. 2a). In contrast, *Calluna* plants showed an increase in nitrogen and phosphorus content in response to nutrient addition when they were growing alone, but a much smaller increase when growing with *Nardus* (Fig. 2b). There was therefore a significant pot type–fertilizer interaction for both species (Table 1).

Defoliation obviously reduced above-ground biomass in both species (Table 1), but it also prevented *Calluna* from increasing its above-ground biomass in response to fertilizer: even in *Calluna*-only pots defoliated plants were the same size irrespective of fertilizer addition. This was not the case for *Nardus* plants, which increased in above-ground biomass in response to fertilizer whether they were defoliated or not, leading to a significant fertilizer–defoliation interaction for *Calluna* but not *Nardus* (Table 1).

These effects of defoliation on above-ground biomass may reflect the effect of defoliation on nutrient uptake in the two species. Defoliation reduced the nitrogen and phosphorus content of *Calluna* shoots (particularly in fertilized pots), but the nutrient content of *Nardus* shoots was not significantly affected by defoliation (Table 1 and Fig. 3a,b for nitrogen levels), suggesting that the effect of defoliation on the ability of plants to take up nutrients was more marked in *Calluna* than in *Nardus*. For *Nardus*, whether growing in monoculture or in mixtures with *Calluna*, defoliation did not affect the increase in shoot nitrogen content in response to fertilizer (Fig. 3a). Thus there were no significant pot type–defoliation or fertilizer–defoliation interactions for *Nardus* (Table 1), and neither defoliated ($F = 0.31$, $P = 0.58$) nor control ($F = 1.15$, $P = 0.29$) plants showed a significant pot type–fertilizer interaction. In contrast, the addition of fertilizer to *Calluna* produced a much smaller increase

Table 1 The results of GLM analyses on the effects of fertilizer, defoliation, and growing with conspecifics or in mixtures, on the above-ground biomass, shoot nitrogen and phosphorus content, root length and mycorrhizal infection of *Calluna* and *Nardus* plants. *F*-values and significance levels for the main effects and the interaction between them are given. n = the number of replicate pots sampled for each species (see text for details)

	Above-ground measurements					
	Above-ground biomass		mg N per plant		mg P per plant	
	Nardus ($n = 56$)	*Calluna* ($n = 56$)	*Nardus* ($n = 53$)	*Calluna* ($n = 52$)	*Nardus* ($n = 53$)	*Calluna* ($n = 52$)
Pot type	$F = 11.2$ $P < 0.01$	$F = 4.86$ $P < 0.05$	$F = 2.58$ NS	$F = 6.56$ $P < 0.05$	$F = 2.48$ NS	$F = 5.56$ $P < 0.05$
Fertilizer	$F = 138$ $P < 0.001$	$F = 19.5$ $P < 0.001$	$F = 6.6$ $P < 0.001$	$F = 35.51$ $P < 0.001$	$F = 39.4$ $P < 0.001$	$F = 14.95$ $P < 0.001$
Defoliation	$F = 8.8$ $P < 0.01$	$F = 37.91$ $P < 0.001$	$F = 0.27$ NS	$F = 11.52$ $P < 0.001$	$F = 0.16$ NS	$F = 12.52$ $P < 0.001$
Pot type × fertilizer	$F = 10.2$ $P < 0.01$	$F = 18.53$ $P < 0.001$	$F = 1.46$ NS	$F = 14.12$ $P < 0.001$	$F = 0.44$ NS	$F = 10.89$ $P < 0.01$
Pot type × defoliation	$F = 0.02$ NS	$F = 1.43$ NS	$F = 1.65$ NS	$F = 0.04$ NS	$F = 1.5$ NS	$F = 0.56$ NS
Fertilizer × defoliation	$F = 2.22$ NS	$F = 4.92$ $P < 0.05$	$F = 0.00$ NS	$F = 6.41$ $P < 0.05$	$F = 0.54$ NS	$F = 1.46$ NS
	Below-ground measurements					
	Root length		Proportion mycorrhizal infection			
	Nardus ($n = 40$)	*Calluna* ($n = 40$)	*Nardus* ($n = 40$)	*Calluna* ($n = 40$)		
Pot type	$F = 6.84$ $P < 0.05$	$F = 5.15$ $P < 0.05$	$F = 0.77$ NS	$F = 0.00$ NS		
Fertilizer	$F = 26.52$ $P < 0.001$	$F = 2.02$	$F = 43.12$ $P < 0.001$	$F = 0.73$ NS		
Defoliation	$F = 0.33$ NS	$F = 6.61$ $P < 0.05$	$F = 3.23$ NS	$F = 10.85$ $P < 0.01$		
Pot type × fertilizer	$F = 2.37$ NS	$F = 5.17$ $P < 0.05$	$F = 2.28$ NS	$F = 0.00$ NS		
Pot type × defoliation	$F = 0.01$ NS	$F = 0.12$ NS	$F = 0.18$ NS	$F = 0.03$ NS		
Fertilizer × defoliation	$F = 0.09$ NS	$F = 0.56$ NS	$F = 16.54$ $P < 0.001$	$F = 0.14$ NS		

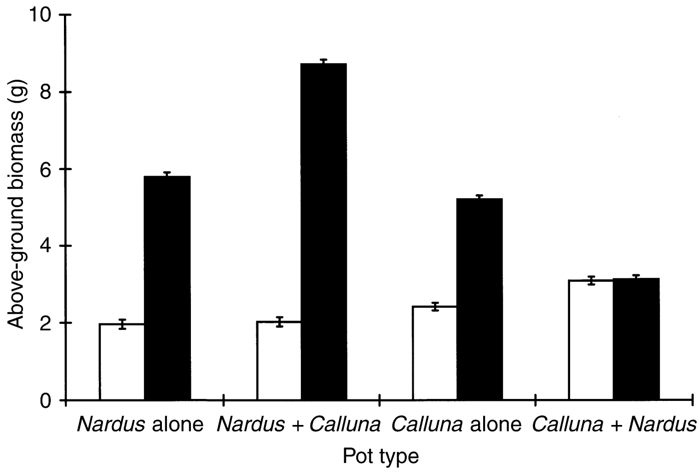

Fig. 1 Above-ground biomass (dry weight in g) of *Nardus* ($n = 56$) and *Calluna* ($n = 56$) plants, grown in pots in monocultures (alone) or in mixtures (+ *Calluna*, or + *Nardus*). Shaded bars are values for plants grown in pots with added fertilizer, unshaded bars are values for plants from control pots with no fertilizer added. Mean values ± SE are shown.

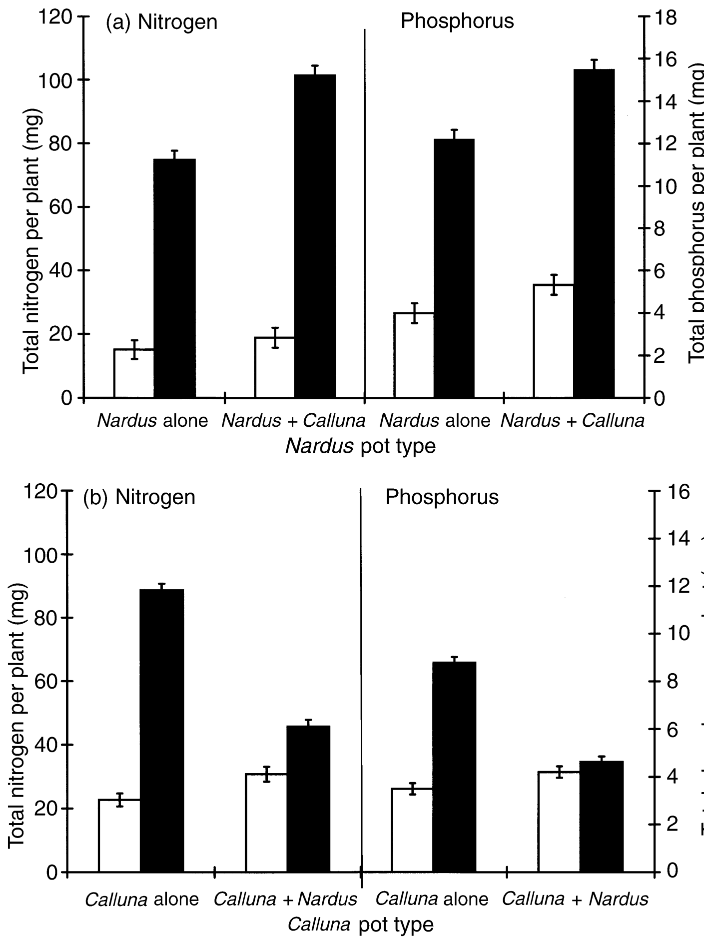

Fig. 2 Nitrogen and phosphorus contents (as total nitrogen or phosphorus in mg per plant) of *Nardus* and *Calluna* plants grown in monocultures or in mixtures, in pots with (shaded bars) or without (unshaded bars) fertilizer addition. Mean values ± SE are shown. (a) *Nardus* plants ($n = 53$), (b) *Calluna* plants ($n = 52$).

in shoot nitrogen content in defoliated plants than in control ones, both for *Calluna* growing in monoculture and in competition with *Nardus* (Fig. 3b). There was a significant fertilizer–defoliation interaction term for *Calluna* nitrogen content (Table 1), and both defoliated ($F = 10.7$, $P = 0.003$) and undefoliated ($F = 6.06$, $P = 0.02$) *Calluna* plants showed a significant fertilizer–pot type interaction for shoot nitrogen content. In summary, the increase in tissue nitrogen content produced by fertilizer in plants grow-

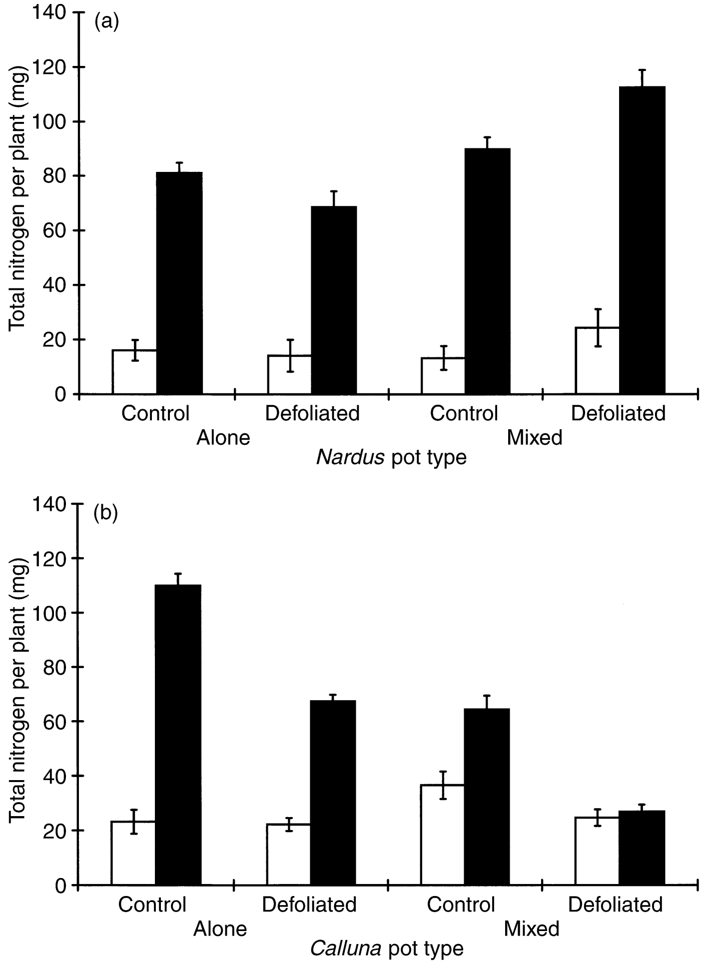

Fig. 3 The nitrogen content (mg per plant) of shoot tissue in control and defoliated plants grown in monocultures (Alone) or with the other species (Mixed). Shaded bars are values for plants from fertilized pots; unshaded bars are values for plants from control pots. Mean values ± SE are shown. (a) *Nardus* plants (n = 26), (b) *Calluna* plants (n = 26).

ing in mixtures was slightly greater for defoliated *Nardus* plants but significantly reduced in defoliated *Calluna* plants, relative to control plants (Fig. 3a,b).

BELOW-GROUND MEASUREMENTS

Fertilizer increased the root length of *Nardus* (Table 1 and Fig. 4 and Fig. 5), particularly when the plants were growing in monocultures, although the pot type–fertilizer interaction was non-significant. Regardless of fertilizer treatment, *Nardus* plants tended to have a greater root length growing in monoculture than when growing with *Calluna* plants, hence there was a significant effect of pot type on root length (Table 1 and Fig. 4). Overall, fertilizer had no significant effect on the root length of *Calluna*, but there was a significant effect of pot type on *Calluna* root length (Table 1): in monocultures, fertilizer increased root length, but decreased it when *Calluna* was growing with *Nardus*. In unfertilized pots, *Calluna* root length was the same whether the plants were grown alone or in mixtures with *Nardus* (Fig. 4). There was therefore a significant pot type–fertilizer interaction on *Calluna* root length. Defoliation had no effect on the root length of *Nardus* plants but caused a marked decrease in the root length of *Calluna* (Table 1 and Fig. 5).

Nardus plants had a higher proportion of root length infected by mycorrhizal fungi than *Calluna* plants, regardless of treatment (Fig. 6). Defoliation alone increased the mycorrhizal infection rate of *Nardus* plants, while fertilizer (with or without defoliation) significantly decreased it. The large decrease in infection rates in fertilized *Nardus* plants as a result of defoliation led to a significant fertilizer–defoliation interaction on infection rates. Fertilizer tended to reduce the infection rate in *Calluna* slightly, while defoliation caused a more marked decrease (Table 1 and Fig. 6).

Discussion

All the treatments applied to the *Calluna* and *Nardus* plants in this experiment, namely fertilizer, defoliation and being grown in competition with conspecifics vs.

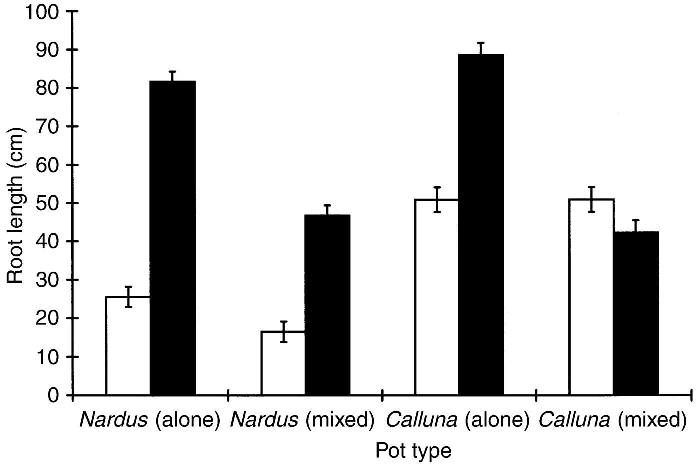

Fig. 4 Root length (cm) of *Nardus* and *Calluna* plants, grown in pots in monocultures (alone) or in mixtures (mixed). Shaded bars are values for plants grown in pots with added fertilizer, unshaded bars are values for plants from control pots with no fertilizer added. Mean values ($n = 40$) $\pm$ SE are shown.

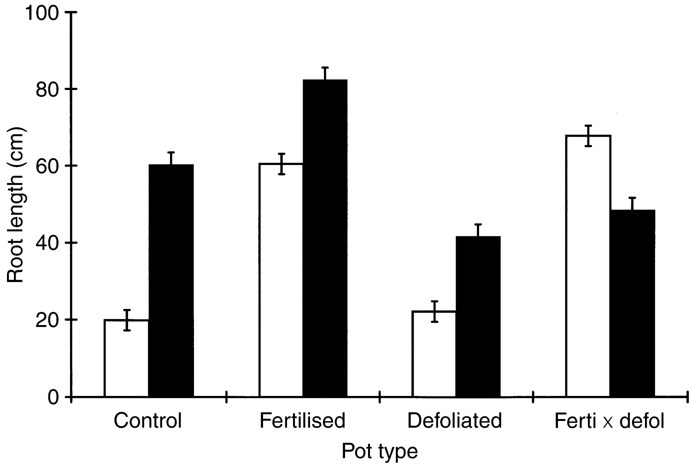

Fig. 5 The root length (cm) of *Nardus* plants (unshaded bars) and *Calluna* plants (shaded bars) receiving no treatment (control), fertilizer, defoliation, or both fertilizer and defoliation treatments. Mean values ($n = 40$) $\pm$ SE are shown, calculated irrespective of whether the plants were in mixtures or in monocultures (see Fig. 4 for monoculture vs. mixture effects).

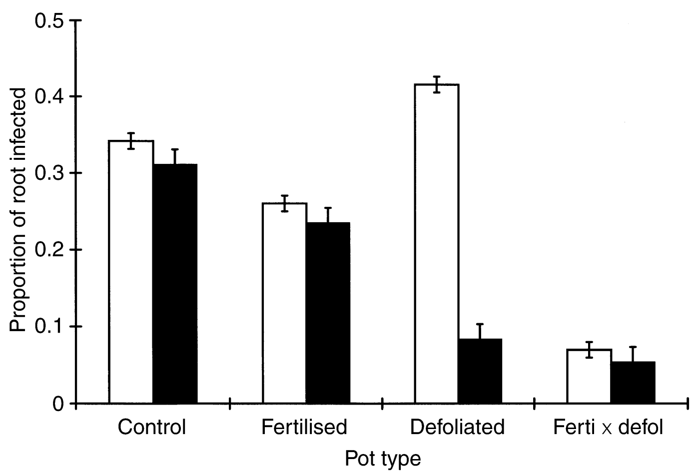

Fig. 6 Proportional mycorrhizal infection of *Nardus* plants (unshaded bars) and *Calluna* plants (shaded bars) receiving no treatment (control), fertilizer, defoliation, or both fertilizer and defoliation treatments. Mean values ($n = 40$) $\pm$ SE are shown, calculated irrespective of whether the plants were in mixtures or in monocultures.

mixtures, produced significant effects on at least some aspects of their above- and below-ground growth. In addition, there were interactions between the treatments: for example, the effects of fertilizer on the plants were modified by defoliation and the identity of the competing species. The treatments altered plant growth and nutrient acquisition by the two species to differing extents, suggesting that the competitive balance between *Nardus* and *Calluna* may be altered by nutrient availability and herbivory.

Under three of the four treatments, *Nardus* was the superior competitor, which explains why *Nardus* performed better in mixtures than in monocultures, while the reverse was true for *Calluna*. Only in unfertilized and undefoliated pots did the competitive advantage lie with *Calluna*. In unfertilized pots *Calluna* produced more biomass growing with *Nardus* than alone, and *Nardus* plants were the same size growing with *Calluna* as with conspecifics. In addition, *Nardus* root length was lower in unfertilized pots where *Calluna* was present. However, when fertilizer was added, the competitive balance changed and *Nardus* seemed better able to take advantage of the nutrient addition than *Calluna*. *Calluna* plants did not increase in size if they were fertilized when growing with *Nardus*, but *Nardus* plants showed a greater response to fertilizer when growing with *Calluna* than when grown in monoculture. The same pattern occurred in shoot nutrient content as in biomass, with a greater benefit to *Nardus* from fertilizer addition in mixtures than monocultures, but the reverse was the case for *Calluna*. Furthermore, the competitive disadvantage to *Calluna* extended below-ground, because fertilizer increased *Nardus* root length in both monocultures and mixtures, but *Calluna* root growth only increased in monocultures.

These results are similar to those from experiments with *Erica tetralix* and *Molinia caerulea* (Berendse & Aerts 1984). In unfertilized conditions, the growth of *Erica* was similar in mixtures and in monocultures, but when nitrogen was added *Erica*'s productivity and shoot nitrogen content were decreased in the presence of *Molinia*. The superior competitive ability of both *Erica* and *Calluna* to *Molinia* in unfertilized conditions has also been demonstrated in the field (Aerts *et al.* 1990); *Calluna* also outcompeted *Molinia* at high fertility, although *Erica* did not. However, several other studies have found that high fertility does favour *Molinia* over ericaceous species (Heil & Bruggink 1987; Aerts 1989; Aerts *et al.* 1991; Berendse *et al.* 1994).

This study suggests *Calluna* has a slight advantage over *Nardus* when the plants are competing without the addition of fertilizer. Although it is difficult to extrapolate from pots to the field situation, this is what might be expected on upland moorlands, with *Calluna* and its mycorrhizal endophyte *Hymenoscyphus ericae* better able to overcome the nutrient limitations of the soil (Stribley & Read 1980; Read 1983; Leake & Read 1991). However, when nutrient availability is increased, *Nardus* benefits to a greater extent than *Calluna* because it acquires the nutrients more rapidly, possibly because of differences in the effect of fertilizer on the root growth of the two species. Root length was increased in the fertilized pots to a greater extent for *Nardus* than for *Calluna*, especially when they were growing together. This may reflect the different strategies of the two plants for acquiring nutrients: *Nardus* has fibrous roots that go deep in the soil, while *Calluna* has fine roots close to the soil surface (Gimingham 1960). In the pot system used here, in which peat and soil were mixed homogeneously, *Nardus* roots may have been able to colonize to a greater depth and so have access to more of the added nutrients. Generally grasses distribute their roots more evenly in the soil profile than ericoid species, which concentrate their roots in the top 10 cm of soil (Aerts 1993). Aerts *et al.* (1991) found that *Molinia* allocated more than twice as much biomass to its root system than did *Calluna* when they were growing in competitive mixtures. Furthermore, the root biomass of *Molinia* present in the soil compartment of competing *Calluna* plants was three times as high in fertilized turves as in unfertilized ones. The authors concluded that the high competitive ability of *Molinia* at high nutrient supply was due to its large biomass allocation to the roots and a root system that can exploit a large soil volume. However, in heather moorlands the soil substrate is more heterogeneous than in turves or pots, and nutrients are concentrated in the organic layer very close to the soil surface. This is where *Calluna* roots form a dense mat, so the advantage to *Nardus* and other grasses may not be so apparent under field conditions. There is evidence from root box experiments using a separate peat layer at the soil surface, that this is indeed the case: *Calluna* is a better competitor for nitrogen than *Nardus* in spatially heterogeneous substrates (I. J. Alexander & S. E. Hartley, unpublished data).

The decrease in mycorrhizal infection rates in both species in the fertilized pots may be due to a direct effect of nutrients on the ability of mycorrhizae to infect successfully, or it may simply reflect 'dilution' of infection by increasing root growth. However, there are results from other pot studies that support the idea that mycorrhizal infection is reduced by increased soil nutrient levels (Stribley & Read 1976; Yesmin *et al.* 1996), although results from field trials have been less consistent (Caporn *et al.* 1995). Infection is costly to the host in terms of carbon, so if soil nutrient levels are such that adequate nutrients can be obtained by the plant without the aid of the mycorrhizae, it seems likely that there is a mechanism by which the plant can reduce infection. There are a number of published experiments on the effects of mycorrhizal infection on the outcome of competition (Allen & Allen 1990; Watkinson & Freckleton 1997), but these have usually used plants that have vesicular-arbuscular (VA) mycorrhizae (West 1996). There seem to be few studies, if any, comparing the performance of plants that have VA mycorrhizae with that of plants with ericoid mycorrhizae. In this study we did not manipulate the levels of infection, so we can make no inference on the importance of either sort of mycorrhizal infection on the competitive ability of plants. Indeed, the interpretation of the results from experiments that do compare plants with and without mycorrhizal infection in order to assess the effects on competition is complex, and effects are often found to be dependant on plant density (Watkinson & Freckleton 1997).

Nardus was a better competitor than *Calluna* not only under conditions of high nutrient supply, but also when defoliation shifted the competitive balance in its favour: defoliation had more adverse effects on *Calluna* than on *Nardus*, in terms of shoot nutrient content, mycorrhizal infection and root length. Defoliation reduced the increase in shoot nutrient content produced by fertilizer to a greater extent in *Calluna* than in *Nardus*, particularly when *Calluna* was grown in competition with *Nardus*. Defoliation decreased both root length and mycorrhizal infection in *Calluna*, but did not decrease root length and actually increased mycorrhizal infection in *Nardus*. The lower levels of shoot resources in defoliated *Calluna* plants, but not in defoliated *Nardus* plants, suggest that *Nardus* may be quicker to recover from defoliation than *Calluna*, reinforcing the advantage *Nardus* already gains from having basal meristems. Heavy grazing is thought to be a major cause of the loss of *Calluna*-dominated moorland in recent years (Welch 1986; Hartley 1997).

Although in these pot experiments both fertilizer and defoliation seemed to shift the competitive balance towards *Nardus*, in the field these factors may not necessarily favour *Nardus* to the same extent, as soil type, the nature of the grazing pressure, and the structure (and hence invasibility) of the *Calluna* canopy will all play a role in modifying their effects (Hartley 1997). For example, the effect of nutrients on the competitive balance between the two species may depend on the extent to which their relative palatability to grazing animals alters in response to increasing nutrient inputs. Any competitive advantage to *Nardus* from increased shoot nutrient concentrations might be lost were it to become a more preferred food for grazing animals. On Scottish moorlands, however, it was found that nitrogen addition benefited *Nardus*, but only in heavily grazed areas where its resistance to grazing gave it a competitive advantage. If grazing animals were excluded by fencing, *Calluna* cover increased in response to fertilizer and its increased growth, in response to both the extra nutrients and the lack of browsing, allowed it to close its canopy over the *Nardus* plants and shade them out (Hartley 1997). This field experiment highlighted the importance of canopy structure in competitive interactions between *Calluna* and *Nardus*: the smaller stature and shade intolerance of the latter species does not come into play in experiments using small transplanted plants in pots.

The results presented here show that the competitive ability of *Nardus* with respect to *Calluna* was enhanced by the addition of fertilizer, as a result of the superior ability of *Nardus* to acquire the added nutrients. Simulated grazing also benefited *Nardus*, due to its more adverse effects on *Calluna*'s root and shoot resources. These results suggest that both grazing and nitrogen inputs could reduce the competitive ability of *Calluna*, particularly below-ground, which may have implications for the future dominance of *Calluna* in heathland ecosystems, particularly those where nutrient inputs are increasing significantly, or where grazing pressures are high.

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