

Competition and coexistence between seven grassland plant species

The effect of spatial soil nutrient heterogeneity

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1. Introduction

1.1. General background

For many years plant ecologists have been working on understanding the mechanisms of competition. One of the main questions is how plant species can coexist in a certain area without one species outcompeting all the others, a process that is called competitive exclusion. Several theories have been formed of which the ones of J.P. Grime (1974, 1977, 1987, 1997) and D. Tilman (1987, 1989, 1990, 1994) are the most well known (see Box A). These two theories seem to be incompatible, although J.B. Grace (1991) pointed out that part of the problem is a difference in the definitions that are used to form the basis of the theories. Grime concentrates on the ability of a plant for resource capture, hereby suppressing the fitness of its neighbours. Tilman emphasises the ability of plants to be able to lower the resource level and survive this low level (low resource requirement), competitive success is measured by the ability to dominate in a habitat.

The definition of competition that will be used in this study is the one of Grime (1977): competition is “the tendency of neighbouring plants to utilise the same quantum of light, ion of a mineral, molecule of water, or volume of space”. This definition has several advantages. It is specific about the resources for which plants compete, and other processes e.g. allelopathy are excluded (Welden & Slauson, 1986).

This study focuses on belowground resource foraging. Soil resources can reach the root surface through three general processes. The first, least important as regards the quantity of nutrients taken up by this means, is root interception, the second is mass flow of water and nutrients which is dependent on e.g. evapo-transpiration, and the last process is diffusion of resources. The uptake of nutrients gives rise to a depletion zone (a concentration gradient surrounding roots). The size of the depletion zone varies with the rate of diffusion, which in turn depends on several factors: the mobility of ions, soil water content, overall nutrient concentration, and the roots ability to depress nutrient concentration at its surface. The degree to which plants will interact negatively through the depletion of a shared resource pool will be determined by variation in the rate of transport between resource pool and plants, and by variation in the size of the zone of resource uptake (Casper & Jackson, 1997). There is disagreement over what resources plants compete for and how this affects plant communities. This problem is formed by three conceptual differences. Different resources have very different dynamics, consequently the mechanisms used to capture these resources will differ, and finally the effect of these differences on coexistence remains yet unclear (Huston & DeAngelis, 1994).

Numerous studies have suggested another explanation for species and vegetation dynamics, which is the heterogeneous distribution of resources in both space and time. The nature and also the outcome of competition will be affected by this heterogeneity of resources, it may even be more important than average resource level (Huston & DeAngelis, 1994, Casper & Jackson, 1997, Tilman, 1994). What is pointed out here is that competition is not uniform, but varies with local depletion of nutrients and water in immediate vicinity of individual roots and light under individual leaves

(Campbell, Grime and Mackey, 1991). It is not yet clear to what extent heterogeneity of soil resources determines species composition or is determined by species growing in a habitat (what is cause, what is consequence?; Ozinga, Van Andel, McDonnell-Alexander, 1997, Stark, 1994). There are several suggestions about processes and mechanisms that affect this interaction between (soil) heterogeneity and plant growth and competition.

Huston and DeAngelis (1994) propose a transport limited competition model. Here small-scale heterogeneity is induced in an initially homogeneous neighbourhood as a result of the interaction among resource uptake by the organisms, resource supply from the environment, and the transport rate of the limiting resource through the medium. Others suggest that a larger root system might have a disproportionate advantage in a patchy soil environment because it should be more likely to encounter a high nutrient patch. The relation between root system size and resource uptake could also depend on the mobility of the limiting resource.

Casper and Jackson (1997) distinguish two general possibilities for the way patchiness influences competition. If co-occurring species differ simply in ability to harvest soil resources from patches, then heterogeneity may affect their relative performance, independent of competition. If heterogeneity directly alters the dynamics of root interactions, this may result in spatial aggregation of competing root systems, potentially intensifying belowground competition.

1.2 Research question

It is important to know what effect heterogeneity in nutrient supply may have on plants and their interactions to be able to draw reliable conclusions from experimental research. In this research an attempt is made to assess the importance of the distribution of nutrients in the soil for competition between plants.

The main research question is:

Is there an effect, and if so, what is the effect of heterogeneity of the distribution of nutrients in the soil on coexistence of, and competition between plants?

2. Materials and methods

2.1 Species

Seven different species have been used in this experiment. All species can occur in a mesotrophic and moist grassland. Three of them are monocots, four are dicots, they differ in degree of dominance.

Species	mono-/dicot	abbreviation	species reference
<i>Anthoxanthum odoratum</i>	M	AO	1
<i>Agrostis capillaris</i>	M	AC	3
<i>Holcus lanatus</i>	M	HL	4
<i>Plantago lanceolata</i>	D	PL	2
<i>Rumex acetosa</i>	D	RA	5
<i>Lychnis flos-cuculi</i>	D	LF	6
<i>Crepis paludosa</i>	D	CP	7

Holcus lanatus is the most dominant monocot, *Agrostis capillaris* is less dominant, but is not really a subordinate, *Anthoxanthum odoratum* is a subordinate. The dicots are less obviously divided, but a certain distinction can be made. *Rumex acetosa* and *Plantago lanceolata* are the more dominant species, *Lychnis flos-cuculi* is intermediate, and *Crepis paludosa* is a subordinate (Rodwell, 1992).

2.2 Planting pattern

The planting pattern is very important in a competition experiment, because all plants have to be each others neighbours, and they all have to be planted equidistant. This can be achieved by using seven species in a hexagonal planting pattern (see fig 1).

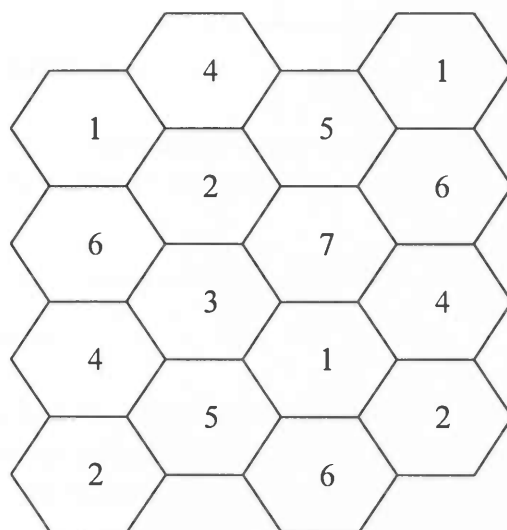


Fig 1. Planting pattern (Van Andel & Dueck, 1982). Each number is a plant, on every junction (in the clustered treatments) are nutrient patches.

Every plant from one species can interact directly with exactly one plant of every other species used. By putting nutrients in the clustered treatments on all intersections between three species every nutrient patch can (at least) be used by the three species surrounding it. Both the distances between the plants and the distances between plants and nutrient patches stay the same all through the pattern. The distance between the plants was 10 cm, the distance from a plant to a nutrient patch was approximately 5.5 cm. Every plant had access to 4 (depths) x 6 nutrient patches in the immediate vicinity. The total number of plants per box was 72, the plants on the edges were not used in the harvest (see 2.4).

2.3 Nutrients and experimental set-up

Wooden boxes of 74 x 93.5 x 39 were lined with cloth and plastic and then filled with substrate and nutrients. A mixture of vermiculite and washed sand (1:1) was used as a substrate for planting. Nutrients were added by mixing osmocote through this substrate (for the 'even' treatments) or by placing osmocote patches on four fixed depths in the substrate (for the 'clustered' treatments, see fig 2).

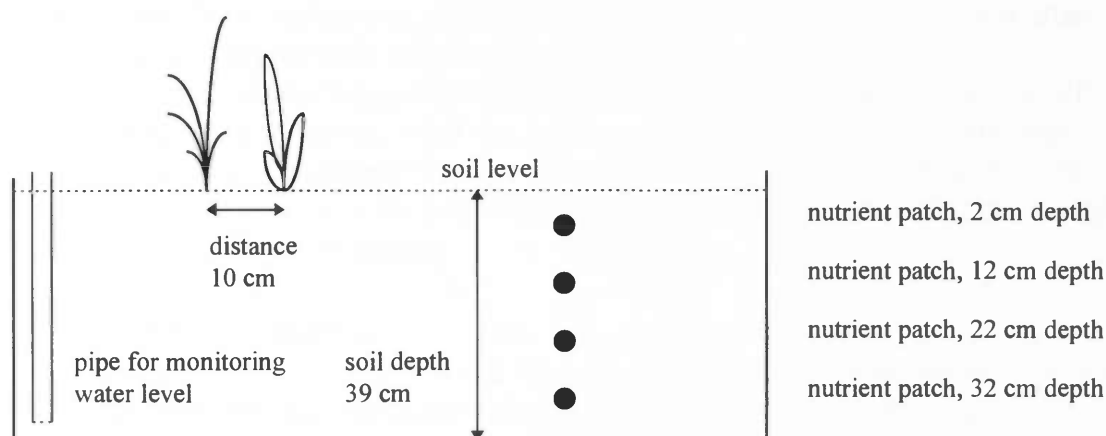


Fig 2. Experimental set-up.

Two different levels of nutrients were used, a high and a low treatment, which results in four different nutrient treatments:

Osmocote	low level (0.67 g/l)	high level (3.36 g/l)
patches / clusters	LC	HC
even distribution	LE	HE (control)

The osmocote had the following composition: N : P : K = 13 : 13 : 13, + 2 Mn + 1 Fe. A Lewis + Powers micronutrient solution (1 ml/l) was applied twice every week.

Composition: per 10 litre standard solution:

H ₃ BO ₃	26.8 g
MnCl ₂ • 4 H ₂ O	18.1 g
Na ₄ MoO ₄ • 2 H ₂ O	1.26 g
ZnSO ₄ • 7 H ₂ O	2.2 g
CuSO ₄ • 5 H ₂ O	0.8 g

The boxes were set up in three climate rooms with the following conditions:

	'day'	'night'
time	12 h	12 h
light	$\pm 400 \mu\text{mol m}^{-2} \text{s}^{-1}$	–
temperature	22 °C	18 °C
rel. humidity	70 %	70 %

Seeds from the species were sown on potting compost, in these same climate rooms, and they were used approximately 2 weeks after germination.

2.4 Harvest and measurements

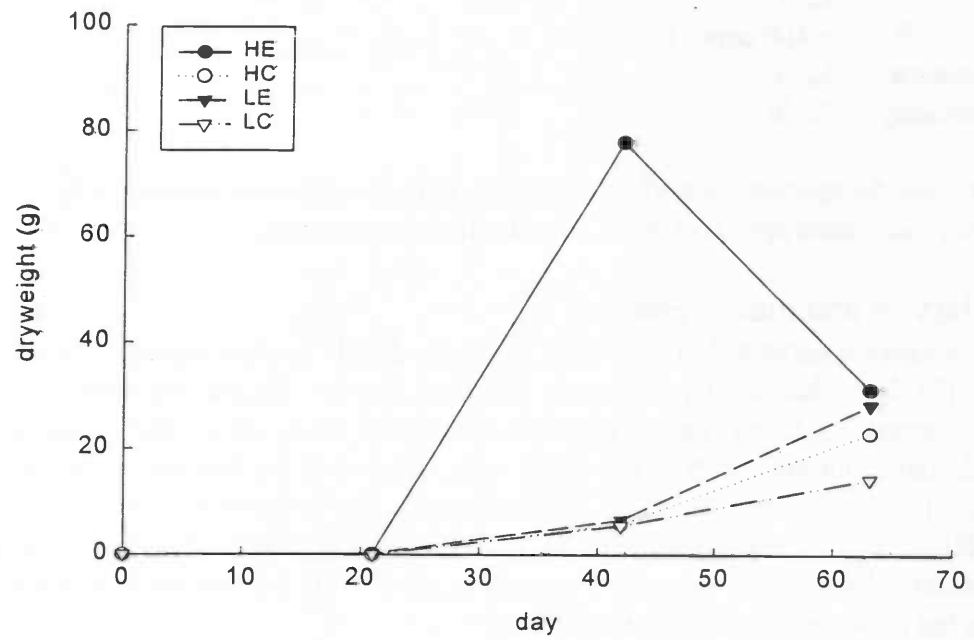
The plants were harvested at the day of planting (day 0, 'control harvest'), three weeks (21 days, 'harvest 1'), six weeks (42 days, 'harvest 2') and nine weeks (63 days, 'harvest 3'). Every harvest equalled one climate room. Every box contained $8 \times 9 = 72$ plants, but the plants on the edges were not used in the harvest. For all seven species, five plants were harvested (per treatment). The plants were divided in stems and leaves. These were weighed separately, and the leaf area was determined with a leaf area meter. The samples were dried in an oven, at ± 70 °C for two/three days after which the dryweights were recorded.

Prior to harvesting the light under the canopy (at soil surface) was measured in all treatments and in all rooms. After the first harvest light measurements were done twice a week. A light meter (Skye Instruments Ltd., SKP 200 ($\times 10 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)) with one sensor was used, the measurements were done in four (and after the second harvest two) rows per treatment.

2.5 Statistical analysis

Several parameters can be calculated from the raw data. Only shoots are used because the experimental design made it practically impossible to harvest the roots for each plant separate from the roots of the others. The parameters that will be examined here are total shoot dryweight and relative growth rate (RGR). The relative growth rate is the change in log (dry) weight per unit time. The dryweights and relative growth rates were analysed by using a two-way Anova with nutrient concentration and nutrient distribution (and the interaction between these two) as explaining factors.

Dryweight *Holcus lanatus*



Relative growth rate *Holcus lanatus*

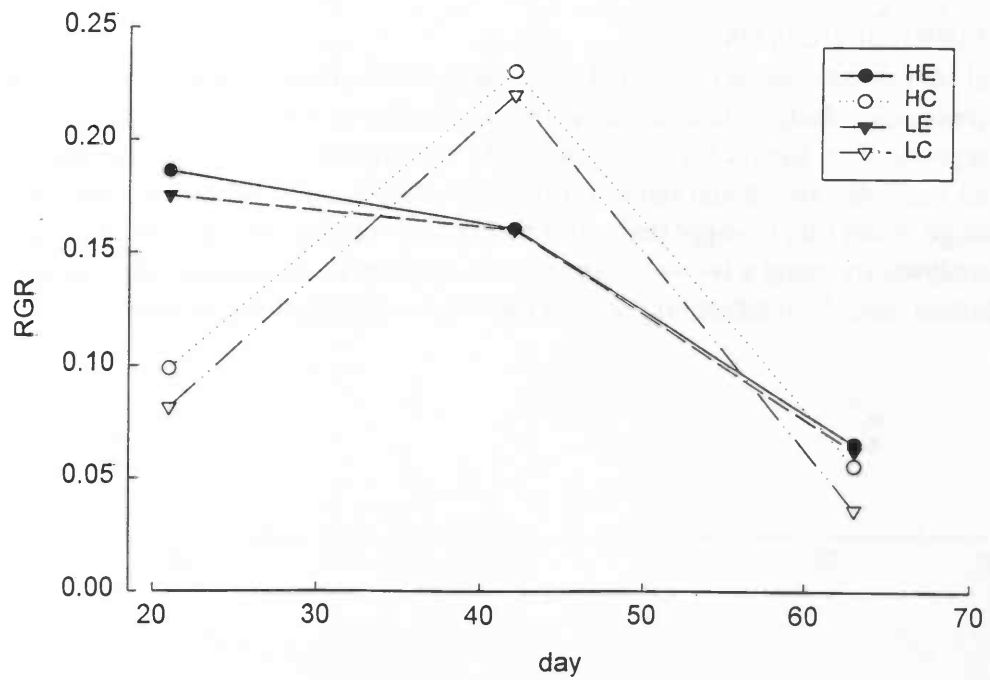


Fig 3a/b. Dryweight and relative growth rate of *Holcus lanatus*

3. Results

In the tables in this section an overview of the results of the Multivariate Analyses of Variances is given. The explaining factors are concentration of nutrients per litre (high and low, C) and distribution of nutrients (D) and the interaction (C x D) between these factors. When the difference between treatments is significant (at $\alpha = 0.05$), the p-value and an asterisk(?) is given in the table, non-significant differences are indicated as n.s. For every species two graphs are given, one with the development of the dryweight of the shoot (of the living material only) and one for the relative growth rate.

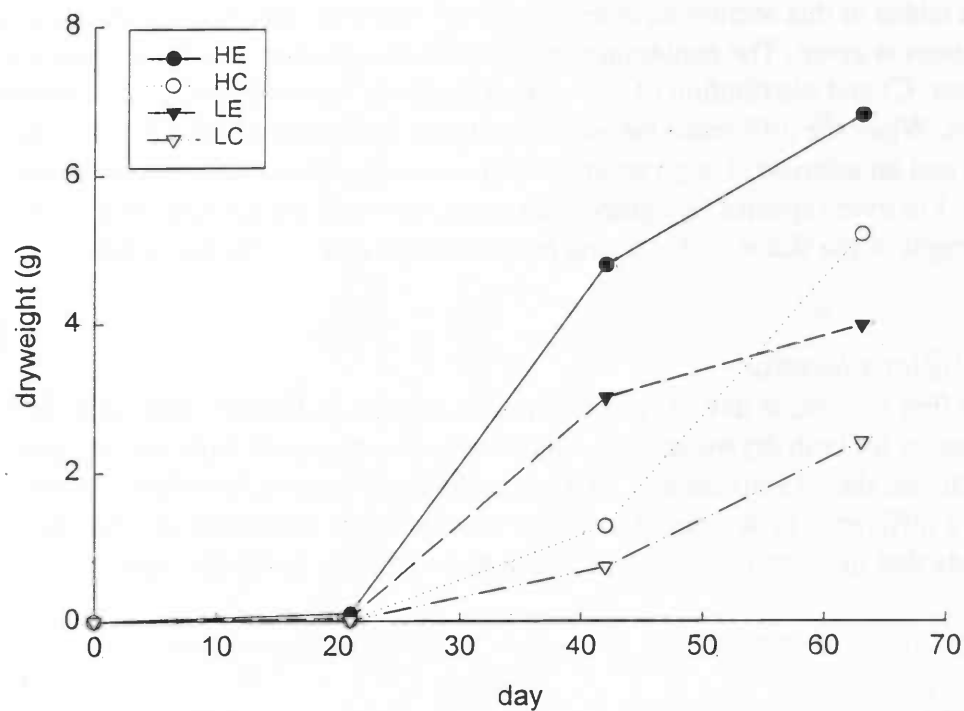
3.1. *Holcus lanatus*

In the first harvest, at day 21, *Holcus* is performing significantly differently in the four treatments for both dryweight and relative growth rate. At 42 days only the relative growth rate shows a difference. At 63 days the low even and low clustered treatments show a difference in dryweight, the high treatments are quite similar. The Manovas indicate that the distribution is a significant determining factor for these two variables.

HL	dryweight			relative growth rate		
	C	D	C x D	C	D	C x D
harvest 1	n.s.	0.000 *	n.s.	n.s.	0.000 *	n.s.
harvest 2	n.s.	n.s.	n.s.	n.s.	0.000 *	n.s.
harvest 3	n.s.	0.007 *	n.s.	n.s.	n.s.	n.s.

The dryweight graph shows that the plants in the high even treatment are a lot bigger than plants from other treatments at the time of the second harvest. In the third harvest most of this difference is gone. In the RGR graph the treatments can be divided in two groups. The patterns of the RGR of the even treatments are very similar, but clearly different from those of the clustered treatments.

Dryweight *Agrostis capillaris*



Relative growth rate *Agrostis capillaris*

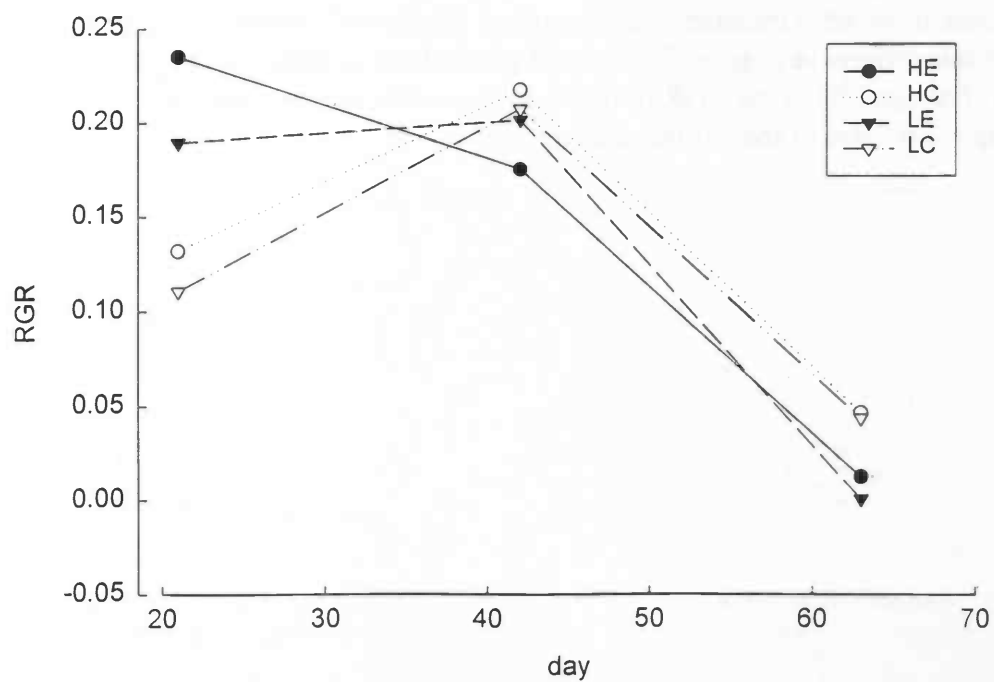


Fig 4a/b. Dryweight and relative growth rate of *Agrostis capillaris*

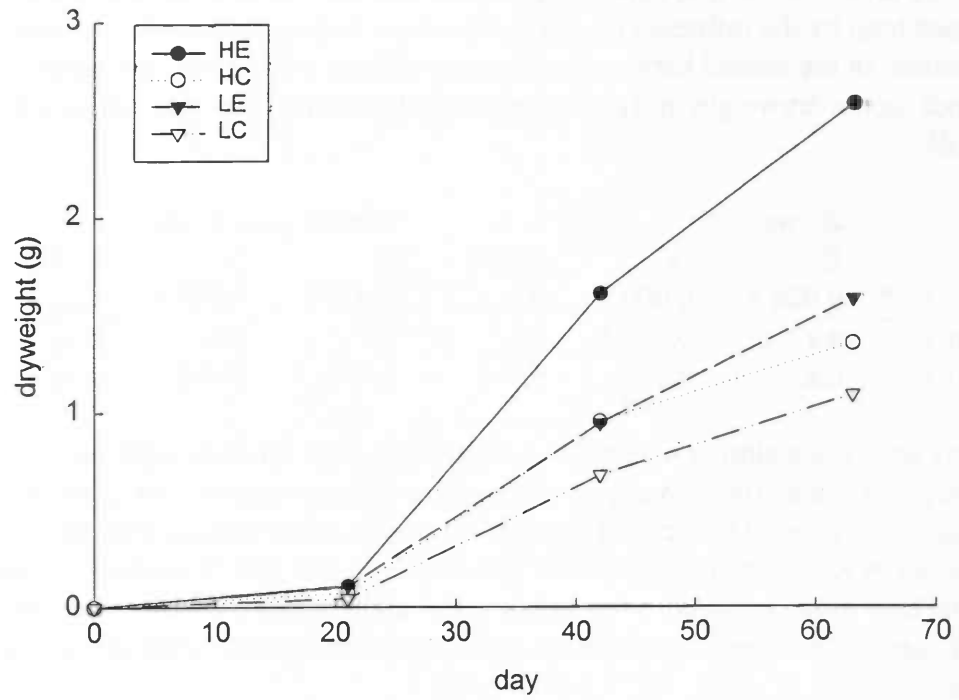
3.2. *Agrostis capillaris*

Agrostis shows significant differences in dryweight for the first and second harvest, RGR only differs at the first harvest day. In the first harvest these differences are explained both by the influence of nutrient levels as well as by the effect of nutrient distribution. In the second harvest the distribution is the only factor that seems to have influence on the dryweight of *Agrostis*, while in the third harvest this has an effect on the RGR.

AC	dryweight			relative growth rate		
	C	D	C x D	C	D	C x D
harvest 1	0.026 *	0.000 *	n.s.	0.039 *	0.000 *	n.s.
harvest 2	n.s.	0.001 *	n.s.	n.s.	n.s.	n.s.
harvest 3	n.s.	n.s.	n.s.	n.s.	0.032 *	n.s.

Agrostis has a quite similar pattern in all treatments, both for dryweight and for relative growth rate. The dryweights of the plants in high clustered are lower than those of low even until the second harvest, but they increase rapidly after day 42. The differences in RGR between treatments that can be seen at day 21 decrease in time. Here the high even treatment is the only one that decreases between the first and second harvest, the other three increase at first and then decrease after the second harvest.

Dryweight *Anthoxanthum odoratum*



Relative growth rate *Anthoxanthum odoratum*

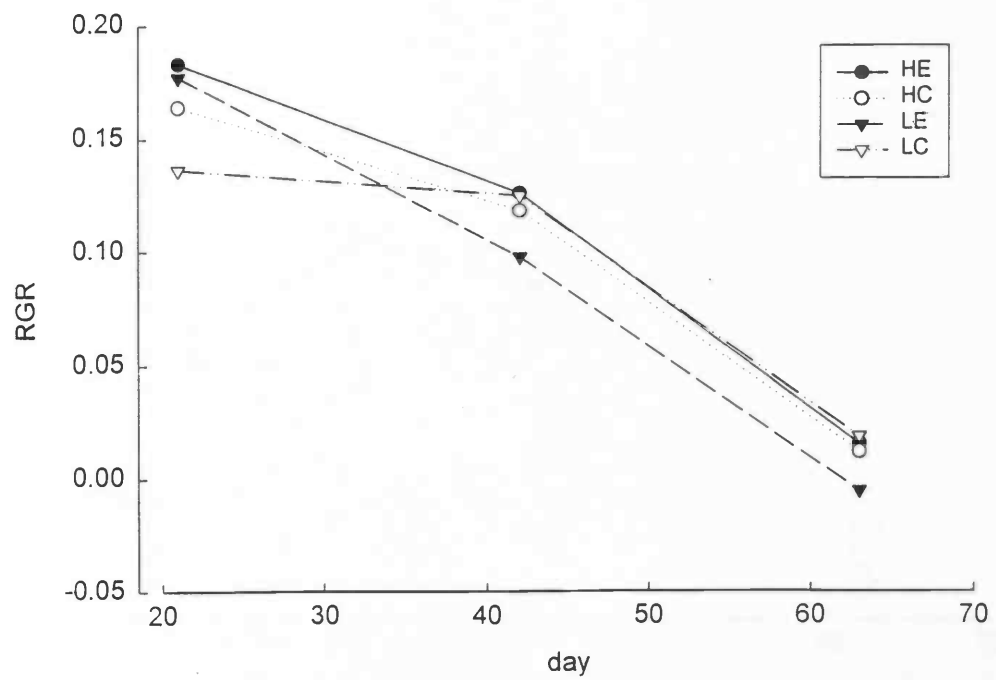


Fig 5a/b. Dryweight and relative growth rate of *Anthoxanthum odoratum*

3.3. *Anthoxanthum odoratum*

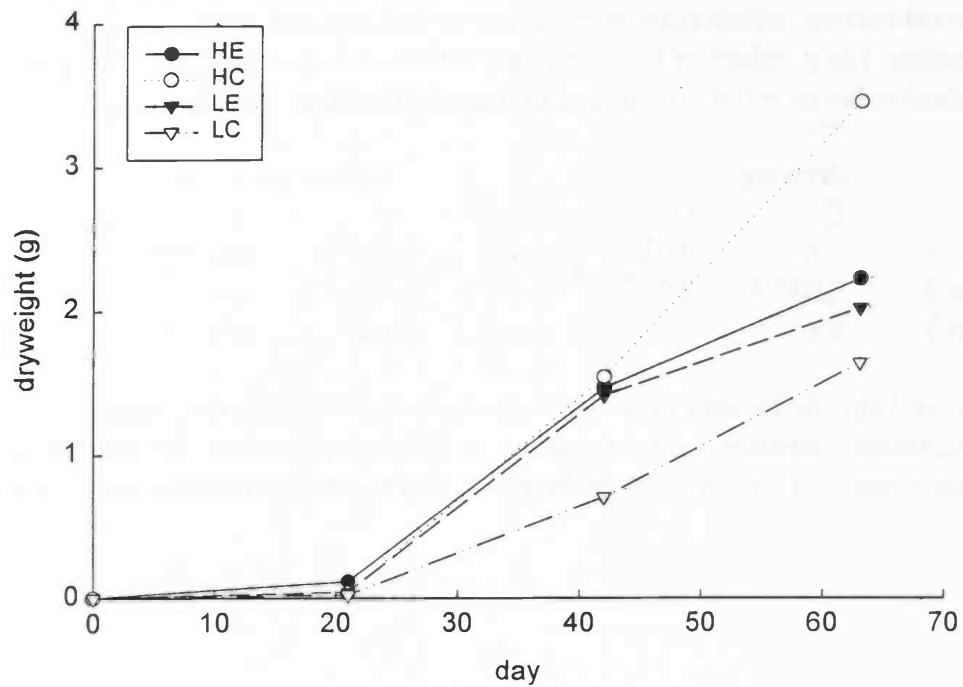
Anthoxanthum behaved quite similarly in all treatments, there is a significant difference ($p = 0.0463$) between the dryweights in 'high clustered' and 'high even' in the second harvest, which may be explained by influence of both nutrient levels and distribution. The p-values of the significant differences are larger, and thus closer to the critical value ($\alpha = 0.05$) than seen in many of the other species.

AO	dryweight			relative growth rate		
	C	D	C x D	C	D	C x D
harvest 1	n.s.	0.027 *	n.s.	n.s.	0.025 *	n.s.
harvest 2	0.033 *	0.037 *	n.s.	n.s.	n.s.	n.s.
harvest 3	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

What could already be seen in the table above is also visible in the graphs.

Anthoxanthum odoratum does not seem to be heavily affected by different nutrient concentrations, and only slightly by homo- or heterogeneous distribution of nutrients.

Dryweight *Plantago lanceolata*



Relative growth rate *Plantago lanceolata*

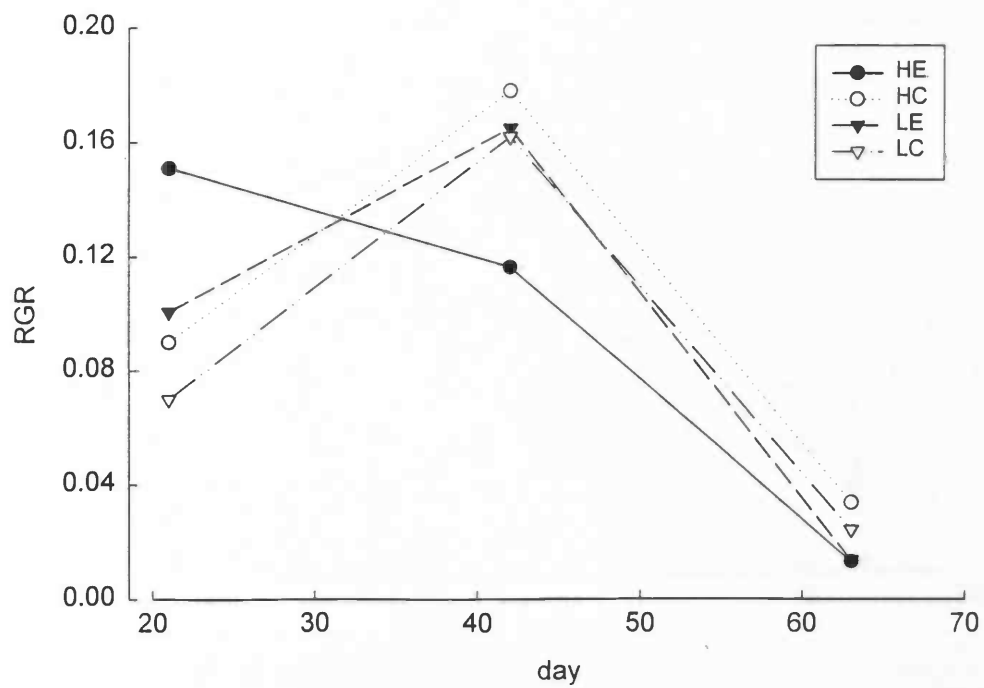


Fig 6a/b. Dryweight and relative growth rate of *Plantago lanceolata*

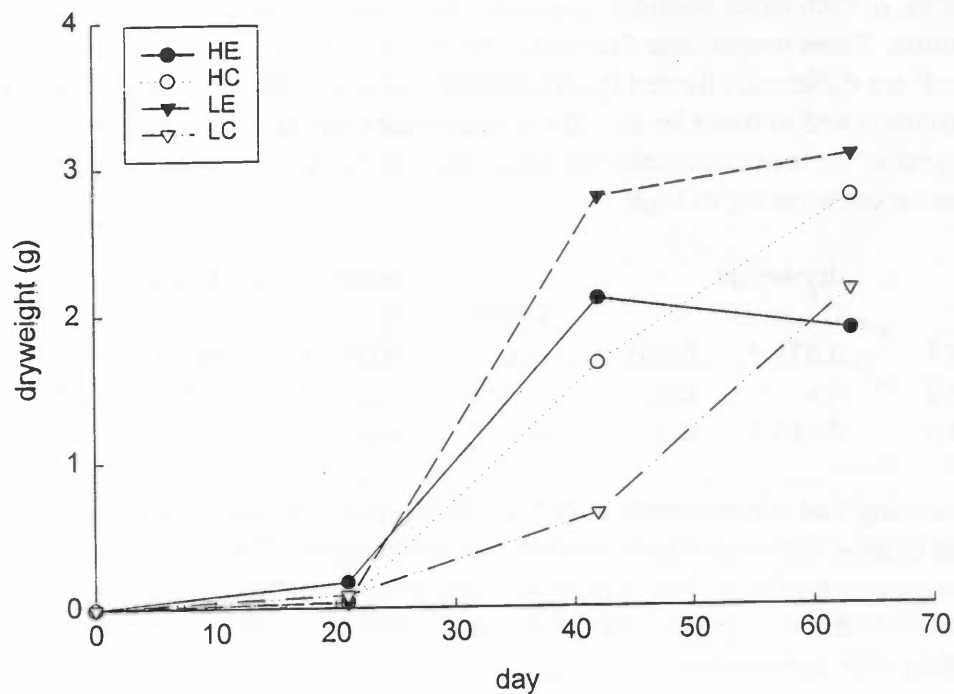
3.4. *Plantago lanceolata*

At day 21 the dryweight and RGR of *Plantago* show a difference in the 'high' treatments, in both cases possibly caused by the effects of nutrient levels and those of distribution. Three weeks later (harvest 2) the RGR's of the 'high even' and 'high clustered' are different, affected by distribution but also influenced by the interaction of distribution and nutrient levels. At the same time there is a difference between the dryweights in the low treatments, the Manovas give no indication of nutrient levels or distribution contributing to this.

PL	dryweight			relative growth rate		
	C	D	C x D	C	D	C x D
harvest 1	0.011 *	0.005 *	n.s.	0.017 *	0.003 *	n.s.
harvest 2	n.s.	n.s.	n.s.	n.s.	0.005 *	0.003 *
harvest 3	0.043 *	n.s.	n.s.	n.s.	n.s.	n.s.

The first thing that is remarkable is that the plants from the high clustered treatment have the highest dryweight in the second and third harvest. The relative growth rate shows a pattern similar to that of *Agrostis capillaris*, with high even as the only one that is already decreasing after the first harvest while the RGR of the others starts decreasing after harvest two.

Dryweight *Rumex acetosa*



Relative growth rate *Rumex acetosa*

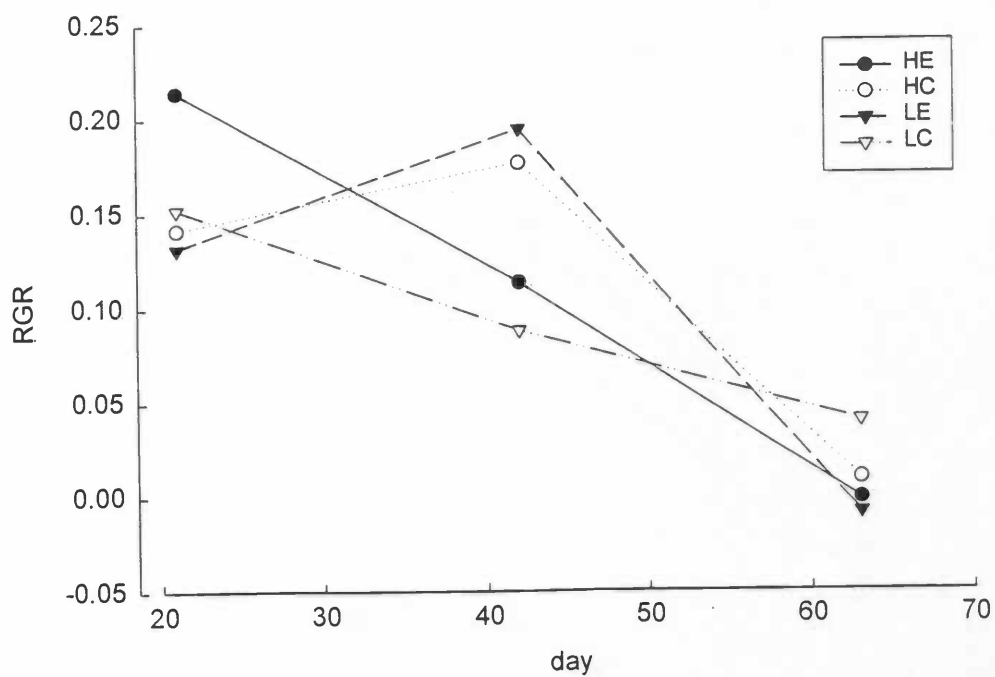


Fig 7a/b. Dryweight and relative growth rate of *Rumex acetosa*

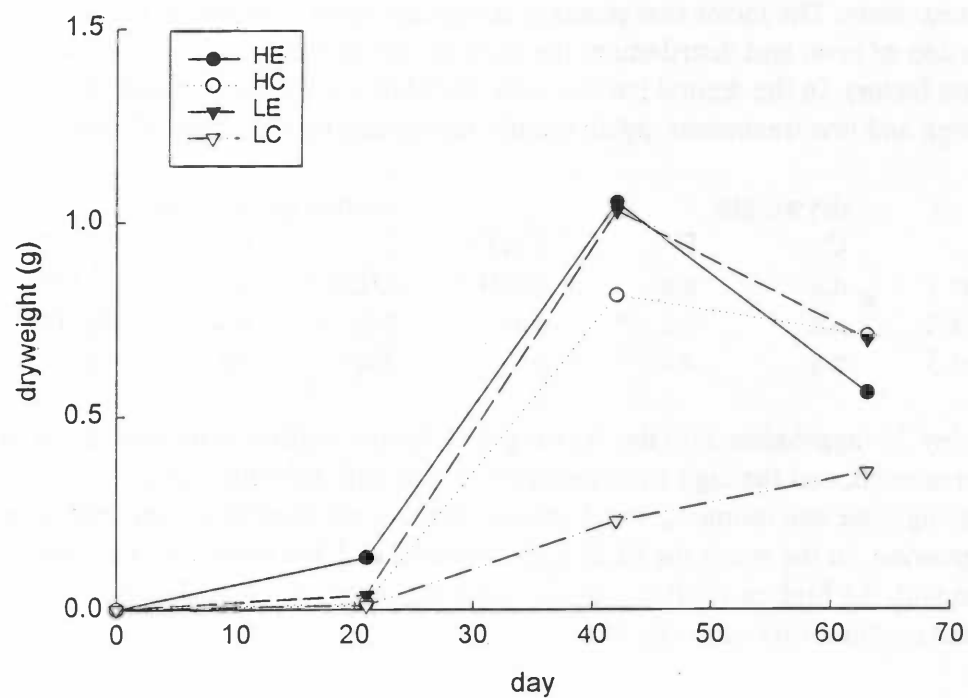
3.5. *Rumex acetosa*

In harvest 1 a distinction can be made for the dryweight and the RGR of *Rumex* in the high treatments. The factor that seems to determine these differences is primarily the interaction of level and distribution, the RGR is also affected by concentration (as a separate factor). In the second harvest only the RGR shows a significant difference, in both high and low treatments, again mainly influenced by the effect of interaction.

RA	dryweight			relative growth rate		
	C	D	C x D	C	D	C x D
harvest 1	n.s.	n.s.	0.004 *	0.034 *	n.s.	0.008 *
harvest 2	n.s.	n.s.	n.s.	n.s.	n.s.	0.000 *
harvest 3	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

After day 24 (approximately) the dryweight of *Rumex acetosa* is highest in the low even treatment, and the high even treatment that is still quite high at day 42 is decreasing after that moment, which means that there is more plant material dying than growing. In the graph for RGR high clustered and low even have the same pattern with the highest RGR at day 42, while high even and low clustered both decrease continuously after day 21.

Dryweight *Lychnis flos-cuculi*



Relative growth rate *Lychnis flos-cuculi*

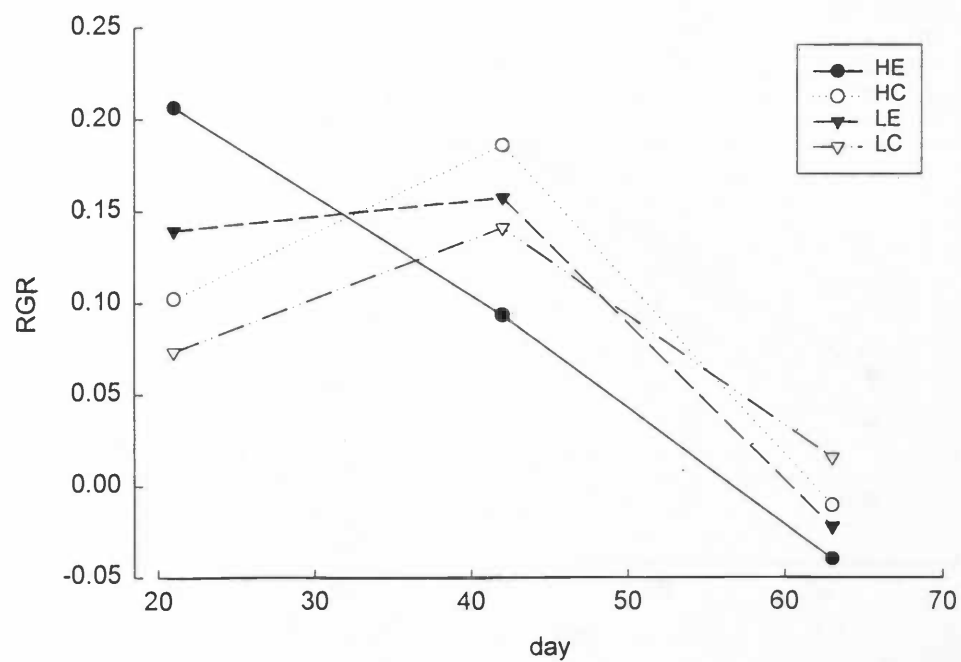


Fig 8a/b. Dryweight and relative growth rate of *Lychnis flos-cuculi*

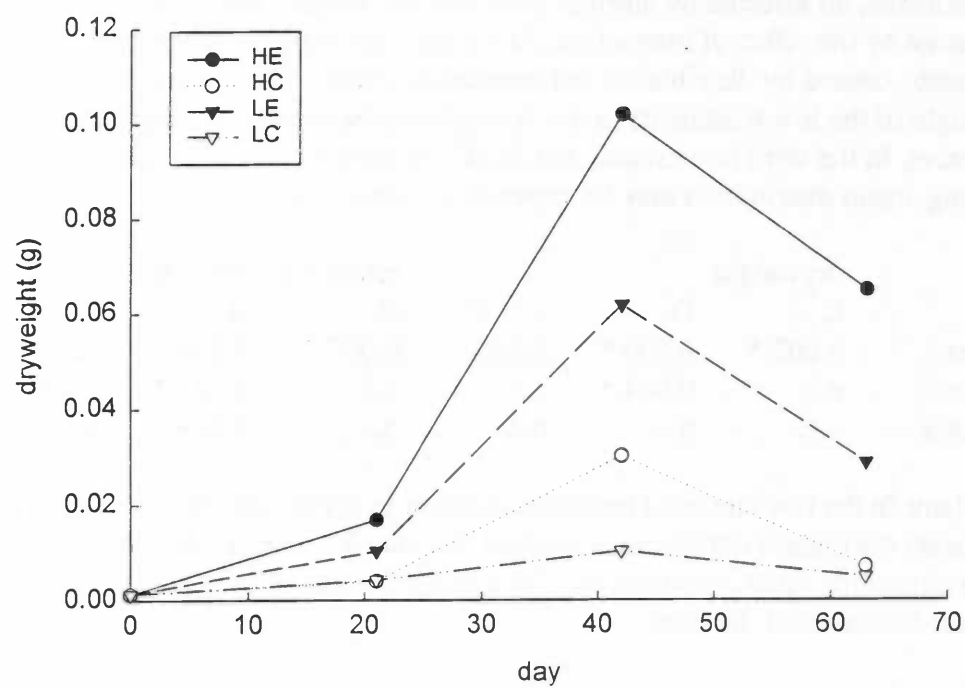
3.6. *Lychnis flos-cuculi*

In the first harvest the performance of *Lychnis* is different for dryweight and RGR in all treatments, all affected by nutrient level and distribution, the dryweight is also influenced by the effect of interaction. At 42 days the RGR is different for the high treatments, caused by distribution and interaction effects. The variances in the dryweight of the low treatments in this harvest may be caused by distribution influences. In the third harvest only the RGR's of the low treatments are significantly differing, again distribution may be expected to cause this.

LF	dryweight			relative growth rate		
	C	D	C x D	C	D	C x D
harvest 1	0.002 *	0.000 *	0.005 *	0.007 *	0.000 *	n.s.
harvest 2	n.s.	0.004 *	n.s.	n.s.	0.001 *	0.000 *
harvest 3	n.s.	n.s.	n.s.	n.s.	0.016 *	n.s.

The plants in the low clustered treatment increase in dryweight while in the other treatments the highest dryweight is reached near day 42. The graph of relative growth rate is almost the same as the one of *Plantago lanceolata*, with high even as the only one that decreases all the time.

Dryweight *Crepis paludosa*



Relative growth rate *Crepis paludosa*

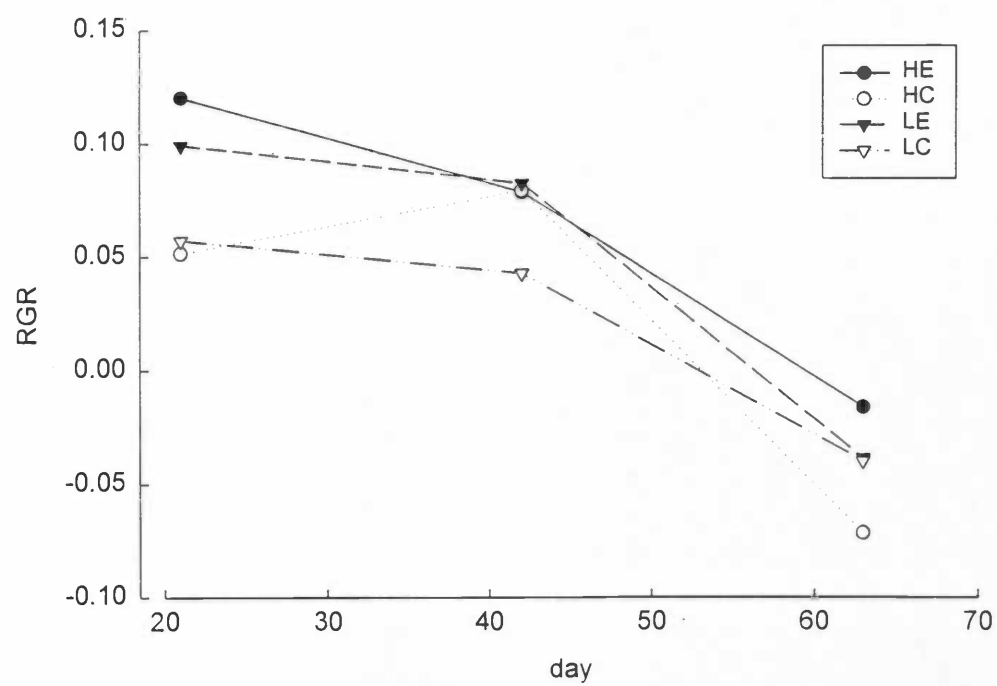


Fig 9a/b. Dryweight and relative growth rate of *Crepis paludosa*

3.7. *Crepis paludosa*

According to the Manovas the growth of *Crepis* is mainly affected by the nutrient distribution, only for the RGR of the second harvest this has no significant effect. The RGR's of the high treatments are different in harvest 1 and 3, those of the low treatments in harvest 1 and 2. The dryweights of *Crepis* differ in harvest 1 and 2 for the high treatments, and in all harvests for the low treatments.

CP	dryweight			relative growth rate		
	C	D	C x D	C	D	C x D
harvest 1	n.s.	0.000 *	n.s.	n.s.	0.000 *	n.s.
harvest 2	n.s.	0.002 *	n.s.	n.s.	n.s.	n.s.
harvest 3	n.s.	0.006 *	n.s.	n.s.	0.043 *	n.s.

All treatments have the same pattern in the dryweight graph, with a slow increase until day 21, a faster increase between day 21 and day 42 and a decrease after day 42. The clear difference between the treatments is in the total dryweight. In the relative growth rate the high clustered treatment is the only one that is not continuously decreasing, but increasing till the second harvest.

3.8 Light under the canopy

The light was measured in all climate rooms prior to harvesting. The mean of the recorded light intensities at soil surface per treatment was used. The differences between the rooms were not significant, these could very well be caused by chance. More interesting is a comparison between the four treatments at a certain time.

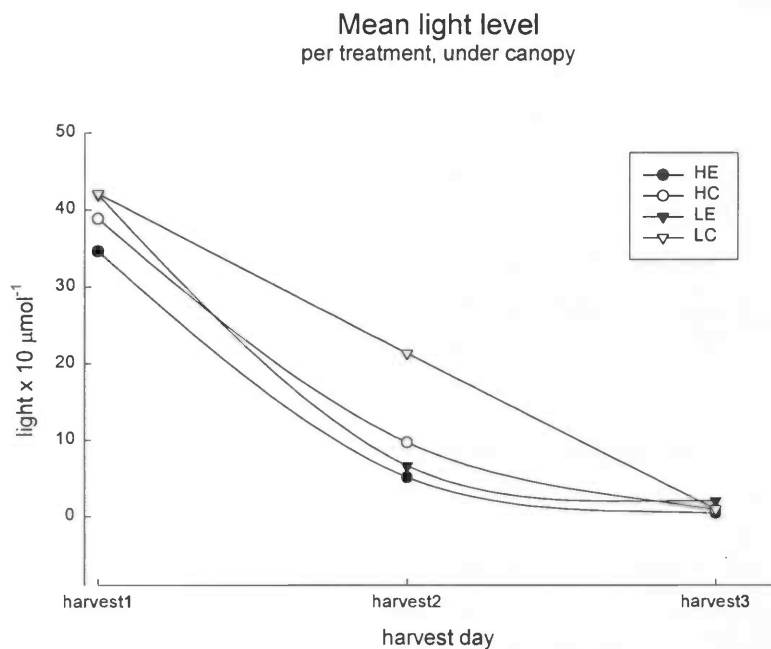


Fig 10. Light under the canopy in all treatments prior to harvesting.

In climate room A, the light shows a quite rapid decrease after the first harvest date, in an 'inverse S-shaped' curve.

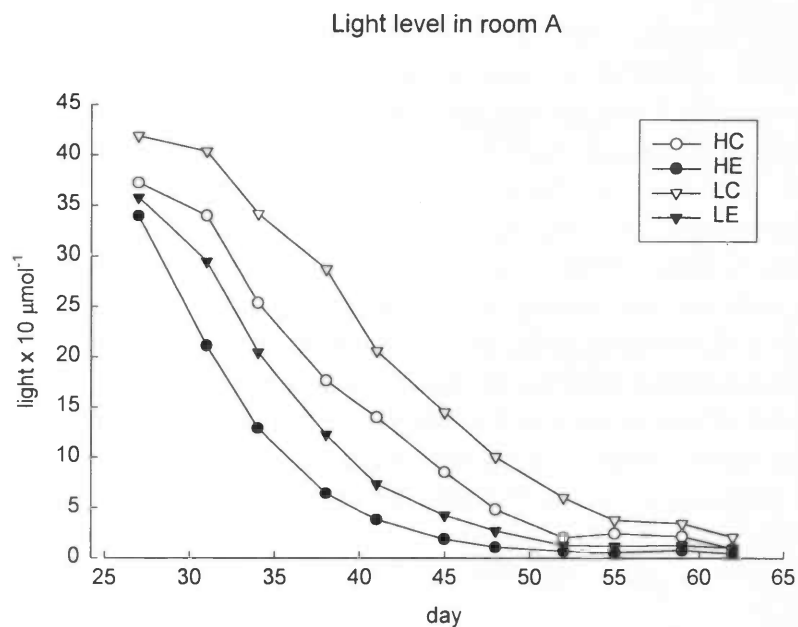


Fig 11. Light under the canopy in room A per treatment.

The fastest decrease in light under the canopy is seen in the high even treatment, followed by the low even and the high clustered treatments. The low clustered treatment is the slowest, at the time of the last harvest this is the only one that is a little bit higher than all other ones. In all treatments the light level under the canopy approaches 0 before the last harvest, which makes it highly probable that not only competition for nutrients but also light competition is playing a role in determining the outcome of this experiment.

4. Discussion

A problem that occurs in this research is the fact that some of the words that are used have no clear definition or have more than one definition. The most important word in this context is competition. As Welden and Slauson (1986) pointed out 'competition' is used for both a process and a product. They suggest to separate competition into intensity and importance. Here intensity qualifies the process of competition (the amount of strain that is induced in an organism by competition), while importance concerns the products of competition (the relative degree to which competition contributes to the overall decrease in e.g. growth rate, survival or fitness of an organism, as compared to importance of other processes and conditions). These two are not necessarily correlated. The advantage of separating them is that it distinguishes competition (the process) and competitive success (the product), which helps to avoid confusion in terminology. The problem that is left is how to measure these two. In this research the competitive success is measured by determining the weight, growth rate etc. of the seven species that were used. With this information one can try to give an indication of the competitive ability of different species.

The experimental design of this research creates several problems. One of them is that because the number of treatments is relatively large, the harvesting becomes a serious limitation. Considering this and the fact that every climate room can hold a maximum of four boxes (as described in 2.3), true replication is practically not achievable. A choice has to be made between the scope of the experiment and true replication, here the aim is to obtain information on the performance of the plants over longer periods in numerous treatments (Hughes & Freeman, 1967). To be able to compare the treatments to each other, all four treatments on one harvest day were taken from one climate room. If there had been differences between the rooms (which were be minimised, and were not found to be significant in the control plants), they would have affected all treatments.

When analysing the data with a two-way ANOVA, a lot of the tests failed to meet the assumption that the variances have a homogeneous distribution. Fortunately, the analysis of variance test is robust, operating well, even with considerable heterogeneity of variances, as long as all samples (n_i) are equal or nearly equal (Zar, 1996, G.V. Glass, P.D. Peckham and J.R. Sanders, 1972). In this case all samples were indeed all equal ($n = 5$). Grime (1974) stated that even though the analytical methods may not be exactly correct, that is a "small price to pay for the more realistic description of the trends in each of the sets of data that this analytical procedure provides".

As mentioned in the introduction several factors are important in competition for nutrients. The zone of uptake and the rate of transport are affected by three factors, shown in fig 12. In the first place there are the properties of the soil, e.g. water content and structure. Very closely related to this is the mobility of the ion or resource. The last factor influencing these processes is the gradient of nutrients that is established by plant uptake. When uptake zones of plants are overlapping, depletion of the shared resource pools can occur. In this case there can be competition for nutrients, if the species are limited by the same resource.

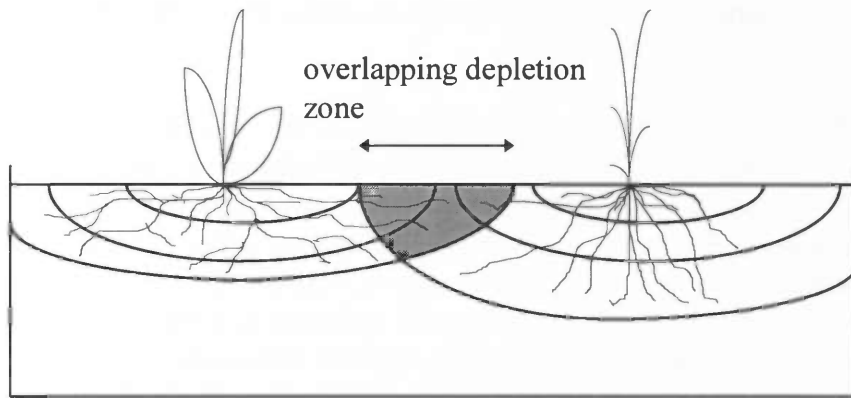


Fig 12. Overlapping uptake zones.

Of course the mechanism of uptake and also of competition will differ for different ions. Various morphological and physiological attributes of plants can improve belowground competitive ability. The capacity of a plant to adjust the size and distribution of shoot canopies and root systems in response to changes in the external supply of resources is called plasticity. Plasticity is determined by potential growth rate and the capacity to make internal reallocations. Plants differ in plasticity, which may contribute to their competitive success, although there are various suggestions on how it might function in different communities. Morphological and physiological plasticity influence both the quantity and the rate of additional resource uptake (Campbell, Grime and Mackey, 1991).

In belowground competition morphological plasticity has three components, rate, scale, and precision. Hanski (1983) already noticed that the outcome of interspecific competition may depend on the scale of space considered. Campbell, Grime and Mackey (1991) presented evidence for 'high-scale' resource foraging by leaf canopies and root systems for dominants and 'high-precision' for subordinates, which fits Grimes theory of interdependence of above- and belowground competitive abilities. (Casper & Jackson, 1997) The effect of physiological plasticity should increase the uptake of relatively mobile ions more than the uptake of less mobile ones, particularly when competition occurs through overlapping depletion zones. Finally spatial and temporal rooting patterns can create 'niche separation' by soil partitioning. This reduces belowground competition.

Very often there is no direct correspondence between root density and the outcome of belowground competition. This may be explained by looking at competition among roots of the same plant, precision in foraging nutrients possibly being at least as important as scale (the possibility of localised patches), the effects of mycorrhizae, and physiological properties related to rate of uptake.

Competition does not only occur belowground, there is interaction with aboveground competition for light. The consequences of these two forms of competition are very different. Even though there are big differences in the theories about this interaction all agree that both competition for nutrients and competition for light are important in the development of the vegetation structure. Light comes from one direction and its availability can only be influenced by biotic and abiotic processes such as shading. It

is not dependent on diffusion or any other kind of transport (Huston and DeAngelis, 1994).

Several researchers have suggested a model with a place for both nutrient and light competition. In communities on poor or medium fertile soils competition for belowground resources will be the main factor that influences vegetation structure. Because belowground competition is competition for a broad range of resources, all with their own properties (charge, mobility, solubility etc.), coexistence of many species is very well possible. When the soil is more fertile, the competition for light will become dominant. As light is an finite and unidirectional resource that can be monopolised, diversity will decrease and the species that is the best competitor for light will exclude all or most other species. This model explains the change of diversity along a productivity gradient as well as the decrease in the diversity of competing species during plant succession. The diversity will be low in very unproductive communities, because the circumstances here exceed the tolerance of most species. When soil resources increase (decreasing depletion zones) the diversity will increase too, as long as competition is primarily belowground. In systems like this an extensive range of coexisting species can be found. When aboveground competition starts dominating the diversity will drop off rapidly and competitive exclusion can occur, this explains the hump shaped curve that is found for the relationship between productivity and species richness (Huston & DeAngelis, 1994, Grace, 1995, Casper and Jackson, 1997).

Another explanation for coexistence that was already mentioned in the introduction is heterogeneity of the distribution of nutrients in the soil. Not only the shift from belowground to aboveground competition can change the vegetation structure, but also the small scale differences in habitats. One possibility is that the soil is initially homogeneous, but small scale differences arise because plants create depletion zones. In response to this other species will establish or disappear. Another possibility is that the soil is never really homogeneous at all, and various species will establish in the habitats that most suit them, and they can intensify the differences in the soil. It is obvious that when the assumption of a well mixed regional resource pool is relaxed and local resource depletion is allowed to occur without a strong influence on the regional pool, the nature of competition is totally altered. Under these conditions, the local coexistence of many potentially competing species is possible, even when they are all limited by the same resource.

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Box A

In Tilman's theory competitive success is predicted as a function of the concentration of limiting resources. The species that can lower the concentration of the limiting resource and survive this low concentration will win the competition in a particular habitat (lowest resource requirement). The number of coexisting species cannot exceed the number of limiting resources. There is a trade-off between the abilities to compete for different resources, plants are good competitors above- or belowground. This leads to the expectation that competition can be equally intense and important in all habitats (productive or unproductive) and in all phases of succession (Tilman, 1987, 1989, 1990, 1994, Grace, 1991, Grace & Tilman, 1990).

1. competitive superiority by low resource requirement
 2. trade-off of competitive abilities for different resources
 3. competition not necessarily less intense in unproductive habitats
 4. competition determines dominance during all successional phases
- (Grace, 1991)

If it is true that competition for the most limiting resource will result in competitive exclusion of all species by the best competitor, how is it possible that a lot of species coexist even when only one resource is limiting? In the explanation of (bio)diversity Tilman introduces the concept of interspecific trade-off between colonisation ability, competitive ability and longevity. If a species is not present at a certain locality this does not necessarily mean that it is absent because of biotic interactions, another possibility is that none of its propagules has yet arrived at that site, this is called colonisation limitation (Tilman, 1994).

Spatial subdivision allows for a potentially unlimited number of species to coexist in a physically homogeneous, equilibrium habitat. An alternative explanation for species diversity is that habitats are spatially heterogeneous, which allows coexistence.

Grime (1977) distinguishes two external factors that limit plant biomass: stress and disturbance. (?) These terms are defined by Grime (1977). Stress consists of the external constraints which limit the rate of dry-matter production of all or part of the vegetation. This can be environment-induced or plant-induced or both. Disturbance is the process that contains all mechanisms which limit the plant biomass by causing its destruction. Three main strategies have developed in plant species that are adapted to the differing circumstances of habitats. All intermediates between these strategies are possible as well.

	stress low	stress high
disturbance low	competitor	stress-tolerator
disturbance high	ruderal	not viable

Competitive success depends on the ability to maximise resource capture. Competitors are good at competing for aboveground (space and light) and belowground (water and nutrients) resources, these traits are interdependent. Competition is a distinct strategy, which implies that it has a set of circumstances

under which it dominate in a vegetation (fertile, relatively undisturbed area, or during mid-succession), and circumstances under which it will lose the 'battle' with others, e.g. stress tolerators in an unproductive habitat or in a late phases of succession or ruderals in a recently disturbed area (early succession). The nature of the strategies is determined by differences in relative importance of the abilities for resource capture, growth, and reproduction (Campbell & Grime 1992). There is a tendency towards dominance by one or a few species in most communities, these species have a major contribution to biomass, monopolising resource capture and influencing the identity of that community (Grime, 1987).

1. competitive superiority by high resource uptake capacities
 2. interdependence of competitive abilities for different resources
 3. competition less intense in unproductive habitats
 4. competitors dominate during mid-succession
- (Grace, 1991)

In addition to this Campbell, Grime and Mackey (1991) suggest the existence of a trade-off between scale and precision in resource foraging. Dominant species have coarse grained, high scale foraging (and plastic responses, see par.), subordinate species have comparatively fine grained, high precision foraging (and plasticity).

(Campbell & Grime, 1992)

In summary, two suggested theories are:

- 'Competition is most important under productive conditions, decreasing when stress or disturbance takes over'. The abilities to capture resources above and below ground are interdependent, they reach a simultaneous maximum in rapidly growing, perennial communities on fertile soil, increasing habitat productivity (Grime).
- 'Competition remains the primary determinant of vegetation structure but there is a change from aboveground to belowground competition'. There is an inverse relationship between above- and belowground competitive abilities: morphological trade-off (Tilman).

Box B

To show when the differences between treatments are significant one can use the following notation: a continuous line indicates a non-significant difference, a break in the line indicates a significant difference.

Day 0: LC LE HE HC

Day 21: LC LE HC HE

Day 41: LC HC LE HE

Day 62: LC HC LE
 LE HE

