

Effects of competition on root–shoot allocation in *Plantago lanceolata* L.: adaptive plasticity or ontogenetic drift?

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Abstract We investigated how shoot and root allocation in plants responds to increasing levels of competitive stress at different levels of soil fertility. In addition, we analyzed whether different responses were due to adaptive plasticity or should be attributed to ontogenetic drift. *Plantago lanceolata* plants were grown during 18 weeks at five plant densities and four nutrient supply levels in pots in the greenhouse. Thereafter root and shoot biomass was measured. There were clear negative effects of increasing plant densities on plant weights revealing strong intraspecific competition. At the lower N-treatments, the proportional allocation to root mass increased with increasing competitive stress, indicating the important role of belowground competition. At the higher N-supply rate, the relationship between competitive stress and shoot to root ratio was neutral. These responses could not be attributed to ontogenetic drift, but could only be explained by assuming adaptive plasticity. It was concluded that at lower N-supplies belowground competition dominates and leads to increased allocation to roots, while at the higher N-supply competition for soil resources and light had balanced impacts on shoot and root allocation. An alternative hypothesis explaining the observed pattern

is that light competition has far less pronounced impacts on root–shoot allocation than nutrient deprivation.

Keywords Root–shoot allocation · Competition · Ontogenetic drift · Adaptive plasticity · *Plantago lanceolata* L.

Introduction

In grassland communities, plant species composition and plant species diversity vary significantly with productivity and soil fertility (Whittaker 1975; Grime 2001). Competition between plant populations is often assumed to have decisive effects on these patterns (Grime 1979; Berendse 1983; Tilman 1988). A classical, but still unresolved issue is whether the relative importance of belowground and aboveground competition shifts with increasing soil fertility and whether this has consequences for competition intensity and the rate of species replacement (Grime 1979, 2001; Tilman 1988; Wilson and Tilman 1991; Goldberg and Novoplansky 1997; Peltzer et al. 1998; Keddy et al. 2000; Wardle 2002). Answering this question would enable us to predict what plant features increase plant fitness at different levels of soil fertility.

Competing plants deprive each other of resources such as light, soil nutrients, and water. Brouwer (1962a, b) and many others showed unambiguously

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that changing levels of resource supply lead to significant changes in the partitioning of growth between the below- and the aboveground parts of the plant. Shading increases the allocation to leaves and stems, while reduced supplies of nitrogen or water increase the allocation to root growth. Recently, these general patterns were reconfirmed by a meta-analysis of literature data (Poorter and Nagel 2000). Brouwer (1962a,b) explained this adaptive response by his Functional Equilibrium Hypothesis, where he assumed that below- and aboveground parts are competing for the resources that the plant has acquired. The consequence is that we should expect that root competition would lead to increased allocation to belowground parts, while aboveground competition would lead to increased allocation to shoots. These opposite responses would enable a sharp distinction between the effects of stress due to above- or belowground competition. Such distinction can possibly help to answer questions about the relative importance of above- and belowground competition from the point of view of the plant.

The single use of shoot:root ratios to test whether plants show an adaptive response in allocation pattern to changes in resource supply has been criticized (Weiner 1990; Jasienski and Bazzaz 1999). It has been argued that biomass allocation patterns may change due to allometric relationships that are maintained during plant development (Evans 1972; Gedroc et al. 1996). Such ontogenetic relations might lead to changes in biomass partitioning only as a consequence of an increase in plant size. Using an allometric analysis, several authors observed that the effects of nutrient supply (Müller et al. 2000) or root competition (Cahill 2003; Litton et al. 2003) on shoot:root ratios could be explained by their effects on individual plant mass.

In this article, we investigate the effects of nutrient supply and competitive stress on allocation to above- and belowground parts. We attempted to distinguish between changes in biomass partitioning due to adaptive plasticity or fixed allometric relationships during development. We tried to answer the following questions: (1) What are the effects of different levels of competitive stress on the proportional allocation to shoot and root mass? (2) Is the response of shoot:root ratios to increasing levels of competitive stress different at low and high nutrient supplies? (3) Are the effects of nutrient supply and competitive

stress on the shoot:root ratio a consequence of adaptive plasticity or should they be attributed to ontogenetic drift?

We attempted to answer these questions by performing an experiment where we compared the allocation to shoot and root mass at a large range of competitive stress and soil fertility levels. It is often impossible to harvest the complete root mass of the target species as roots of the competing species are strongly intermingled. We resolved this problem by creating different levels of competitive stress by growing *Plantago lanceolata* L. plants at different monospecific densities, so that we were able to harvest all roots in all treatments. *Plantago lanceolata* L. is a perennial herb that grows in hay meadows at a wide range of soil fertilities.

Materials and methods

Design of the experiment

The experiment was designed to investigate the effects of different levels of N supply on the stress that plant individuals experience by intra-specific competition. The plants were grown in the greenhouse in pots with a diameter of 20 cm and a depth of 20 cm. In order to avoid edge effects that would reduce the differences in light environment between densities and nutrient supply levels, the plants were grown in pots surrounded by an outer pot in which plants were grown at the same density. The target plants were grown in the inner pot with a ground area of 314 cm² and a pot volume of approximately 6 l. These pots were placed in larger pots that had dimensions such that the outer part also had a ground area of 314 cm² and a soil volume of 6 l. The diameter of the pot including the buffer part was 28.3 cm. These buffer zones were planted with the same numbers of plants as the inner pots, so that not only plant densities, but also ground area and soil volume per individual were equal in the inner and outer pots.

We compared five plant densities (1, 2, 4, 8, and 16 plants per 314 cm²) and 4 N-fertilization levels (N0, N5, N10, and N20) in a complete factorial combination. Each combination of plant density and N-treatment was repeated in five replicated blocks. In each of these blocks the treatments were located randomly.

Experimental procedures

Plants were grown in the greenhouse at day and night (12/12 h) temperatures of 20 and 18°C, respectively. Air humidity was maintained at 70%. A nutrient-poor soil substrate was prepared by mixing five parts sand without organic matter and one part black top soil removed from an arable field on a sandy subsoil. The organic matter content of the mixture was 1.3%, and pH(H₂O) and pH(KCl) were 6.4 and 6.0, respectively. Total N and P contents were 345 and 163 mg kg⁻¹, respectively. We supplied both the inner and outer pot weekly with 50 ml of nutrient solution with 37 mg N, 5 mg P, and 12.5 mg K at the highest fertilization level. The total amount applied during the course of the experiment were 0, 4.4, 8.8, and 17.7 g N m⁻² (and corresponding amount on P and K) in the N0, N5, N10, and N20 treatments, respectively. Pots were supplied daily with water to prevent water limitation. The soil water content was maintained at field capacity (14.4%, w/w) by weighing the pots twice a week and adding sufficient amount of water to maintain constant pot weights. On the five days each week when this was not done, the amount of water to be added were determined from estimates based on the weights of a random sample of pots from each N treatment.

On 26 April 2001 seeds of *Plantago lanceolata*, collected from natural populations in a hay meadow near Wageningen, were planted in trays containing fine sand. On 17 May 2001 the seedlings were planted in the pots. Plants were harvested on 3 September 2001. All shoots in the inner pots were cut off at ground surface (including the caudex). Roots in the inner pots were washed out of the soil and thereafter cleaned by hand using tweezers to remove humus particles. All plant parts were dried at 70°C during 48 h and subsequently weighed.

Statistical analysis

The homogeneity of variances of log-transformed individual plant weights and shoot:root ratios were investigated using a Gamma GLM (GENSTAT 1993). The assumptions with respect to the homogeneity of the variances were met by our data. Subsequently, a GLM was applied with plant density and nutrient treatment as factors and the log-transformed values of individual plant weights and

shoot to root ratios as dependent variables. Blocks were included as random factor. In a second analysis of the shoot to root ratios (S_w/R_w) we included plant density (D) and N-treatment (N) as fixed factors with plant weights (P_w) as a covariate. We used the model

$$\log(S_w/R_w) = a + b \cdot \log P_w + N + D + N \cdot D + N \cdot \log P_w + D \cdot \log P_w \quad (1)$$

We also analyzed the allometric relation between log-transformed shoot and root weights. Shoot weight (S_w) was set as a dependent variable, root weight (R_w) was set as a covariate, and density and N-treatment were set as factors. Here, we applied the following model

$$\log S_w = a + b \cdot \log R_w + N + D + N \cdot D + N \cdot \log R_w + D \cdot \log R_w \quad (2)$$

Three way interactions, which did not have significant effects, were excluded since they would lead to an undesired loss of degrees of freedom given the number of data. Significant effects of the factors N and D are assumed to reveal differences between the intercepts of the relationships across fertilization treatments and plant densities, respectively. Significant interactions between N or D and the covariates P_w or R_w are supposed to reveal significant differences among the slopes of the allometric relation across different levels of nutrient supply or intra-specific competition, respectively (Shipley and Meziane 2002). Pair-wise differences between regression coefficients were tested using variances and covariances of the estimates.

Results

Individual plant weights

At all N-supply rates, individual plant weights declined strongly with increasing plant density, indicating the great stress that the plants experienced due to intra-specific competition (Fig. 1). Plant density and N-treatment each had significant effects ($P < 0.001$). The interaction between these two factors was not significant ($P = 0.11$), but distinction between the linear, quadratic, and cubic terms of these effects shows that the interaction between the linear effects was highly significant ($P < 0.001$),

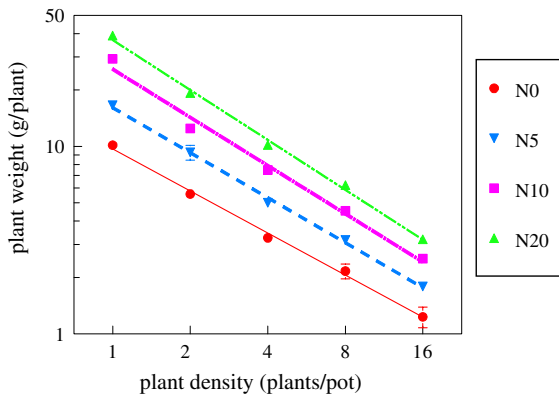


Fig. 1 Effects of increasing plant densities on individual plant weights at four levels of nutrient supply (dots, N0; reverse triangles, N5; squares, N10; triangles, N20). Bars indicate standard errors of the mean. Both the vertical and the horizontal axis have a logarithmic scale

while the other interactions were not. The slope of the effects of plant density on plant weight became steeper with increasing N-supply (-0.52 , -0.55 , -0.59 , -0.61 in the N0, N5, N10, and N20 treatments, respectively). The slope for treatment N20 was significantly steeper than for the treatments N0 ($P = 0.001$) and N5 ($P = 0.024$) and that for treatment N10 differed from that for treatment N0 ($P = 0.014$).

Shoot to root ratios

Shoot to root ratios declined with increasing plant density ($P < 0.001$) and decreasing N-supply ($P < 0.001$; Fig. 2). The interaction between plant density and N-treatment ($P = 0.023$) shows that the effects of plant density on shoot to root ratios varied across different N-levels. Distinction between linear and higher order terms revealed a highly significant interaction between the linear terms ($P < 0.001$), while the interactions which included higher order terms were not significant. The slope for the N20 treatment was less steep than for the N0 ($P < 0.001$) and N5 treatment ($P = 0.004$). The difference between the slopes in the N10 and the N0 treatment was marginally significant ($P = 0.059$).

Including individual plant weight as a covariate showed that within each nutrient treatment this variable explained a large part of the variation in shoot to root ratio (Fig. 3). Shoot to root ratios declined with decreasing plant weight. Since there

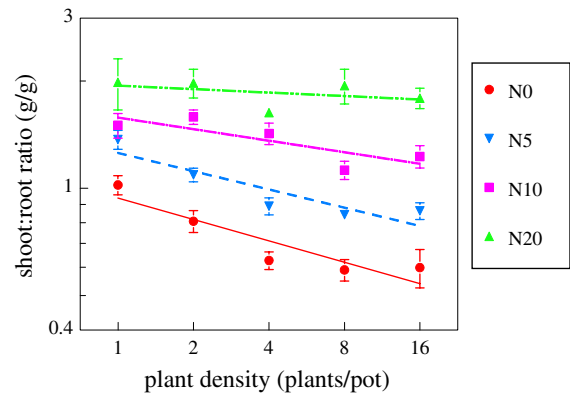


Fig. 2 Effects of increasing plant densities on shoot to root ratios at four levels of nutrient supply (dots, N0; reverse triangles, N5; squares, N10; triangles, N20). Bars indicate standard errors of the mean. Both the vertical and the horizontal axis have a logarithmic scale

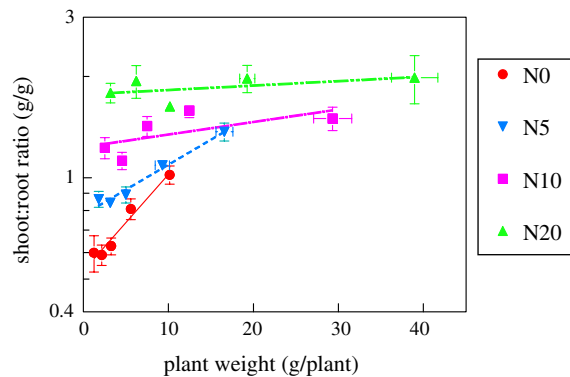


Fig. 3 The relation between shoot to root ratios and individual plant weight at four levels of nutrient supply (dots, N0; reverse triangles, N5; squares, N10; triangles, N20). Vertical and horizontal bars indicate standard errors of the means. The vertical axis has a logarithmic scale

was a highly significant interaction between the effects of N-supply and individual plant weight ($P < 0.001$), we compared the slopes of the regression lines (Fig. 3). These slopes decreased with increasing N supply. In the N0, N5, N10, and N20 treatments the slopes were 0.25, 0.21, 0.11, and 0.01, respectively. The slope for the N0 treatment differed significantly from the slope in the N10 and N20 treatments ($P = 0.041$ and $P = 0.001$, respectively) and the slope of the N5 treatment differed from that in the N20 treatment ($P = 0.003$). The interaction between plant weight and plant density was not significant.

Allometric relation between shoot and root mass

An analysis of the relationships between shoot and root weights produced similar results (Table 1). The interaction between the effects of root weight and N-treatments was highly significant, while the interaction with plant density was not. The relationships between shoot and root mass had declining slopes with increasing N-supply: 1.24, 1.21, 1.09, and 0.96 in the N0, N5, N10, and N20 treatments, respectively. The slope for the N20 treatment was significantly smaller than that for the N0 and N5 treatments ($P = 0.003$ and $P = 0.001$, respectively). In the N0, N5, and N10 treatments the slopes were significantly ($P < 0.05$) greater than 1, meaning that the shoot to root ratios declined with decreasing plant size, while in the N20 treatment the slope did not deviate from unity. The single factors nutrient treatment and plant density had significant effects indicating different intercepts both among nutrient treatments and plant densities.

Discussion

We found that at the lower nutrient supplies the proportional allocation to root mass increased with increasing competitive stress, while in the higher nutrient treatment the relationship between competitive stress and shoot to root ratio was neutral. The relation observed in the nutrient-poor treatments has earlier been found in field studies (Cahill 2003; Litton et al. 2003). These authors attributed the effects of competitive stress on the shoot to root ratio entirely to

the ontogenetic relation between shoot and root mass (sensu Gedroc et al. 1996) rather than to adaptive phenotypic plasticity. In most experiments it is not possible to distinguish between the effects of plant size and the effects of competitive stress, since these two variables are strongly correlated. However, in our experiment, in the high N-supply treatment the variation in plant sizes was not only much greater, but also overlapped the variation in the three other treatments (cf. Fig. 3). Nevertheless, in the higher N treatment there was no relationship between individual plant mass and shoot to root ratio, while there was a strong relationship in the low N supply treatments. Also the allometric analysis of the relations between shoot mass and root mass (cf. Table 1) supports the conclusion that at the different nutrient supply levels there were different effects of competitive stress on the allocation to shoots and roots. The relationships between root and shoot mass were different both across the four nutrient treatments (intercepts and slopes) and five levels of competitive stress (intercepts; cf. Shipley and Meziane 2002). Apparently, the negative relation between plant density and shoot to root ratio in this experiment cannot be attributed to ontogenetic drift. However, the observed patterns can be explained very well by adaptive plasticity in accordance with the functional equilibrium hypothesis (Brouwer 1962a, b).

The intensity of competition was measured as the slope of the decline of plant weight with increasing density. There were small, but significant differences between these slopes among fertilization levels. At the highest nutrient supply level the slope of the relationship between plant density and plant weight was 17% steeper than in the treatment where no nutrients were applied. The higher intensity of competition at the higher nutrient supplies was probably due to the more rapid growth of the seedlings, so that the plants started sooner to interfere with each other. Although intra-specific competition in the high N treatment appeared to be even more intense than at the lower N-supplies, there was no response of allocation pattern to increased plant densities. The aboveground biomass that was present at the higher N supplies seemed to be sufficient for light competition to develop. At the higher plant densities, the harvested aboveground biomass was 236, 424, 706, and 1,044 g m⁻² in the inner pots with the N0, N5, N10, and N20 treatments, respectively,

Table 1 Effects of plant density (D), nutrient supply (N), and root mass (R_w) on shoot mass

	df	F	P
Intercept	1	82.73	<0.001
Density	4	20.24	<0.001
Nutrients	3	24.72	<0.001
Density * nutrients	12	1.59	0.114
Log(root weight)	1	1.59	0.114
Density * log(root weight)	4	0.49	0.773
Nutrients * log(root weight)	3	4.28	0.008

A General Linear Model was applied with plant density and nutrient supply as fixed factors and root mass as covariate (cf. Eq. 2). Blocks did not have significant effects

so that the aboveground biomass in the highest N-supply treatment was clearly well beyond the level (400–500 g/m²) at which Grime (1979, 2001) predicted light competition would become the dominant process.

Twolan-Strutt and Keddy (1996) measured the effects of full and belowground competition in wetlands varying in standing crop and soil fertility. The belowground competition intensity did not differ between sites with low and high standing crops, but the estimated aboveground competition intensity was clearly higher at the high productive site. Peltzer et al. (1998) found no change in root competition intensity along a soil fertility gradient, but other studies found a decrease in root competition after fertilization (Cahill 1999). Many of these field studies suffer from great methodological difficulties. Root competition is often excluded by the insertion of tubes in the soil that not only exclude roots, but also change the volume of soil available for the target plants. In the treatments without tubes it is often extremely difficult to harvest all roots, since they are intermingled with the roots from the surrounding vegetation. In other studies, the intensity of aboveground competition is estimated on the basis of the difference between the effects of full and belowground competition, ignoring possible interactions.

In our experiment these pitfalls were avoided, but it should be emphasized that we measured the response of the whole population of plants in the pot. It is possible that there is correlated variation in plant size and allocation pattern among plant individuals within the pot with smaller plants showing a stronger response (cf. Fig. 3), but larger individuals contributing more to the response that we measured. Since large plants had probably experienced less competitive stress than smaller plants, we might have underestimated the change in allocation in response to increased competition. So, taking this possible pitfall into account, we can still only conclude that there are strong effects of competitive stress on the allocation of biomass to below- and aboveground organs.

The relationships between shoot to root ratios and plant weights show that at high levels of competitive stress these ratios vary markedly among the four N-supply levels (Fig. 3). At the low levels of competitive stress this variation is much smaller. It even appears that the four lines converge to a constant shoot to root ratio at lower plant densities, i.e., under

conditions where both nitrogen and light limitation are low.

We did not find a complete shift from a negative to a positive effect of plant density on the shoot to root ratio with increasing nutrient supply as we expected, but rather a shift from a negative to a neutral relationship. We suggest that there are two possible hypotheses that explain this pattern. The first explanation is that belowground competition is relevant both on nutrient-poor and nutrient-rich substrates, while the relevance of aboveground competition increases with increasing aboveground biomass. In the low N treatment only belowground competition plays its role, while in the high N treatment the effects of above- and belowground competition would more or less balance each other. This hypothesis would be in agreement with the finding of Twolan-Strutt and Keddy (1996), that total and aboveground competition were greater in wetlands with higher standing crop, while belowground competition intensity did not differ between sites. The second hypothesis is that the effects of nutrient deprivation on root–shoot allocation are far more important than the effects of light competition, while we would expect such nutrient depletion effects to be stronger on poor substrates. Casper et al. (1998) did not find any effect of increased plant densities on shoot to root ratios, when they excluded root competition, while the plants grown at high densities exhibited typical aboveground responses to neighbors, such as higher ratios of stem to leaf biomass and greater specific leaf areas. Poorter and Nagel (2000) attempted to evaluate the adaptive value of changes in shoot to root ratio in response to changes in light and nutrient supply using a growth analysis, taking into account the effects of various parameters on the relative growth rate. They concluded that changes in allocation to roots had strong adaptive effects on plant growth, while the consequences of changes in allocation to aboveground biomass were relatively small as compared to the effects of changes in other parameters such as specific leaf area and rate of photosynthesis per unit leaf area. It is important that future experiments attempt to test these two alternative hypotheses so that we can conclude at last what plant features contribute to the competitive ability of plant individuals on fertile and less fertile substrates.

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