

Effects of herbivory and competition on growth and reproduction of *Triglochin maritima* in a gradient of primary succession



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SUMMARY

In this study the effects of competition and disturbance through herbivory are investigated in a gradient of primary succession. The objective was to test two theories on plant community structure (Grime's life-history theory and Tilman's mechanistic resource competition theory). These two theories yield different predictions about the role of competition and other factors (like herbivory) in determining plant community structure. Grime predicts that the importance of competition will increase when primary production increases, whereas Tilman predicts that competition will always be important, but will shift from competition for soil resources to competition for light. These predictions can be tested in a gradient of primary succession. One plant species, *Triglochin maritima*, was studied in a chronosequence of salt marsh plant communities on Schiermonnikoog, near three transects (transects 1, 2 and 3; age of successional stage increases from 1 to 3). Transplants of *Triglochin* (both mature plants and seedlings) were subjected to treatments with no neighbours, with only the roots of neighbours or both roots and shoots of neighbours. These treatments were either protected from grazing by Brent Geese, hares and rabbits with an enclosure, with only a cage around the transplant or not at all (control). As it is a precondition that a resource is limiting in order to expect competition for this resource, and because N was earlier found to be growth limiting, N fertilisation was applied in order to check limitation of this nutrient. Growth of the mature plants was measured from May 1995 through July 1995, and biomass of mature plants and seedlings was harvested in July, in order to assess the effects of competition and herbivory. Flowering of transplants was recorded three times. Growth and biomass of mature plants was increased by fertilisation at transects 1 and 2, but not at transect 3. Biomass was not affected by competition treatments, though. The plants showed phenotypic response instead, from short plants with many leaves in no-neighbours treatments to high plants with a few leaves in control treatments. Plants at transect 3 were higher than plants with equal biomass at transects 1 and 2, implying light limitation. Seedling biomass was not increased by fertilisation, yet a competition effect was found at transect 3, indicating competition for light. Seedling survival was not significantly affected by grazing or competition, but survival at transect 1 was very low. Grazing effects on mature plant biomass and growth was found at transect 2 in May (during spring staging of Brent Geese) and at transect 1, where grazed plants weighed three times less than ungrazed plants. Flowering of *Triglochin* was strongly affected by grazing, also at transect 3, and was reduced in the all-neighbours treatment at transects 2 and 3. Comparing both results of mature plants and seedlings together to the theoretical predictions yields indecisive conclusions on the importance of competition and the possible shift from competition for soil resources to competition for light. Distinguishing between the effect and response components of competition (Goldberg, 1990) in the two theories, yields more precise predictions that dictate a separate evaluation of results for mature plants and seedlings and fit closer to the results in this study. Applying this distinction to the two theories does seem to prove useful and explicitly holds the possibility that both theories are true in their own context. Extending the length of this experiment may provide more insight in the importance of competition and herbivory for the growth and reproduction of *Triglochin maritima*.

INTRODUCTION

In the last two decades, much attention in plant ecology has been paid to the role of competition in structuring plant communities (Grace & Tilman, 1990). Current debate concentrates on apparent controversies between Grime's (1979) theory on life histories and Tilman's (1985, 1988) mechanistic resource competition theory (Thompson, 1987; Tilman, 1987a,b; Thompson & Grime, 1988; Grace, 1990, 1991, 1995).

Grime's theory is based on the idea that two major factors limit plant biomass in any habitat (Grime, 1977). The first is stress, defined as the external constraints which limit the rate of dry matter production of all or part of the vegetation. The constraints comprise a wide variety of environmental factors, among which temperature and supply of water and mineral nutrients. The second factor is disturbance, defined as the mechanisms which limit the plant biomass by causing its destruction. Examples of such mechanisms are grazing, mowing or frost (Grime, 1977).

Based on these two factors, Grime proposes three life-history strategies in plants: 'Ruderal', 'Competitive' and 'Stress-tolerant' strategies. The 'Ruderal' strategy is predicted to occur in habitats with low stress and high disturbance and is associated with high growth rates and high reproductive effort. The 'Stress-tolerant' strategy is predicted to occur in habitats with high stress but low disturbance and is associated with low growth rates and low reproductive effort. Lastly, the 'Competitive' strategy is predicted to occur in habitats with low stress and low disturbance and is characterised by low reproductive effort but high growth rate. Although this theory primarily deals with life-history traits, an important part is concerned with the role of competition in processes of vegetation succession and dominance (Grace, 1991).

Tilman (1988) takes a different approach on competition by focusing on resource limitation instead of life-history characteristics. His theory is based on the assumption that the eventual outcome of competition between plant species can be predicted, using the concentration to which limiting resources can be depleted by monoculture populations of each species (R^*). Furthermore, he states that, due to the physical separation of soil nutrients and light, plants face a trade-off between these two types of resources. Plants can either allocate more to their root systems (to become better soil resource competitors) or to leaves and stem (to become better competitors for light).

Tilman (1988) developed a numerical model of cohorts of plant species with different allocation patterns to roots, leaves, stems and seeds, based on his ideas of the mechanism of resource competition. Because he considers resources of greatest importance in plant competition (Tilman, 1990), other factors (like herbivory: Grime's disturbance) that influence plant growth rate are simply represented in his model as one factor, the 'loss rate'.

A fundamental difference between these two theories is that Tilman assumes a trade-off in the allocation pattern of plants to compete for soil resources or for light, whereas Grime assumes that 'Competitors' are better able to take up all resources. Also, Tilman predicts that the intensity of competition does not differ between habitats of high or low productivity (e.g. over vegetation succession), while Grime predicts that competition is more important in habitats with high productivity (e.g. later in vegetation succession). More generally, Tilman states that resource competition is the determining factor in plant dominance, whereas Grime states that disturbance or stress can instead be decisive.

The difference in approach and definitions (especially the definition of competition) has caused a lot of confusion about the precise meaning of the predictions and assumptions of the two theories. A great deal of the debate on the apparent controversies can be attributed to this semantic confusion (Grace, 1990, 1991). The differences in the definitions of the two theories have to be clarified before their validity can be discussed.

Yet, clarifying the confusion alone will not clarify the validity of either theory in nature. To be able to evaluate the assumptions and predictions of both theories, experimental data are needed on the mechanisms of interspecific competition in plants. Although some studies have been performed (Aarssen & Epp, 1990; Tilman & Wedin, 1991a,b; Wilson & Tilman, 1991; Campbell & Grime, 1992; Goldberg & Barton, 1992; Wedin & Tilman, 1993; Wilson, 1993; Wilson & Tilman, 1993; Chapin *et al.*, 1994), more data on resource competition in different habitats is required.

The salt marsh vegetation on the Dutch island of Schiermonnikoog may provide a good environment for experimental studies on resource competition in a gradient of primary succession (Bakker, 1989a,b; Olff *et al.*, 1992). As the island gradually extends eastwards, salt marsh development repeatedly started again on newly formed land. This has resulted in a progressive developmental range from 200 years of age (the most western part of the salt marsh) to 2 years of

age (the most recently developed part in the east), providing a successional chronosequence of the salt marsh vegetation.

Comparison of vegetation development inside and outside exclosures has shown, that herbivory can have a major impact on community structure (Bakker, 1985, 1989b, Olf *et al.*, 1992). Apart from cattle grazing on the older parts of the salt marsh, the vegetation is being grazed throughout the year by hares and rabbits. Intense grazing occurs each spring, due to spring staging by Brent Geese (*Branta bernicla bernicla*). The geese arrive in April and stay in the area until the end of May, when they leave to breed in Siberia (Teunissen *et al.*, 1985; Prop & Loonen, 1989; Prop & Deerenberg, 1991; Bergmann *et al.*, 1994). Barnacle Geese (*Branta leucopsis*) also stage on the salt marsh in spring, but they arrive earlier than the Brent Geese and leave at the end of April.

Qualitatively, one of the best food plants for the Brent Geese is *Triglochin maritima*, a rush-like cryptophyte (Prop & Deerenberg, 1991). This plant (hereafter referred to as *Triglochin*) has a distribution over the chronosequence, that more or less coincides with the intensity of Brent Geese grazing (Fig. 1a & b) and reaches its highest abundance in approximately 25 year old vegetation. Here, *Triglochin* is locally one of the dominant species. Yet, light availability in the vegetation decreases from young to older vegetation (Fig. 1c), whereas nitrogen (N) pool size in the soil increases, due to clay accumulation (Olf *et al.*, 1992). Earlier investigations have shown that N is the major limiting nutrient in these plant communities (van Wijnen, unpublished results).

Considering the distribution of *Triglochin*, its main herbivore and resources, this plant seems to provide a good case to evaluate the theories of Grime and Tilman. All plant species on the salt marsh can be considered 'Stress-tolerant', because they have to be adapted to high salinity. According to Grime, competition for resources should then be of less importance, whereas Tilman states that resource competition should still determine species dominance. If the latter statement is true, then the distribution of *Triglochin* may be explained by a shift from competition for soil N to competition for light. The resource conditions would then be optimal for *Triglochin* in the 25 year old vegetation, whereas it may be competitively displaced in younger stages due to N limitation and in older stages due to light limitation. On the other hand, Grime's theory might explain the higher abundance of *Triglochin* due to *Triglochin* being best at tolerating the disturbance, imposed by grazing. Grazing pressure is highest in the 25 year old vegetation, therefore *Triglochin* should grow best in that area.

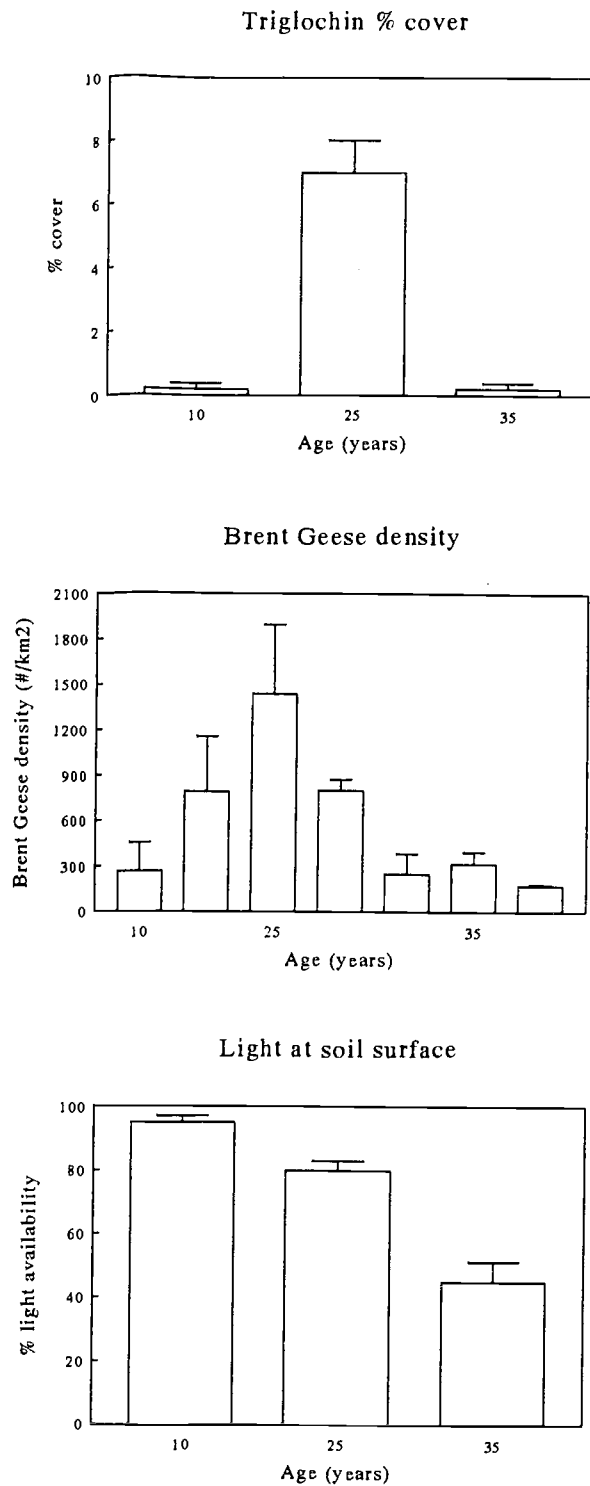


Fig. 1 a (top): *Triglochin* abundance (mean percentage cover in 5 1x1 m. plots) vs age of successional stages; b (middle): grazing pressure (mean density of Brent Geese from two field counts) vs age of successional stages; c (bottom): average light availability (expressed as the percentage of incoming light that reaches the soil surface) vs age of successional stages. Error bars indicate 1 standard error of the mean; data are measured in 1995.

In order to test in how far either of these predictions hold true, this study is intended to investigate the effect of competition for light and nutrients and the effect of disturbance through herbivory on the growth and reproduction of *Triglochin maritima*.

METHODS

Experimental sites and plant material

Transplantation experiments with competition and grazing treatments were carried out in 10, 25 and 35 years old vegetation, near transects that have been used for several years to investigate the salt marsh system. Transects 1, 2 and 3 correspond to resp. 10, 25 and 35 years old vegetation. The transect areas cover the range in *Triglochin* abundance, grazing intensity and resource availability (Fig. 1). The sites were located in a zone, consisting of a mosaic of plant communities. This mosaic pattern follows the geomorphological pattern of small elevations (5-25 cm high), separated by shallow gullies, and is persistent from transect 1 through transect 3. *Triglochin* only reaches local dominance around transect 2 on the slopes of these elevations, therefore all experimental sites were positioned on such slopes. Elevation is a determinant factor for inundation frequency and duration during floods, therefore elevation in m. + N.A.P. (Dutch Ordnance Level) was measured within the zones around each transect. Table 1 shows mean elevation and inundation duration for each transect, these are in the same order of magnitude.

Table 1 Mean elevation and inundation duration for the experimental sites.

	transect 1	transect 2	transect 3
elevation (m + N.A.P.)	1.28 (sd=0.016)	1.31 (sd=0.029)	1.24 (sd=0.016)
inundation duration (h/year)	265	236	310

Both mature plants and seedlings were used in the experiments. Seeds of *Triglochin*, collected in 1994 in the area near transect 2, were germinated in climatic chambers and grown for two weeks in a mixture of half peat and half sand before transplanting into the field. The first transplantation was carried out from 25 to 27 April 1995, but all seedlings died, due to a week of warm and dry weather following transplantation. All seedlings were replaced between 24 and 26 May 1995. In order to increase survival and obtain a better average measure of growth, seedlings were planted in triplets. Mature plants were sampled with a root corer from one place at transect 2 between 3 and 12 April 1995 and transplanted directly into all three experimental sites. In order to obtain clean

Triglochin tussocks, other plant species were removed by hand before transplanting.

Competition treatments and fertilisation

Three competition treatments were applied to measure the above- and below-ground effect of neighbours on the transplanted seedlings and mature plants of *Triglochin*, according to the setup of Wilson & Tilman (1991). Transplants were grown in subplots with no neighbours, or in subplots with the roots but not the shoots of neighbours, or in control subplots with all above- and belowground parts of neighbours present. One tussock of mature *Triglochin* was grown in the centre of each subplot, and likewise one triplet of seedlings.

The no-neighbours (NN) treatment was accomplished by removing all plants in a 50x50 cm. square (25x25 cm. for seedlings) with a hand mower. Roots were not removed, because that would disturb the soil. Instead, regrowth was regularly mown again (every 2 to 4 weeks). To prevent the soil from desiccation, green plastic agricultural mats were pinned to the ground with four steel pins. The bare soil beneath the mats was observed to remain moist throughout the experiment. A hole was made in the centre (7 cm. diameter for mature plants, 2 cm. for seedlings) to allow transplanting. The plots were established between 3 and 12 April 1995.

To grow transplants with only neighbour roots (RN treatment), nets of black cloth (50x50 cm. for mature plants, 25x25 cm. for seedlings; mesh: 2 mm.) tied back the shoots of the neighbouring plants to prevent shading of the transplants in the centre of the nets. The nets were fastened at the soil surface with 3 steel pins (20 cm. long) and the outer corners of the nets were held approximately 10 to 20 cm. above the ground with pins of 40, resp. 60 cm. long. This tie-back method may induce increased self-shading in the neighbours, which might result in increased availability of soil resources (Aarssen & Epp, 1990). If this effect occurs, one runs the risk of measuring 'apparent' instead of 'real' competition (Connell, 1990). Transplants may grow faster in such treatments, not because of the experimentally increased light availability, but due to the increased N availability provided by the self-shaded neighbours. However, in several comparable studies no such effect of tying back was found (Aarssen & Epp, 1990; Wilson & Tilman, 1991; Wilson, 1993). Because the stand in this experiment was not dense and increased self-shading was not evident in the field, the tie-back method was assumed to have no effect on soil resource availability. The nets

were established between 10 and 15 May 1995 (between 24 and 26 May 1995 for seedlings).

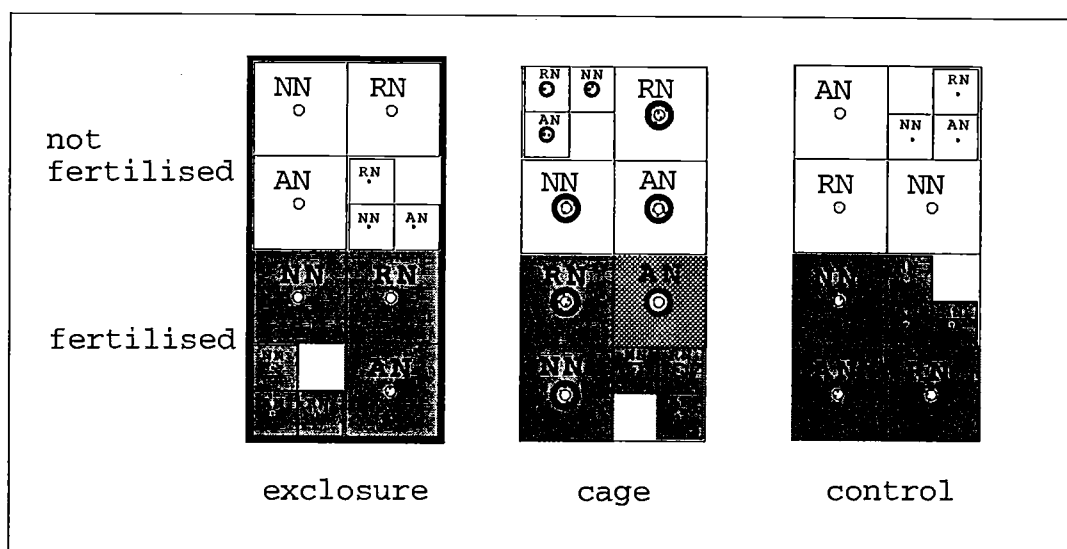
The all-neighbour (AN) treatment consisted of a transplant grown in the centre of a 50x50 cm. (25x25 cm. for seedlings) subplot of undisturbed vegetation. Transplantation was carried out between 3 and 12 April 1995.

In order to test for soil nitrogen limitation, all competition treatments were duplicated in subplots, fertilised with 20 g N per m² (applied as commercial NH₄NO₃ in two equal portions on 3-4 May 1995 and 6-7 June 1995).

The fertilised and non-fertilised competition treatment subplots were randomly grouped in a 1x2 m. plot.

Grazing treatments

Three grazing treatments were applied: grazing of all plants in the subplot excluded, grazing of *Triglochin* but not of the neighbours excluded, and grazing not excluded (control). The grazing treatments were applied over the competition plots. Thus there were three grazing treatment plots, each containing 6 competition subplots for both mature plants and for seedlings:



The no-grazing treatment (exclosure) was established by fencing a 1x2 m. plot with wire-netting (mesh: 2.5 cm.). Geese are excluded from such plots, since they walk while foraging. Fences were installed between 3 and 12 April 1995.

Grazing of *Triglochin* but not of the neighbours was excluded by wrapping the tussocks of mature plants in wire-netting (height: 25 cm.; mesh: 1.5 cm.), thus providing a cage. Seedlings were protected with a similar cage (height: 5 cm.; mesh 1 cm.). The cages were installed during transplantation.

The control plots were unchanged competition plots, as described above. The treatment plots were replicated 10 times at all three transects to allow for statistical analysis. Thus, all three experimental sites consisted of 30 plots (3 grazing treatments x 10 replicates), each containing 6 subplots for mature plants (3 competition treatments x 2 fertilisation treatments) and 6 identical subplots for seedlings. In total, 540 tussocks of mature plants and 540 triplets of seedlings were transplanted.

Measurements

Three, randomly chosen, mature plants per tussock were marked with a small plastic ring at the base of the shoot. The height (as the length of the longest leaf) of these marked plants was measured roughly every two weeks (but only once in June). In this way, the growth rate during the experiment could be calculated as the average increase in height. Tussocks with one or more marked plants missing or dead were excluded from the calculation. New plants were then marked and measured to allow for calculation of the growth rate over the next period. Between 10 and 12 July the marked plants from 5-6 randomly selected plots were harvested (all vegetative aboveground material), dried at 70 °C to constant mass and weighed. Height and number of leaves of these plants were recorded. Furthermore, the number of tussocks with flowers was counted on three occasions (30-31 May, 25-26 June and 10-12 July 1995).

Fifty triplets of seedlings were not transplanted, but dried to constant mass and weighed to acquire an average initial seedling biomass. The surviving transplanted seedlings were harvested on 11 and 12 July, dried at 70 °C to constant mass and weighed. As far as possible, root and shoot of a number of samples were separated to assess shoot/root ratio (most seedlings were too small to separate root and shoot with acceptable accuracy).

The biomass growth rate of each seedling transplant was calculated, following Wilson & Tilman (1991), as:

$$r = [\ln(M2/M1)]/d$$

where M1 is initial biomass, M2 is final biomass and d is the length of the growing period in days. The intensity of competition (again following Wilson & Tilman, 1991) could then be calculated:

$$CI = (r_{NN} - r_{AN})/r_{NN}$$

where CI is competition intensity, r_{NN} is growth rate with no neighbours present and r_{AN} is growth rate with all neighbours present.

Statistical analysis

Data on the growth rate of mature plants during the experiment, the final above-ground biomass, height and number of leaves and the seedling biomass were analysed with MANOVA for effects of fertilisation, grazing, competition and any interaction between these factors. For that purpose, data of seedling biomass and aboveground biomass of mature plants were $^{10}\log(x + 1)$ transformed to reduce heteroscedasticity (Zar, 1984). The correlation of final aboveground biomass with plant height and number of leaves was examined, using Pearson's product-moment correlation coefficient. Overall differences between the three experimental sites for final seedling biomass and mature plant growth were analysed with ANOVA, for final aboveground mature plant biomass with the Kruskal-Wallis test. The data on flowering were analysed with G-tests. The data on the intensity of competition were compared between the experimental sites, using Student's t-test. Differences in survival of seedlings over the treatments were tested with log-linear models.

RESULTS

Grazing and growth during the experiment

The first flocks of Brent Geese arrived in the second week of April. By 26 May almost all geese had left the island. Due to the necessity to replace the seedlings (which required germination of new seeds), these were not subjected to potential grazing by the geese. Transplantation of the new seedling triplets could not be started before the end of May, by which time the geese were already departing. A field check a few days after transplantation confirmed that all seedling triplets were still present, which confirms that the geese did not graze seedlings.

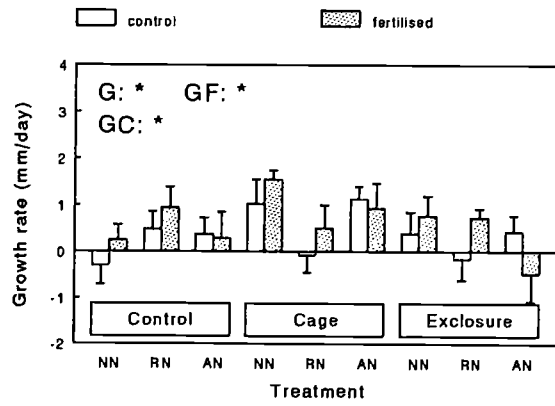
The growth of mature plants (Fig. 2a-c) showed a significant grazing effect during presence of the Brent Geese. After the geese departed, grazing still affected growth at transect 1, but not at transects 2 and 3. Apparently, intense grazing of *Triglochin* by hares and rabbits only occurs at transect 1. Plants released from grazing at transects 2 and 3 grew equally fast as non-grazed plants, showing neither over- nor undercompensation to herbivory. Fertilisation effects on the growth rate of mature plants were found only after applying the second portion of nitrogen. These fertilisation effects were significant for transects 1 and 2, but not for transect 3. Differences between neighbour treatments occurred after May and show that plants in AN treatments grow higher (Fig 2a-c).

Table 2 Significance tests of differences in growth rates between transects (Tukey test).

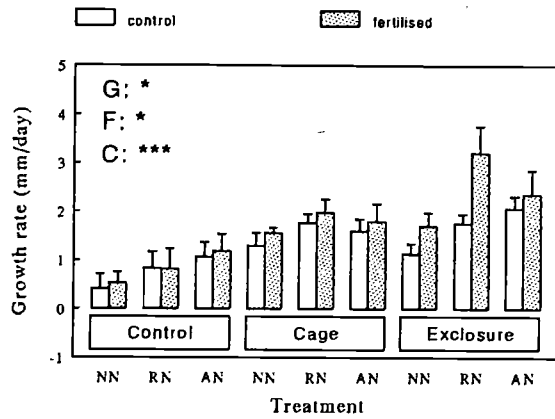
	T1 vs T2	T1 vs T3	T2 vs T3
17/5 - 30/5	p>0.5	p<0.001	p<0.001
30/5 - 25/6	p>0.8	p<0.001	p<0.001
25/6 - 11/7	p<0.05	p<0.05	p<0.001

Analysis of growth rates between transects showed significant differences for all periods (ANOVA, $p<0.001$ for all three periods). Growth rates at transect 3 were highest in May and June, but smallest in July (Table 2 and Fig. 2). Plants at transect 2 grew significantly faster than at transect 1 in July only (Table 2 and Fig. 2).

Transect 1, 17/5 - 30/5



Transect 1, 30/5 - 25/6



Transect 1, 25/6 - 11/7

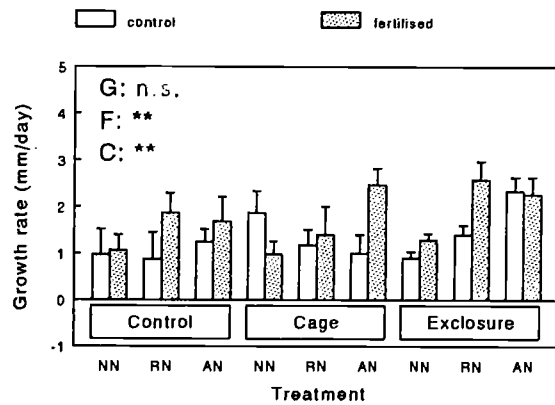
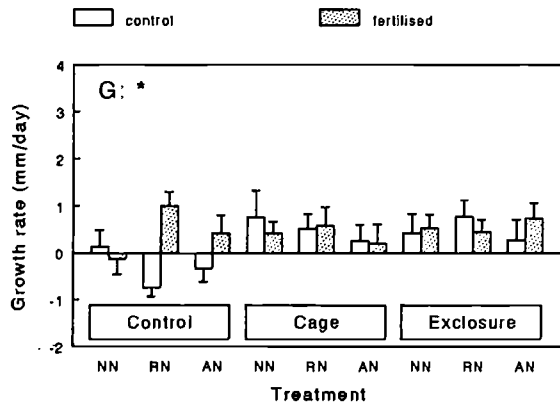
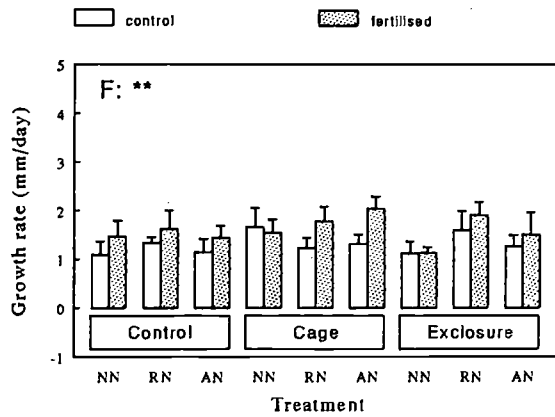


Fig. 2a Mean growth rate of mature plants per treatment at transect 1 between 17 and 30 May (top), 30 May and 25 June (middle) and between 25 June and 11 July (below). Error bars indicate 1 standard error of the mean. Significant effects are indicated as follows: G = grazing, F = fertilisation, C = competition, combinations of characters are interaction effects. Levels of significance are indicated with * ($p < 0.05$), ** ($p < 0.01$) and *** ($p < 0.001$).

Transect 2, 17/5 - 30/5



Transect 2, 30/5 - 25/6



Transect 2, 25/6 - 11/7

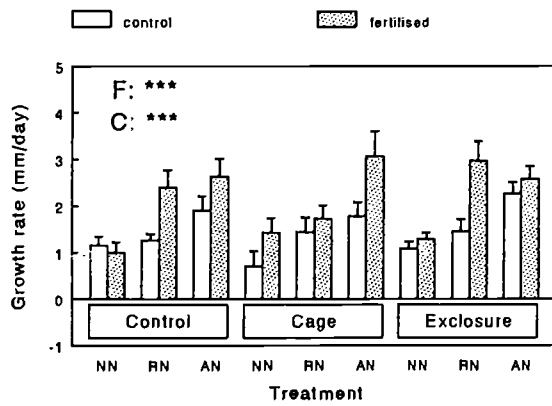
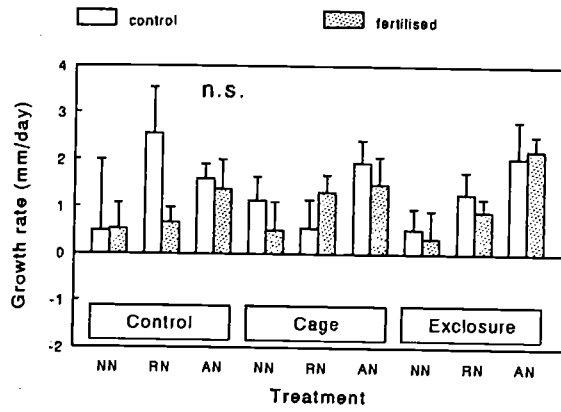
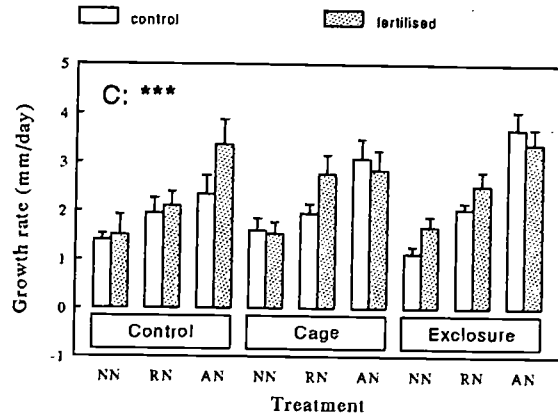


Fig. 2b Mean growth rate of mature plants per treatment at transect 2 between 17 and 30 May (top), 30 May and 25 June (middle) and between 25 June and 11 July (below). Error bars indicate 1 standard error of the mean. Significant effects are indicated as follows: G = grazing, F = fertilisation, C = competition, combinations of characters are interaction effects. Levels of significance are indicated with * ($p < 0.05$), ** ($p < 0.01$) and *** ($p < 0.001$).

Transect 3, 17/5 - 30/5



Transect 3, 30/5 - 25/6



Transect 3, 25/6 - 11/7

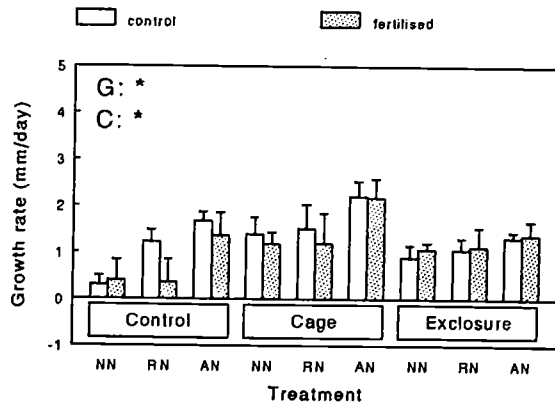


Fig. 2c Mean growth rate of mature plants per treatment at transect 3 between 17 and 30 May (top), 30 May and 25 June (middle) and between 25 June and 11 July (below). Error bars indicate 1 standard error of the mean. Significant effects are indicated as follows: G = grazing, F = fertilisation, C = competition, combinations of characters are interaction effects. Levels of significance are indicated with * ($p < 0.05$), ** ($p < 0.01$) and *** ($p < 0.001$).

Seedlings

The survival of seedlings (Fig. 3a) was strongly reduced at transect 1 compared to transects 2 and 3 (G-test, $G=118.2$, $df=2$, $p<<0.001$). For the latter two transects no significant differences in survival was found. The low number of surviving seedlings at transect 1 does not allow for statistical analysis of survival or biomass, nor for calculation of the intensity of competition. The few surviving seedlings at transect 1 were mostly found in grazed plots, which suggests that grazing here is not the determining factor for survival. However, 8 out of 9 seedlings were found in NN treatments, which may indicate that competition is important for seedling survival at this site.

Analysis of the survival at transects 2 and 3 revealed no significant treatment effects, although seedlings in RN treatments seemed to have a higher frequency of survival (Fig. 3b). Survival seemed reduced in grazed plots (compared to cages and exclosures) (Fig. 3a). This decrease cannot be assigned to direct geese grazing (they had already left the area) or to indirect grazing effects on the neighbouring vegetation, because seedlings in cages (whose neighbouring vegetation is grazed) survived better. Possibly, grazing by hares and rabbits had this (statistically insignificant) effect on survival.

Average total seedling biomass decreased from 1.2 mg at transect 1 to 0.8 mg at transect 3 (ANOVA, $F=20.895$, $p<0.001$). Comparison of seedling biomass (Fig. 4) over the treatments for transect 2 showed that grazing significantly reduced biomass. Addition of nitrogen did not yield a significant increase of seedling biomass (contrarily, fertilised seedlings at transect 3 had a significantly lower biomass!). Furthermore, both at transects 2 and 3, seedlings grown in AN treatments had less biomass than those in RN or NN treatments, but only significantly so at transect 3. Thus, the seedlings at transect 3 appear to be subjected to light competition, and for the seedlings at transect 2 the same conclusion possibly may apply.

Analysis of the intensity of competition and shoot/root ratios is summarised in Table 3. Differences in the intensity of competition and shoot/root ratios were not significant between transects 2 and 3.

Table 3 Mean intensity of competition and shoot/root ratio of transect 2 (T2) and transect 3 (T3). There is no significant difference in intensity of competition (t-test, $t=-1.19$, $df=27$, $p>0.05$). Likewise, the shoot/root ratios are similar (ANOVA, $F=0.735$, $p=0.396$)

intensity of competition			shoot/root ratio		
	mean	se		mean	se
T2	0.085	0.07	T2	1.16	0.09
T3	0.214	0.08	T3	1.29	0.11

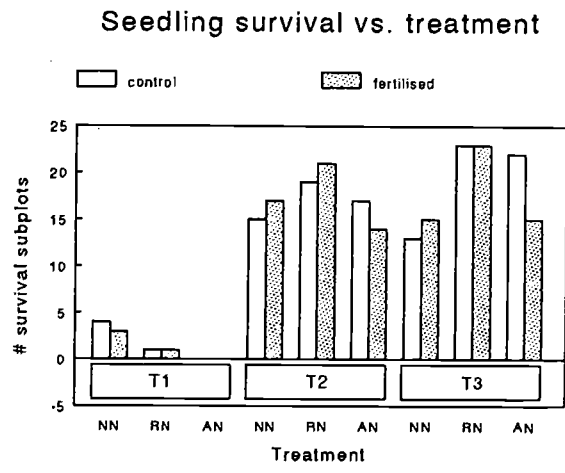
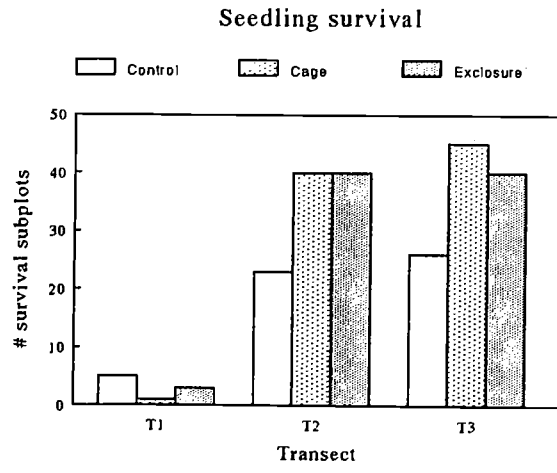


Fig. 3 a (top): number of subplots with surviving seedlings per grazing treatment for all three transects; b (bottom): number of subplots with surviving seedlings per competition treatment

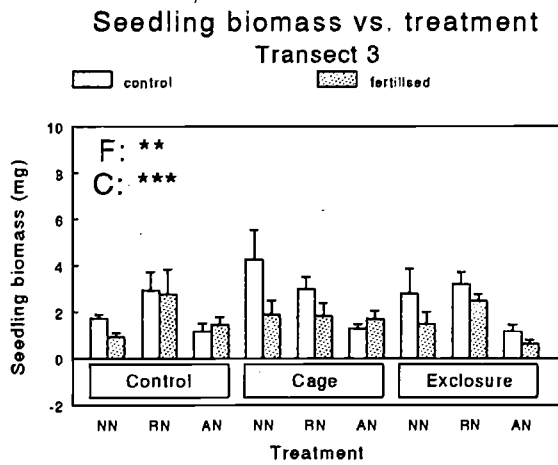
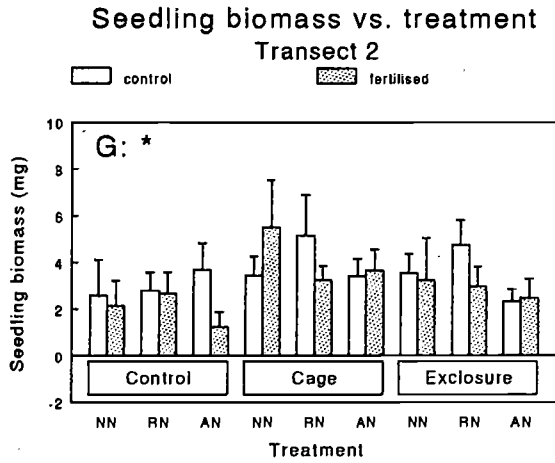
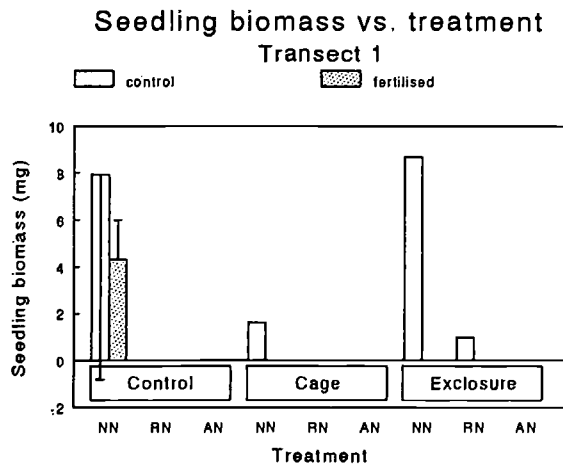


Fig. 4 Mean biomass of seedlings per treatment for each of the three transects. Error bars indicate 1 standard error of the mean. Significant effects are indicated as follows: G = grazing, F = fertilisation, C = competition, combinations of characters are interaction effects. Levels of significance are indicated with * ($p < 0.05$), ** ($p < 0.01$) and *** ($p < 0.001$).

Mature plants

Analysis of the final plant height and number of leaves (Figs. 5 & 6) revealed a contrasting pattern. Both parameters showed a clear competition effect, but where the plant height increases from NN to AN treatments, the number of leaves decreases. The final aboveground biomass (Fig. 7) was highly correlated with both plant height and number of leaves (Table 4). Therefore, the two contrasting patterns of plant height and number of leaves were neutralised in the aboveground biomass, yielding no effect of competition treatments. So although aboveground biomass did not change from NN to AN treatments, plant morphology did change from low plants with many leaves to high plants with few leaves.

Table 4 Correlation coefficients (Pearson's R) for the correlation of aboveground biomass with plant height and number of leaves. All correlation coefficients are significant at the $p < 0.001$ level.

	Height	Number of leaves
Transect 1	0.77	0.69
Transect 2	0.70	0.45
Transect 3	0.58	0.57

Furthermore, the rate of biomass increase per leaf over the increase in height (i.e. the slope of the regression lines in Fig. 8) is lower for transect 3 plants (ANOVA, $F=21.2$, $df=2$, $p < 0.001$; t-test, for T1 vs T2: $t=0.551$, $df=179$, $p > 0.5$; for T1 vs T3: $t=3.449$, $df=197$, $p < 0.001$; for T2 vs T3: $t=2.086$, $df=168$, $p < 0.05$). This indicates that *Triglochin* plants at this transect grow higher with the same amount of structural tissue, which may be expected if growth is light limited.

Aboveground biomass significantly increased with fertilisation for transect 2, and for transect 1 as well if only cage plots and enclosure plots are considered. Leaving out the grazed plots may be appropriate, as *Triglochin* plants in this area were still intensely grazed, regardless of fertilisation treatment. Therefore, nitrogen appears to be limiting at transects 1 and 2, but not at transect 3.

Final aboveground biomass differed significantly between transects (Kruskal-Wallis, $KW=9.811$, $p < 0.01$). *Triglochin* plants at transect 2 had grown significantly less biomass than those at transects 1 and 3 (Mann-Whitney, T1 vs T2: $U=5033.5$, $p < 0.01$; T1 vs T3: $U=5227$, $p > 0.6$; T2 vs T3: $U=2738$, $p < 0.01$).

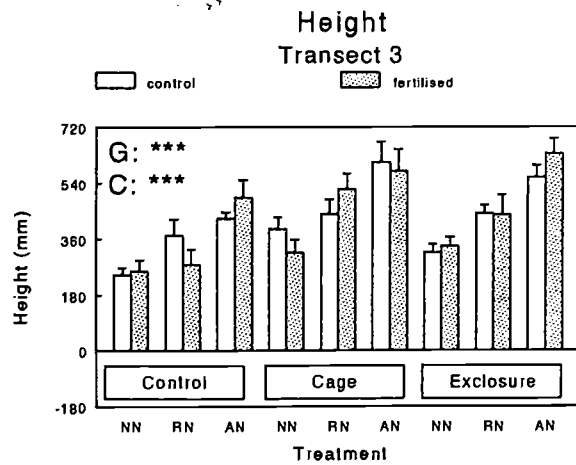
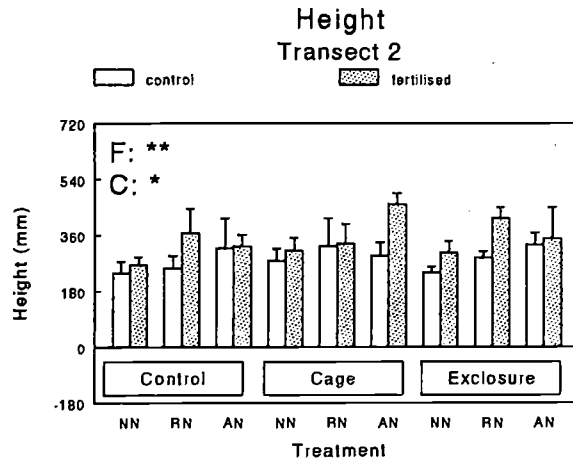
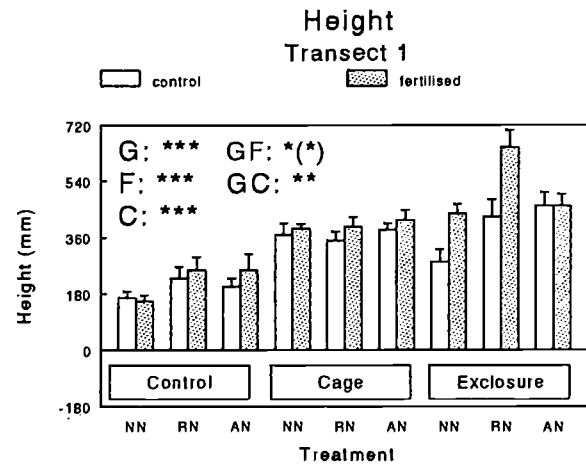


Fig. 5 Mean final plant height (three marked plants added together) per treatment for each of the three transects. Error bars indicate 1 standard error of the mean. Significant effects are indicated as follows: G = grazing, F = fertilisation, C = competition, combinations of characters are interaction effects. Levels of significance: * ($p < 0.05$), ** ($p < 0.01$) and *** ($p < 0.001$).

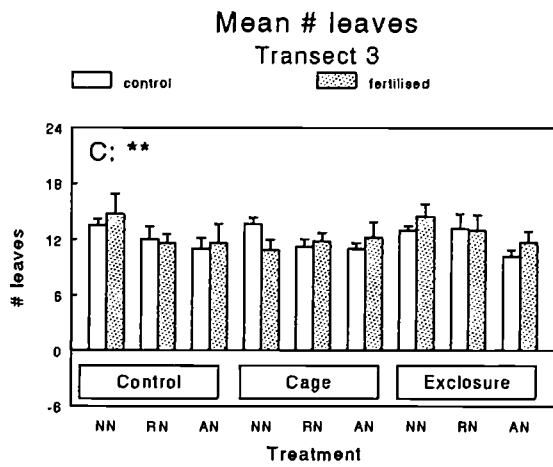
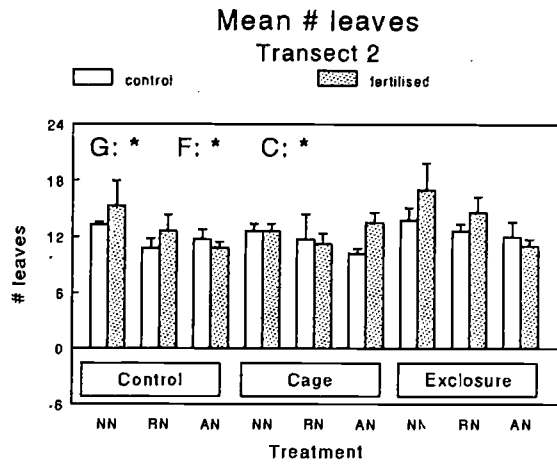
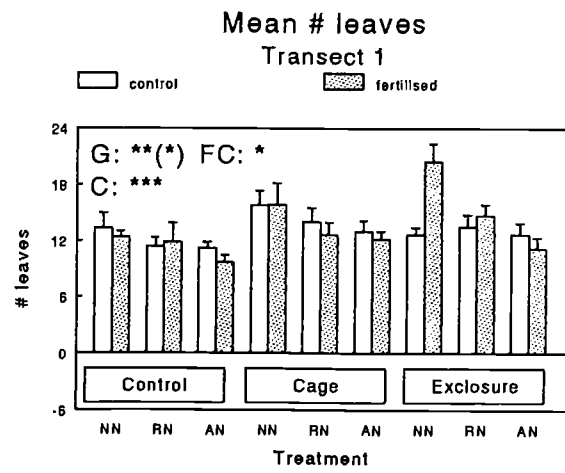


Fig. 6 Mean final number of leaves (three marked plants added together) per treatment for each of the three transects. Error bars indicate 1 standard error of the mean. Significant effects are indicated as follows: G = grazing, F = fertilisation, C = competition, combinations of characters are interaction effects. Levels of significance are indicated with * ($p < 0.05$), ** ($p < 0.01$) and *** ($p < 0.001$).

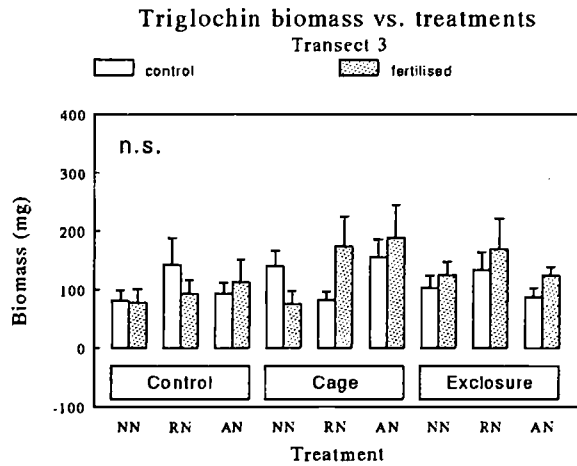
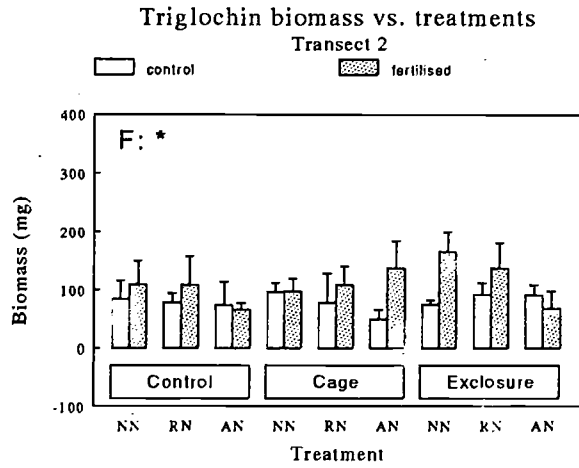
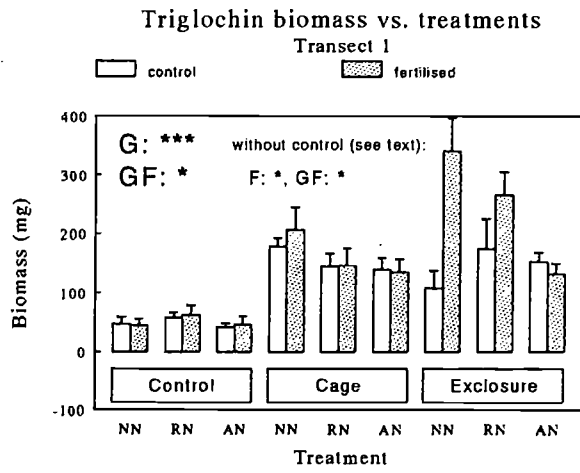
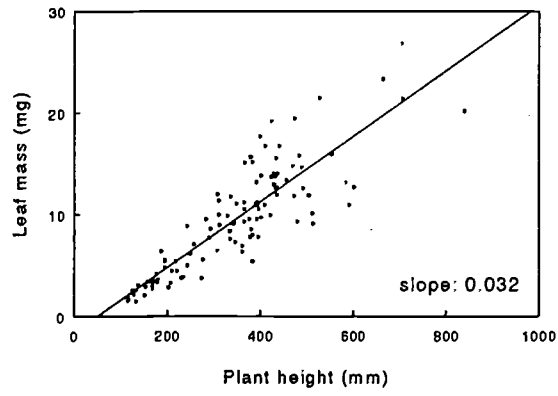
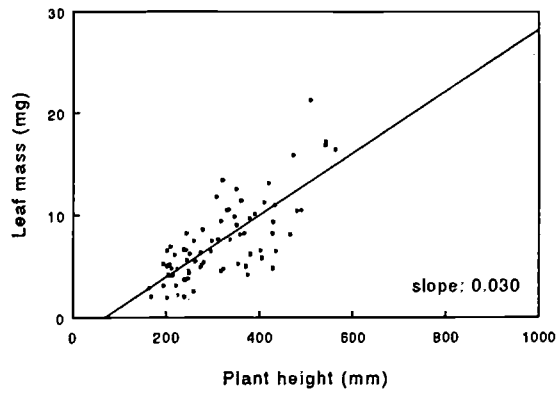


Fig. 7 Mean final biomass (three marked plants added together) per treatment for each of the three transects. Error bars indicate 1 standard error of the mean. Significant effects are indicated as follows: G = grazing, F = fertilisation, C = competition, combinations of characters are interaction effects. Levels of significance: * ($p < 0.05$), ** ($p < 0.01$) and *** ($p < 0.001$).

Triglochin leaf mass vs height
Transect 1



Triglochin leaf mass vs height
Transect 2



Triglochin leaf mass vs height
Transect 3

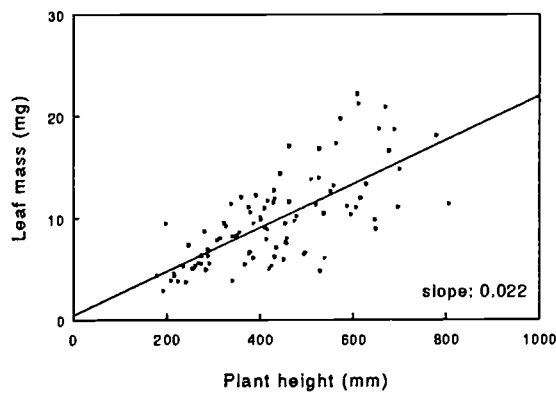


Fig. 8 The relation between biomass per leaf and height of Triglochin for each of the three transects. Biomass increase with height is significantly less at transect 3.

Flowering

The number of flowering tussocks was recorded three times. The total number of flowering tussocks was highest at transect 1 and lowest at transect 3 (G-test, $G=8.94$, $df=2$, $p<0.025$). Grazing had a considerable impact on flowering frequency of tussocks (Fig. 9) at all transects. This effect decreased from transect 1 to transect 3, though. Direct grazing of flowers has been observed in the field, but the influence of grazing on flowering can also have arisen indirectly. Whether directly or indirectly, the reproductive success of *Triglochin* was considerably reduced by herbivory.

In order to assess the effect of competition treatments on flowering without grazing interaction, only the data of cage and exclosure plots were used. No significant effect of competition was found for transect 1, but the data of transects 2 and 3 showed reduced flowering for the AN treatment in June and July (Fig. 10). Apparently, an increase in light availability allows more plants to produce flowers.

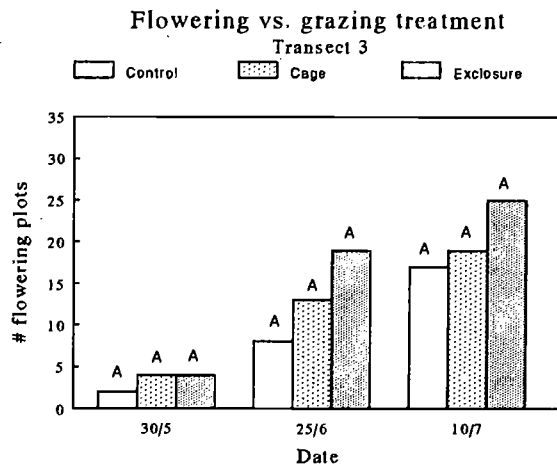
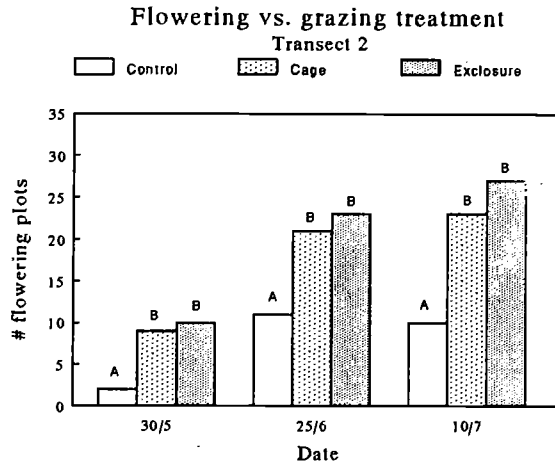
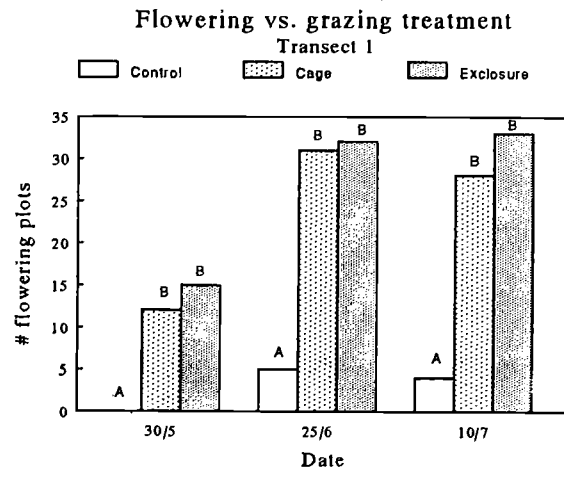


Fig. 9 The number of flowering tussocks per grazing treatment at the three recording dates, for each of the three transects. Measurements with different capitals differ significantly.

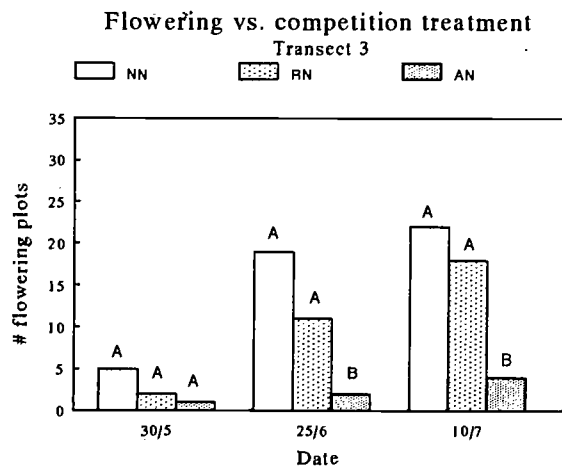
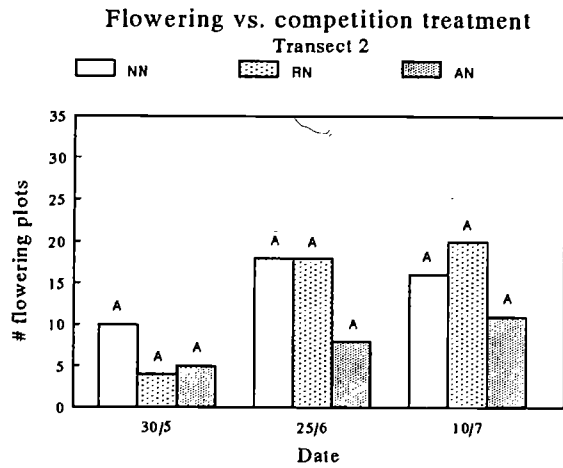
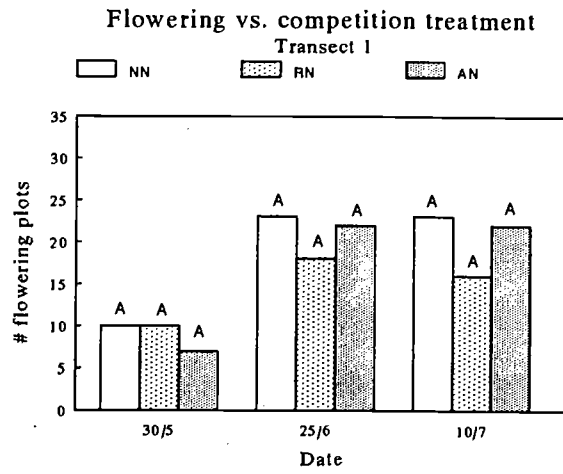


Fig. 10 The number of flowering tussocks (cages and exclosures only) per competition treatment at the three recording dates, for each of the three transects. Measurements with different capitals differ significantly.

DISCUSSION

The case study: Triglochin maritima

Over all transects, *Triglochin* growth and reproduction was highest in the non-grazed plots of transect 1. Therefore, it seems that of the three sites in consideration transect 1 provides the best conditions for *Triglochin* dominance. However, colonisation of this area will be difficult, since seedling mortality was very high. Furthermore, growth and reproduction of mature *Triglochin* was severely suppressed in the grazed plots at transect 1, even after the period of spring staging of the Brent Geese, causing a threefold reduction in aboveground biomass and severely reduced flowering. In contrast, competition treatments imposed no significant effects on *Triglochin* growth and reproduction. It may be that longer-term experiments are required to assess competition effects. Yet, it appears more likely that grazing on the short term will be decisive for the establishment of *Triglochin* as a dominant plant species in this area. This is consistent with Grime's assertion that disturbance or stress factors, instead of competition, may determine plant growth. Summarising, it is concluded that herbivory, and not resource competition, is the important factor in determining the abundance of *Triglochin* at transect 1. Repeating the experiment in subsequent years may determine the consistency of this observation.

In general, the effect of grazing decreased from transect 1 to transect 3. At transects 2 and 3 *Triglochin* hardly suffered grazing after the geese departed. This pattern of grazing differs from the overall grazing pressure (Fig. 1 and van de Koppel *et al.*, 1995). Apparently, *Triglochin* is highly preferable to herbivores in the species composition of the vegetation at transect 1 after geese departure, while at transect 2 other attractive food plants may be available.

Indications for a shift from nutrient competition to light competition between transect 2 and 3 were indecisive. Nitrogen limitation of mature plant growth was found at transect 2 and not at transect 3. Furthermore, mature plants grew higher at transect 3, implying light limitation. Yet, flowering was light limited at both transects. Also, seedling growth was light limited at transect 3 and may have been so at transect 2. However, the competition treatments do not show clear effects of either light or nutrient limitation for mature plants. Therefore, the hypothesis that low abundance of *Triglochin* is maintained at transect 3 by light competition can neither be accepted nor rejected yet. Again, extending the length of the experiment may provide more insight.

In a recent greenhouse experiment, in which a number of salt marsh plant species were grown under different light conditions, it appeared that *Triglochin* was one of the plant species least affected by a decrease in light availability (van der Wal, unpublished data). However, the plants did not experience salt stress in this experiment. The results of this experiment can therefore not readily be applied to salt marsh plant communities.

Phenotypic plasticity

A remarkable feature was the phenotypic plasticity, shown by the mature plants over the different competition treatments (Fig. 5 & 6). Plants in NN treatments remained relatively low, but had a high number of leaves, whereas plants grown in AN treatments were higher, but had a lower number of leaves. On the advantages of these morphological changes can only be speculated. For instance, it may be that the plants adapt their morphology to make better use of the resource availabilities, including those not incorporated in this study, like water (see e.g. Bloom *et al.*, 1985).

How can phenotypic plasticity be interpreted in view of the theories of Grime and Tilman? In perspective of Grime's theory, *Triglochin* employs the 'stress-tolerant' strategy (low growth rate and low reproductive output). It may be assumed that increased growth in response to increased resource availability imposes high costs to the plants, due to salt stress (increasing biomass may result in increasing transpiration). Instead of increasing growth, the plants in the NN treatment can change morphologically, thereby increasing resource uptake.

Tilman (1988) elaborated on the implications of incorporating phenotypic plasticity strategies in his resource competition model. He argues that phenotypic plasticity will not affect the outcome of competition to a great extent, as the potential range of plasticity is small compared to the range of all possible morphologies and physiologies. Furthermore, the natural limitation on plasticity would still constrain a plant to being a superior competitor in a narrow range of habitat types. Tilman's model explicitly applies to plant interactions under equilibrium conditions. Therefore, the experiment should run for a number of years, during which it should become apparent which strategies within the range of phenotypic plasticity fit the resource conditions best.

The controversy: Grime vs Tilman

Recently, Grace (1990, 1991) provided clarification on the contrasting predictions of the theories of Grime and Tilman. He has argued that a lot of the controversy is only due to semantic confusion on the definition of competition. In the eyes of Grime, a good competitor is a plant that has a high ability to capture available resources, thereby depleting the resources for neighbouring plants. In contrast, Tilman defines competition in terms of depleting resources to low levels and the ability to tolerate these low levels (reflected in his parameter R^*). Therefore, predictions of the two theories on competition cannot be contrasted, but have to be evaluated separately.

Goldberg (1990) stresses the importance to distinguish between the effect and response components of competition. These two components correspond to two ways of being a good competitor: by rapidly depleting the available resources (i.e. competition *sensu* Grime) or by maintaining growth at low resource levels (i.e. competition *sensu* Tilman). She further points to the usefulness of this distinction for interpreting competition experiments. If the target species and the neighbouring plants in a competition experiment are of comparable stature, each can potentially deplete the other's resources. Such an experimental design can be used to test predictions of Grime's theory. In contrast, if the target species is small, compared to the neighbour plants, it is unlikely to cause a significant depletion of resources. Instead, it will be 'condemned' to tolerating the levels of resources, imposed by the neighbours. Such response-to-resource experiments can be used to test predictions of Tilman's model.

In this experiment both seedlings and mature plants were used. Therefore, the distinction of effect and response components of competition can be applied to the results of the experiment. Tilman's mechanistic ideas of resource competition should then be compared with seedling performance and Grime's ideas on the importance of competition with mature plant performance. This distinction between seedlings and mature plants seems to make the possible indications for a shift from nutrient competition to light competition less indecisive. Seedlings did not show a clear light limited growth at transect 2, but did so at transect 3. Mature plant biomass did not show a shift to light competition, but did not show an increase in competition intensity either. The distinction between effect on and response to resources does seem to prove useful for a more precise evaluation of the predictions of the two theories..

As a last point, I wish to stress that, apart from testing predictions, testing of the specific assumptions of the two theories is required (equilibrium vs non-equilibrium conditions, trade-off in the ability to compete for different resources or not). Predictions may be the logical outcome of the underlying model. If resource competition was tested for a number of species in a system with light limitation, it may be unavoidable that the species that grow highest turn out to become dominant. What we need to know is how often the assumptions of either theory are met in nature.

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