

The relation between above- and belowground biomass allocation patterns and competitive ability

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Summary. In a 2-year experiment, the evergreen shrubs *Erica tetralix* and *Calluna vulgaris* (dominant on nutrient-poor heathland soils) and the perennial deciduous grass *Molinia caerulea* (dominant on nutrient-rich heathland soils) were grown in replacement series in a factorial combination of four competition types (no competition, only aboveground competition, only belowground competition, full competition) and two levels of nutrient supply (no nutrients and 10 g N + 2 g P + 10 g K m⁻² yr⁻¹). Both in the unfertilized and in the fertilized treatments *Molinia* allocated about twice as much biomass to its root system than did *Erica* and *Calluna*. In all three species the relative amount of biomass allocated to the roots was lower at high than at low nutrient supply. The relative decrease was larger for *Molinia* than for *Erica* and *Calluna*. In the fertilized monocultures biomass of all three species exceeded that in the unfertilized series. *Molinia* showed the greatest biomass increase. In the unfertilized series no effects of interspecific competition on the biomass of each species were observed in either of the competition treatments. In the fertilized mixtures where only belowground competition was possible *Molinia* increased its biomass at the expense of both *Erica* and *Calluna*. When only aboveground competition was possible no effects of interspecific competition on the biomass of the competing species were observed. However, in contrast with the evergreens, *Molinia* responded by positioning its leaf layers relatively higher in the canopy. The effects of full competition were similar to those of only belowground competition, so in the fertilized series belowground competition determined the outcome of competition. The high competitive ability of *Molinia* at high nutrient supply can be attributed to the combination of (1) a high potential productivity, (2) a high percentage biomass allocation to the roots, (3) an extensive root system exploiting a large soil volume, and (4) plasticity in the spatial arrangement of leaf layers over its tall canopy. In the species under study the allocation patterns entailed no apparent trade-off between the abilities to

compete for above- and belowground resources. This study suggests that this trade-off can be overcome by: (1) plasticity in the spatial arrangement of leaf layers and roots, and (2) compensatory phenotypic and species-specific differences in specific leaf area and specific root length.

Key words: Competition – Allocation – Canopy structure – Rooting pattern – Plasticity

In recent years, there has been a lively debate on the nature and the importance of competition as determinant of the structure and dynamics of plant communities (Grime 1979, 1988; Grime and Hodgson 1987; Tilman 1985, 1987, 1988; Thompson 1987; Thompson and Grime 1988). An important aspect of the controversy is the disagreement on the characteristics of successful competitors. Tilman (1988) defines a high competitive ability as the capacity to reduce a resource to a level too low to support the growth of competitors. He postulates that due to the physical separation of above- and belowground resources plants face an unavoidable trade-off between the abilities to compete for these resources: in order to obtain a higher portion of one resource plants must allocate more biomass to structures involved in the acquisition of that resource at the expense of allocation of biomass to structures involved in the acquisition of another resource. Grime and Hodgson (1987) listed the following plant characteristics that confer a high competitive ability: (1) a robust perennial life form with a strong capacity to ramify vegetatively throughout the aerial and edaphic environment, (2) the rapid commitment of captured resources to the construction of new leaves and roots, (3) high morphological plasticity during the differentiation of leaves and roots, and (4) short life spans of individual leaves and roots. Thus, Grime and Hodgson (1987) propose an interacting foraging response to enable escape from zones of low resource availability both above- and belowground. Another point of

disagreement is the intensity of interspecific competition on nutrient-poor soils, which is low according to Grime et al. (1987), especially in the presence of mycorrhizal infection, and high according to Tilman (1988).

In these theories the main emphasis is on the relation between biomass allocation patterns and competitive ability. However, it has been shown that both the spatial arrangement of leaf layers (Mahmoud and Grime 1976; Grime 1979; Spitters and Aerts 1983; Mitchley 1988; Barnes et al. 1988, 1990; Aerts et al. 1990) and of roots (Caldwell and Richards 1986; Crick and Grime 1987; Eissenstat and Caldwell 1988, 1989; Grime et al. 1990) may be important determinants of competitive ability for above- and belowground resources, respectively.

The aim of this study was threefold: (1) to assess the intensity of competition and the relative importance of above- and belowground competition at different levels of nutrient supply, (2) to assess if there is a trade-off between the abilities to compete for above- and belowground resources, respectively, and (3) to assess the relationship between species-specific and environmentally induced variation in biomass allocation (including the spatial arrangement of leaves and roots) and the competitive ability of plant species. Therefore an experiment was conducted in which the relation between competitive ability and biomass allocation patterns of *Erica tetralix*, *Calluna vulgaris* and *Molinia caerulea* was determined in a factorial combination of different types of competition (i.e. both above- and belowground, only aboveground, only belowground and no competition at all) and two levels of nutrient supply. The different competition types were used to test the hypothesis that there is a trade-off between the abilities to compete for above- and belowground resources, respectively (Tilman 1988). If this hypothesis is correct, the exclusion of the possibility of competition for above- or belowground resources should lead to a reversal of the outcome of competition.

Erica and *Calluna* are evergreen dwarf shrubs with a low potential growth rate, whereas *Molinia* is a deciduous perennial grass with a relatively high potential growth rate (Aerts et al. 1990). In most nutrient-rich Dutch heathlands *Erica* and *Calluna* have been replaced by *Molinia*. In a 3-year competition experiment in the field with these species it was found that competitive ability was positively correlated with the ability to compete for light interception. However, it could not be excluded that the ability to compete for light was determined by a high ability to compete for nutrient uptake (Aerts et al. 1990).

Methods

Erica and *Calluna* plants were grown in turf soil for 2 years until they were similar in size and height to the plants in the field experiment with *Erica* (E), *Calluna* (C) and *Molinia* (M) described in Aerts et al. (1990). *Molinia* plants, also similar in size to the plants in that field experiment, were collected in the field. At the start of the experiment (May 1987), all plants were gently transferred to nutrient-poor sandy soil in an experimental garden. The plants were then allocated to each of the factorial combinations of competition types and nutrient supplies described in Table 1.

Table 1. Experimental treatments in the competition experiment. Fertilizer applications given in $\text{g m}^{-2} \text{yr}^{-1}$

<i>Competition type</i>			
I-I	: full isolation		
I-C	: aboveground isolation – belowground competition		
C-I	: aboveground competition – belowground isolation		
C-C	: full competition		
<hr/>			
	N	P	K
<hr/>			
<i>Fertilizer application</i>			
Unfertilized (U)	0	0	0
Fertilized (F)	10	2	10

In the C-I and I-I treatments belowground competition was prevented by placing the plants in cubical plastic pots measuring $13 \times 13 \times 13$ cm. When belowground competition was allowed for (I-C and C-C treatments), 5 plants were placed at intervals of 13 cm in containers measuring 65×13 cm with a depth of 13 cm (monocultures) and in the mixtures 6 plants were placed at intervals of 13 cm in containers measuring 78×13 cm with a depth of 13 cm. Thus the rooting volume per plant was equal in all treatments. In the I-I and I-C treatments aboveground competition was prevented by placing white nylon stockings around each plant over a vertical framework of sticks which were placed at intervals of 13 cm, so each plant had an equal volume of aerial space. The height of the stockings was adjusted to maximum plant height during the growing season.

The three species were grown in monoculture (E, C, M) and in 1:1 mixtures with each other (E/C, E/M, C/M). In each treatment an area of 13×13 cm was allotted to each plant, so plant density was 59 plants per m^2 . This density corresponds very close to the density found in heathlands five years after the start of secondary succession (Aerts et al. 1990). In the monocultures 20 plants were placed in blocks of 52×65 cm (four rows of five plants). In the mixtures 15 plants of each competing species were placed alternately in blocks of 65×78 cm (five rows of six plants). To avoid edge effects only the inner 6 plants (monocultures) or 12 plants (mixtures) were analysed.

For two consecutive years nutrients were supplied to each plant once a week during the growing season dissolved in 25 ml of tapwater. The nutrient supply (Table 1) was equal to the "O" and "2NPK" treatments in the field experiment (Aerts et al. 1990). To stimulate growth at the beginning of the growing season the control was supplied twice with the same nutrient solution as the fertilized series. This amount corresponded to 10% of the total nutrient supply to the fertilized series. Nitrogen was given as ammonium chloride, phosphorus as sodium dihydrogen phosphate and potassium as potassium chloride. The plants were regularly watered to prevent water stress. Nevertheless, due to very high temperatures in the first month of the experiment almost all the *Erica* plants died due to water stress. They were replaced within 1 month after the start of the experiment.

At the end of the second growing season (September 1988) the vertical canopy structure was measured in the C-I and C-C treatments (Table 1) using the horizontal point-quadrat method described in detail in Aerts et al. (1990). In this way the relative distribution of leaf mass over the canopy height was determined. Next, plants in the I-I and C-I treatments were harvested by cutting the shoots and gently washing out the roots in the pots. In the I-C and C-C treatments the shoots were cut off and the contents of each container placed on a pin-board, leaving its original spatial structure intact. Due to the close intermingling of *Molinia* roots and roots of the evergreens, it was not possible to determine the lateral extension of individual roots. Therefore, the soil monolith on the pin-board was cut in blocks of $13 \times 13 \times 13$ cm (with the shoot of each plant in the centre of the block) and the roots were washed out

of every block. When roots of two species were present in a block they were separated by species. In this way it was possible to assess the penetration of roots of each species into the soil compartment of a competing neighbour. In each treatment the shoots were separated into leaf and non-leaf material. After drying for 48 h at 70° C, dry weights of each fraction were determined.

Data were statistically analysed using the General Linear Models procedure of the Statistical Analysis System (SAS Institute Inc. 1985). The calculations used log-transformed data. Multiple comparisons among pairs of means were made using Tukey's Studentized Range Test. The effects of competition (both intra- and interspecific) were measured by comparing the tested parameter in the competition treatments (I-C, C-I and C-C) with the tested parameter in the non-competitive situation (the I-I treatment). This type of comparison is only valid when there are no statistical differences between the tested parameter in the I-I treatments for a given species and a given nutrient supply. This assumption was tested a posteriori and in no case was a significant difference detected, although there were sometimes large differences between means in the I-I treatments. This was due to occasional very high coefficients of variation in the data set.

Results

Total biomass

Monocultures. In the unfertilized monocultures (all treatments) the total biomass of *Erica* and *Molinia* significant-

ly exceeded that of *Calluna* ($P < 0.05$). In the fertilized monocultures (all treatments) total biomass of *Molinia* significantly exceeded that of *Erica* ($P < 0.0001$), which in turn significantly exceeded that of *Calluna* ($P < 0.01$) (Figs. 1, 2, 3). Analysis of variance showed a significant ($P = 0.05$) effect of fertilization on total biomass of *Erica*. The ANOVA also revealed a significant effect of fertilization on total biomass of *Calluna* and of *Molinia* ($P < 0.005$ and $P < 0.0001$, respectively).

In none of the species was there a significant effect of competition type on total biomass in the monocultures (Figs. 1, 2, 3), so there were no net effects of intraspecific competition within the given duration of the experiment and the given sizes of the plants.

Mixtures. In neither of the unfertilized series was there a significant effect of competition type on total biomass of *Erica* (Fig. 1). In competition with *Calluna*, total biomass of *Erica* in the fertilized C-I treatment was significantly higher than in the I-I treatment. In the fertilized competition series with *Molinia*, total biomass of *Erica* was significantly lower in the C-C treatment when compared with the I-I treatment.

In neither of the unfertilized series was a significant effect of competition type observed on total biomass of

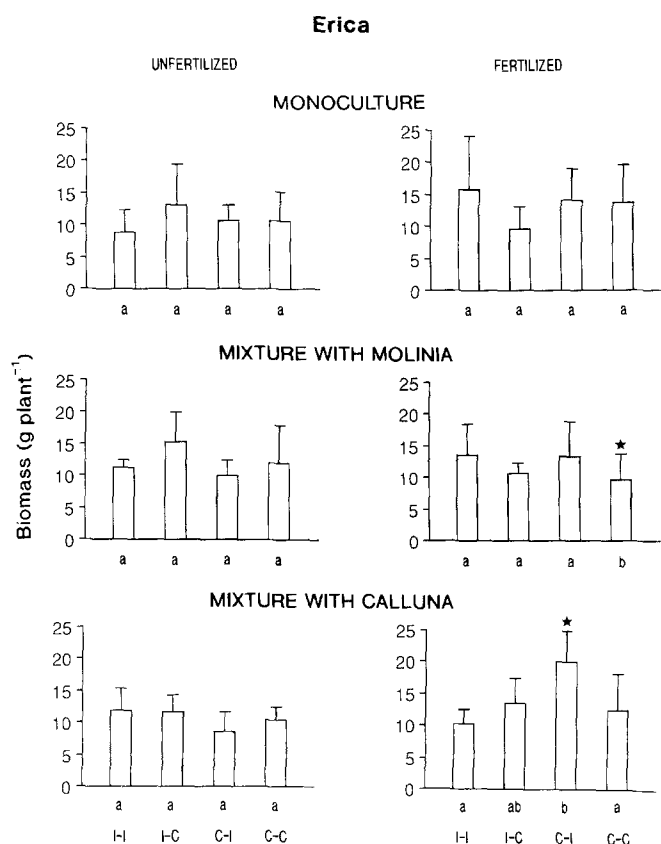


Fig. 1. Total biomass (g plant^{-1}) of *Erica tetralix* grown in monoculture and in mixture at four competition types and two levels of nutrient supply (see Table 1). Error bars are 1 SD ($n = 6$). Within each sub-figure different letters indicate significant difference ($P < 0.05$). * indicates significant difference from I-I treatment

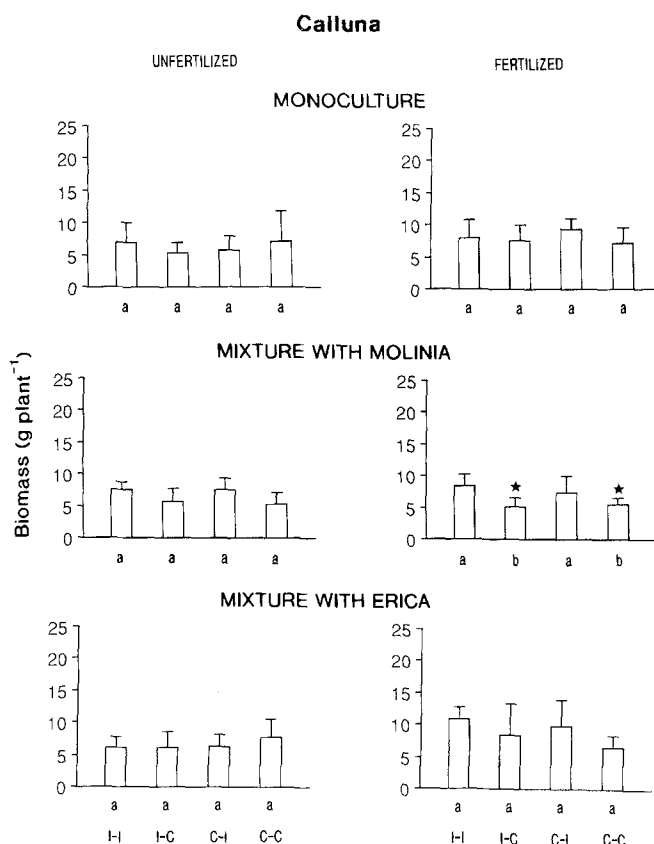


Fig. 2. Total biomass (g plant^{-1}) of *Calluna vulgaris* grown in monoculture and in mixture at four competition types and two levels of nutrient supply (see Table 1). Error bars are 1 SD ($n = 6$). Within each sub-figure different letters indicate significant difference ($P < 0.05$). * indicates significant difference from I-I treatment

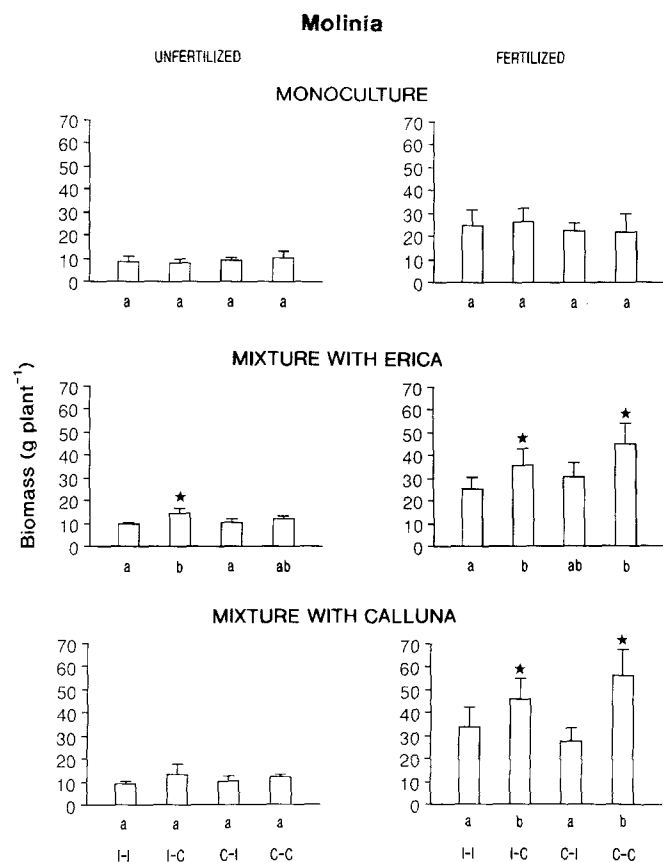


Fig. 3. Total biomass (g plant⁻¹) of *Molinia caerulea* grown in monoculture and in mixture at four competition types and two levels of nutrient supply (see Table 1). Error bars are 1 SD ($n=6$). Within each sub-figure different letters indicate significant difference ($P<0.05$). * indicates significant difference from I-I treatment. Note that y axis is scaled differently from Figs. 1 and 2

Calluna (Fig. 2). In the fertilized competition series with *Molinia* total biomass of *Calluna* in the I-C and C-C treatment was significantly lower than in the I-I treatment.

In the unfertilized competition series with *Erica* biomass of *Molinia* in the I-C treatment was higher than in the I-I treatment (Fig. 3). In the fertilized competition series both with *Erica* and *Calluna* biomass of *Molinia* in the I-C and C-C treatment exceeded that in the I-I treatment considerably.

Percentage allocation of biomass to the roots and lateral extension of the root system

In all three species percentage biomass allocation to the roots decreased with increasing nutrient supply (*Erica*: $P<0.01$; *Calluna*: $P<0.0001$; *Molinia*: $P<0.0001$). Percentage biomass allocation to the roots differed significantly between species ($P<0.0001$) and was highest in *Molinia* and lowest in *Calluna*, whilst *Erica* had an intermediate allocation (Table 2). In *Erica* percentage biomass allocation to the roots was lower in the unfertilized C-C mixture with *Molinia* compared with the I-I treatment, but in the fertilized C-C mixture it was higher (Table 2). In *Calluna* biomass allocation to the roots in the unfertilized C-I mixture with *Molinia* exceeded that in the I-I treatment, but it was higher in the fertilized C-I monoculture (Table 2). In *Molinia* percentage biomass allocation to the roots was lower in the unfertilized C-I monoculture compared with the I-I treatment, and also in the unfertilized I-C, C-I and C-C treatments in the mixtures with *Erica* (Table 2). In the fertilized mixture

Table 2. Percentage allocation of biomass to roots in relation to competition type and fertilization level (see Tab. 1) in *Erica tetralix* (E), *Calluna vulgaris* (C) and *Molinia caerulea* (M), grown in monoculture and in mixture with each other. * indicates significant difference from I-I treatment ($P<0.05$) $n=6$

	Unfertilized			Fertilized		
	Mono	Mix E/C	Mix E/M	Mono	Mix E/C	Mix E/M
<i>Erica</i>						
I-I	28	28	31	27	21	19
I-C	23	30	26	21	25	22
C-I	31	28	30	31	24	23
C-C	24	27	23*	23	22	36*
	Unfertilized			Fertilized		
	Mono	Mix E/C	Mix C/M	Mono	Mix E/C	Mix C/M
<i>Calluna</i>						
I-I	20	21	24	19	23	18
I-C	21	24	22	18	18	17
C-I	26	25	34*	27*	20	24
C-C	27	23	22	17	26	20
	Unfertilized			Fertilized		
	Mono	Mix E/M	Mix C/M	Mono	Mix E/M	Mix C/M
<i>Molinia</i>						
I-I	64	69	56	55	50	43
I-C	60	50*	53	46	41*	41
C-I	56*	51*	58	45	47	49
C-C	67	49*	54	49	44	43

with *Erica* biomass allocation to the roots was lower in the I-C treatment (Table 2).

The extent to which root systems intermingle or explore the same soil volume as neighbouring competing species can be estimated by determining the percentage of the root mass of a plant which is present in the soil

Table 3. Percentage of the root system penetrating the soil compartment of a competing species for *Erica tetralix*, *Calluna vulgaris* and *Molinia caerulea* when grown in mixture with each other at different fertilizer supplies and competition types (see Table 1). Means \pm SD are given ($n=6$)

	Mixture with <i>Calluna</i>		Mixture with <i>Molinia</i>	
	I-C	C-C	I-C	C-C
<i>Erica</i>				
U	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0
F	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0
	Mixture with <i>Erica</i>		Mixture with <i>Molinia</i>	
	I-C	C-C	I-C	C-C
<i>Calluna</i>				
U	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0
F	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0
	Mixture with <i>Erica</i>		Mixture with <i>Calluna</i>	
	I-C	C-C	I-C	C-C
<i>Molinia</i>				
U	29 \pm 6	30 \pm 9	27 \pm 6	37 \pm 7
F	25 \pm 6	26 \pm 6	32 \pm 6	27 \pm 3

Table 4. Total leaf mass (g plant⁻¹) of *Erica tetralix* (E), *Calluna vulgaris* (C) and *Molinia caerulea* (M), grown in monoculture and in mixture with each other in relation to competition type and fertilization level (see Table 1). * indicates significant difference from I-I treatment ($P < 0.05$) $n=6$

	Unfertilized			Fertilized		
	Mono	Mix E/C	Mix E/M	Mono	Mix E/C	Mix E/M
<i>Erica</i>						
I-I	1.5	1.9	1.8	3.5	2.1	3.0
I-C	3.0	1.6	1.8	1.9	2.8	1.6*
C-I	1.4	1.3	1.6	2.4	4.3*	2.9
C-C	1.5	1.6	2.0	2.7	2.6	1.0*
	Mono	Mix E/C	Mix C/M	Mono	Mix E/C	Mix C/M
<i>Calluna</i>						
I-I	1.5	1.1	1.3	1.7	3.1	1.7
I-C	0.7	1.6	1.4	1.7	2.0	1.3
C-I	1.1	1.2	2.0	2.7	2.8	2.1
C-C	1.6	1.3	1.2	1.9	1.7	0.8*
	Mono	Mix E/M	Mix C/M	Mono	Mix E/M	Mix C/M
<i>Molinia</i>						
I-I	0.8	1.0	0.9	2.0	1.9	2.0
I-C	0.9	1.1	1.3*	2.2	3.2	3.3
C-I	0.8	0.8	0.8	1.9	1.9	3.0
C-C	0.8	0.9	1.0	1.7	3.8*	4.1*

volume of a competing neighbour. Neither *Erica* nor *Calluna* expanded their root systems into the soil volume of a competing species (Table 3). *Molinia*, on the other hand, both in the unfertilized and in the fertilized series, extended about 30% of its root system into the soil compartment of competing *Erica* and *Calluna* plants. Due to the high biomass increase of *Molinia* after fertilization (Fig. 3), the absolute root mass of *Molinia* present in the soil compartment of competing *Erica* and *Calluna* plants was about 3 times as high in the fertilized series as in the unfertilized series (19.1 and 6.5 g per plant; $P < 0.0001$).

Total leaf mass and vertical leaf mass distribution

Analysis of variance showed significant differences in total leaf mass between species ($P < 0.0001$) and fertilization levels ($P < 0.0001$).

In both the unfertilized *Erica* and *Calluna* series there was no difference in leaf mass between the I-I treatments and the competition treatments (Table 4). In the unfertilized *Molinia* mixture with *Calluna*, leaf mass of *Molinia* in the I-C treatment significantly exceeded that in the I-I treatment.

In *Erica* total leaf mass in the fertilized C-I mixture with *Calluna* was higher than in the I-I treatment (Table 4). In the fertilized mixture with *Molinia*, leaf mass was significantly lower in both the I-C and the C-C treatments than in the I-I treatment.

In the fertilized competition series with *Molinia* leaf mass of *Calluna* was lower in the C-C treatment than in the I-I treatment (Table 4).

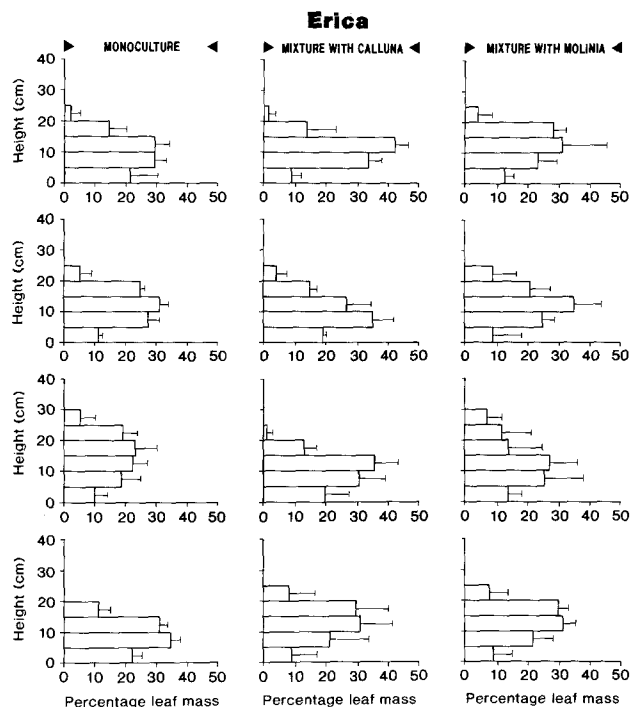


Fig. 4. Percentage leaf mass distribution over the canopy of *Erica tetralix* when grown in monoculture and in mixture at two competition types and two levels of nutrient supply (see Table 1). Error bars are 1 SD ($n=3$ in monoculture, $n=4$ in mixture)

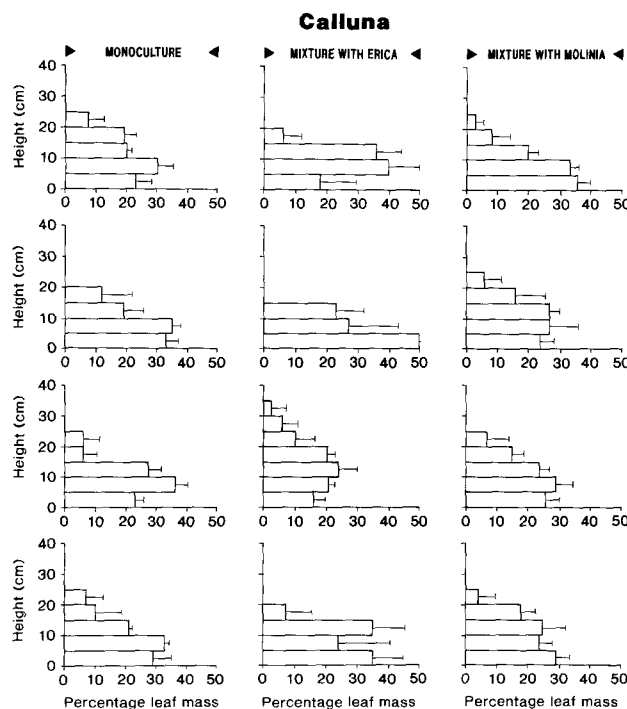


Fig. 5. Percentage leaf mass distribution over the canopy of *Calluna vulgaris* when grown in monoculture and in mixture at two competition types and two levels of nutrient supply (see Table 1). Error bars are 1 SD ($n=3$ in monoculture, $n=4$ in mixture)

In competition with either *Erica* or *Calluna* the leaf mass of *Molinia* in the C-C treatment significantly exceeded that in the I-I treatment (Table 4).

Vertical leaf mass distribution is expressed as the

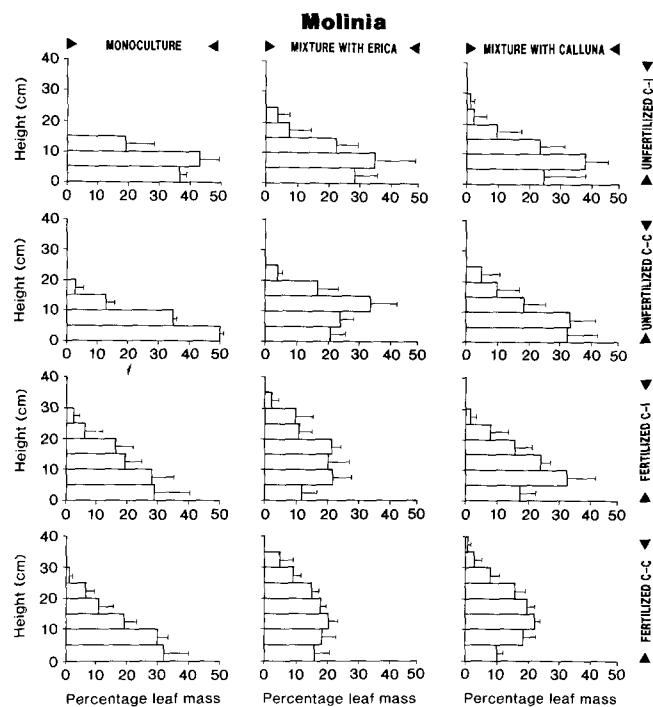


Fig. 6. Percentage leaf mass distribution over the canopy of *Molinia caerulea* when grown in monoculture and in mixture at two competition types and two levels of nutrient supply (see Table 1). Error bars are 1 SD ($n=3$ in monoculture, $n=4$ in mixture)

percentage of total leaf mass present in canopy layers of 5 cm. In *Erica* leaf mass showed a rather similar pattern in all series: leaves were present up to 30 cm, with the bulk of leaf mass concentrated between 10 and 20 cm above the soil surface (Fig. 4). There was no conspicuous effect of fertilization level or competition (monoculture vs. mixture) on this distribution pattern. In *Calluna* a somewhat different pattern was observed (Fig. 5): leaves were present up to 35 cm, with the bulk of leaf mass concentrated in the lower leaf layers (0–15 cm). As was the case with *Erica*, there was no clear effect of fertilization level or interspecific competition on this pattern.

The vertical leaf distribution pattern of *Molinia* was quite different from that of the evergreens (Fig. 6). Leaves were present up to a height of 40 cm. There was a clear effect of fertilization level on maximum canopy height. More striking, however, was the effect of interspecific competition on the vertical leaf distribution. When grown in mixture with *Erica* or *Calluna*, *Molinia* positioned its leaves higher than in the monocultures and a shift of leaf mass allocation from lower to higher leaf layers occurred.

Discussion

The experimental design

The analysis of competition experiments is often obscured by the dependence of the outcome of these experiments on the starting conditions and the duration of the experiment (Spitters and Aerts 1983; Wilson 1988a; Conolly et al. 1990). The experimental design for this

study was based on the design we used in a field experiment (Aerts et al. 1990). We therefore used plant densities and plant sizes characteristic of Dutch heathlands after 5 years of secondary succession and fertilizer applications within the range of mineralization rates measured in these heathlands during secondary succession (cf. Berendse 1990). The pot-volume we used corresponded with about 90% of the rooting volume occupied by the heathland species under field conditions (Aerts et al. 1989; Aerts, unpublished work). Moreover, we grew the plants outside under prevailing weather conditions. In our opinion this experimental design mimics the natural situation as closely as possible. Nevertheless, this experiment still suffers from the limitations of a pot experiment, notably from the limited rooting-volume and the relatively short duration of the experiment (two growing seasons). Moreover, it is hard to generalize the results, because the experiment involved only three species. These aspects should be kept in mind when interpreting the results.

Both in the unfertilized and in the fertilized series the *Molinia* roots did penetrate the *Erica* and *Calluna* soil compartments to a great extent (Table 3). From this we conclude that the experiment did last long enough to allow competitive interactions to occur in both series.

Neither in the unfertilized nor in the fertilized monocultures were there any net effects of intraspecific competition, so the effects which occurred in the mixtures were due to interspecific competition.

Competition at low and high nutrient supply

In the unfertilized series no apparent effect of interspecific competition was observed (Figs. 1, 2, 3). The most obvious conclusion is that this result supports the contention of Grime et al. (1987) about the low intensity of interspecific competition on nutrient-poor soils. As was pointed out earlier (Grime 1979; Berendse et al. 1987; Aerts 1990) the dominance of perennial plant species in low-nutrient habitats is determined by their ability to conserve mineral nutrients rather than to maximize the rate of capture. Both *Erica* and *Calluna* have a higher nutrient retention capacity than *Molinia* (Aerts 1990). This probably balances *Molinia*'s higher competitive ability for nutrient uptake, because in the unfertilized belowground competition series *Molinia* was unable to outcompete *Erica* and *Calluna* despite its higher investment of biomass in the root system (Table 2) and its larger volume of soil explored (Table 3). In a field experiment we even found that at a low nutrient supply *Molinia* was outcompeted by both *Erica* and *Calluna* (Aerts et al. 1990). A possible reason for this difference might be that in the field experiment plant density was somewhat higher than in this experiment. This resulted in closure of the canopy of both evergreens very early in the growing season thus reducing light interception by the *Molinia* plants (deciduous) to the extent that they were crowded out. Due to the lower plant density in this experiment no such phenomenon occurred and there appeared to be no net effects of competition between *Molinia* and the evergreens in the unfertilized series. In a competition experi-

ment with *Calluna* and *Molinia* a similar effect of total plant density on the outcome of competition was found by Heil and Bruggink (1987).

The biomass of all three species increased significantly after fertilizer application. The growth response of *Molinia* to fertilization considerably exceeded that of the evergreens (Figs. 1, 2, 3). This was also the case in the field experiment (Aerts et al. 1990). In the fertilized series clear effects of interspecific competition were found. In mixture with *Molinia* the biomass of both *Erica* and *Calluna* was lower in the treatments with belowground competition (I-C and C-C) as compared with the I-I treatment (Figs. 1, 2), while the biomass of *Molinia* in these treatments exceeded that in the I-I treatment (Fig. 3). Apparently, at high levels of nutrient availability the high competitive ability of *Molinia* with respect to *Erica* and *Molinia* was due to its higher competitive ability for belowground resources. So under these circumstances the higher nutrient losses of *Molinia* are more than compensated for by its higher competitive ability for nutrient uptake. When only aboveground competition was possible (C-I treatment) there were no net effects of interspecific competition on the biomass of the competing species.

The relative importance of above- and belowground competition

In an extensive review of studies on the relative importance of above- and belowground competition Wilson (1988b) found that belowground competition usually affected the balance between the competing species more than aboveground competition. Moreover, competitive effects appeared to be more severe at high levels of resource availability. The results of this study are in agreement with these general trends. Unfortunately, competition for belowground resources is known more by its manifestations than by its mechanisms (Caldwell 1987), but this study offers some indications about possible mechanisms. In all treatments the relative allocation of biomass to the roots in *Molinia* was about 2–3 times as high as in *Erica* and *Calluna* (Table 2). When only belowground competition was possible (I-C treatment) about 30% of the extensive root system of *Molinia* penetrated the soil volume allotted to *Erica* and *Calluna*, while no roots of these evergreens were present in the *Molinia* soil compartment (Table 3). Hence the high competitive ability for belowground resources of *Molinia* was due to its potentially high productivity (Aerts et al. 1990), its high percentage of biomass allocated to the roots, and its strong capacity to proliferate through the edaphic environment (cf. Grime and Hodgson 1987; Eissenstat and Caldwell 1988, 1989). Similarly, Baan Hofman and Ennik (1980, 1982) and Ennik and Baan Hofman (1983) found that the competitive ability of different clones of *Lolium perenne* was positively correlated with their high root-shoot ratio and/or their high root mass.

No net effects of aboveground competition only were observed (Figs. 1, 2, 3), except in the fertilized *Erica/Calluna* mixture where biomass of *Erica* increased significantly without causing a reduction of the biomass of

Calluna. A striking aspect of the C-I mixtures was that *Molinia* positioned its leaf biomass in higher leaf layers compared with the monoculture (Fig. 6), whilst no such pattern was observed in *Erica* or *Calluna* (Figs. 4, 5). In this way *Molinia* increased its competitive ability for light interception (Spitters and Aerts 1983; Roush and Radosevich 1985; Mitchley 1988; Aerts et al. 1990; Barnes et al. 1990). In the full competition treatment (C-C) *Molinia* will have benefited from both its high degree of root extension and its plasticity in the spatial arrangement of leaf layers over its tall canopy (Fig. 6). These results show that at high nutrient supply *Molinia* has a high competitive ability for both above- and below-ground resources.

Biomass allocation and competitive ability

In an analysis of biomass allocation patterns during succession from nutrient-poor to nutrient-rich soils Tilman (1988) postulated that due to the shift from nutrient-limited to light-limited growth late successional species allocate more biomass to the shoot, thus increasing their competitive ability for light interception. In contrast with this equilibrium resource ratio hypothesis, the late successional species of this study (*Molinia*) had the lowest biomass allocation to the shoot. When comparing five species from a grassland succession series Olff et al. (1990) also found that the late successional species had the lowest biomass allocation to the shoots. A similar pattern was found by Berendse and Elberse (1989) when comparing grassland species from nutrient-poor and nutrient-rich sites. Similarly, Tilman and Cowan (1989) and Gleeson and Tilman (1990) reported that in a chronosequence of secondary succession from nutrient-poor to nutrient-rich soils the percentage biomass allocation to the shoots decreased in the course of succession. These observations do not correspond with the equilibrium resource ratio hypothesis.

Morphological plasticity may increase the competitive ability of a plant over a range of different resource availabilities (Grime et al. 1986; Crick and Grime 1987; Tilman 1988). This raises the question how nutrient supply and competition type affect biomass allocation patterns. Both the evergreens and *Molinia* allocated relatively more biomass to the roots at low nutrient supply (Table 2), thus increasing their competitive ability for belowground resources. This phenotypic response is common to all plant species (Brouwer 1962a, b; Chapin 1980; Boot and Mensink 1990). In the monocultures the percentage decrease of biomass allocation to the roots in *Molinia* exceeded that in both evergreens (Table 2) thus pointing to a higher phenotypic plasticity in the partitioning of biomass between shoots and roots. However, there were no clear patterns of plasticity in biomass allocation as a response to different types of competition (Table 2).

Contrary to Tilman's (1988) resource ratio hypothesis, the allocation patterns of the species under study entailed no apparent trade-off between their competitive abilities for above- and belowground resources. *Molinia*

was a superior competitor for belowground resources, but not at the expense of its ability to compete for above-ground resources, despite its low leaf biomass (Table 4), which was less than 10% of total plant biomass compared to 25–30% for both evergreens. Crucial to Tilman's (1988) hypothesis is the assumption that light interception and nutrient uptake are proportional to leaf biomass and root biomass, respectively. However, light interception is dependent on leaf area (Monsi and Saeki 1953) and nutrient uptake is dependent on root length (Boot 1989). There are substantial phenotypic and species-specific differences in specific leaf area (SLA: $\text{m}^2 \text{ leaf g}^{-1} \text{ leaf}$) (Karlsson 1985; Lambers and Dijkstra 1987; Konings et al. 1989; Poorter and Remkes 1990) and specific root length (SRL: $\text{m root g}^{-1} \text{ root}$) (Caldwell and Richards 1986; Robinson and Rorison 1988; Boot 1989; Berendse and Elberse 1989; Poorter and Remkes 1990). Thus, a low allocation of biomass to the leaves can be compensated by a high SLA, and a low biomass allocation to the roots by a high SRL, as was shown for two species of dry nutrient-poor inland dunes (Boot and Den Dubbelden 1990). Such compensatory patterns were also found in the three species of this study. The lower allocation of biomass to the leaves in *Molinia* as compared with *Erica* and *Calluna* (Table 4) is compensated by its higher SLA (Aerts, unpublished work). On the other hand, the lower biomass allocation to the roots of *Erica* and *Calluna* as compared with *Molinia* is compensated for by their higher SRL (Boot 1989). Similarly, the compensation of a low biomass allocation to the leaves by a high SLA was found by Pegtel (1976) comparing two ecotypes of *Sonchus arvensis*.

In conclusion, the ability to compete for above- or belowground resources of the plant species under study is not merely a function of their biomass allocation pattern, but also depends on other morphological characteristics, notably specific leaf area and specific root length. Moreover, this study suggests that a low biomass allocation to the leaves can be compensated by plasticity in the spatial arrangement of leaf layers over the canopy (Fig. 6).

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