Belowground competition increases root allocation in agreement with game-theoretical predictions, but only when plants simultaneously compete aboveground.

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Abstract

Evolutionary game theory posits that plants competing with neighbours preferentially allocate resources towards resource-foraging structures, which reduces the marginal gain per investment unit and the ability of plants to produce seeds. This phenomenon is known as the tragedy of the commons (TOC), and undesirable in grain crops. Specifically, changes in light quality due to neighbour plants often induce costly responses like petiole or stem elongation, increasing individual competitiveness at the expense of stand-level yield. Similarly, it has been postulated that belowground competition can induce increased root production in the vicinity of neighbours, which can also reduce seed yield.

There has been a long-standing debate about the interpretation of resource allocation patterns observed in plant-plant competition experiments in crops. Experimental setups using pot systems and artificial dividers to manipulate competitive interactions have been questioned because of the difficulty of simultaneously controlling pot volume, nutrient amount, and nutrient concentration. Moreover, observations of root growth under competition have been inconsistent, ranging from increased root production to spatial root system segregation. Here, using soybean as a model system, we conducted a competition experiment to disentangle above- and belowground drivers of biomass allocation patterns. Specifically, we used above- and belowground physical dividers and varied inter-plant distances (between 3 and 24 cm) to avoid a confounding of divider treatments with plant-available soil volume. Plants closer together had higher root-to-shoot ratios, indicating that an increased fraction of assimilated was diverted to root growth, but this only happened when they competed both above- and belowground (no dividers). Aboveground competition triggered shade avoidance responses, resulting in slender plant habit and reduced total root and shoot biomass. Overall, our results provide evidence for a preferential allocation to root biomass in soybean plants when exposed simultaneously to above and belowground competitions. As effects of belowground competition became only evident when plants were allowed to also compete aboveground, we interpret the competition cues to be processed hierarchically, with aboveground signals having precedence over belowground signals. More generally, our findings show that varying the distance

between competing plants allows to avoid the confounding of divider treatments with plant-available soil volume. A reduced total biomass production of plants competing above- and belowground may be interpreted as a consequence of lowered marginal gains arising from allocation patterns that optimize individual but not group performance.

Introduction

Competition among plant individuals is a major driver of evolution and an important determinant of the functioning of ecosystems or communities (Aschehoug et al., 2016; Harper, 1977). Despite the interest competition elicits in population ecological and evolutionary studies, competition has received relatively less attention in agronomy and breeding. At the same time, it has long been postulated and experimentally shown that population-level productivity in crop plants can be increased by minimizing allocation to competitive structures (Denison, 2017; Donald, 1968; Jennings & Herrera, 1968; Weiner, 2019). This notion is in line with evolutionary game theory that posits that natural or artificial selection in competitive environments often favours resource acquisition strategies that benefit the individual but are detrimental at the level of the population (Anten & Vermeulen, 2016; Gersani et al., 2001; Zhang et al., 1999). In other words, the strategy that would favor population-level productivity is not an evolutionary stable strategy (ESS), and a group of individuals using it can be invaded by individuals optimizing their own resource acquisition at the expense of the group (Anten & Vermeulen, 2016).

In crops, there exist some well-described traits which enhance individual competitiveness to the detriment of population-level performance, particularly when plants “overinvest” into them. Minimizing this effect by breeding can increase stand yield. For example, varieties with reduced plant height and increased compactness contributed to substantially increased yield in crops such as maize, rice and wheat (Duvick et al., 2003; Hedden, 2003; Jennings & Herrera, 1968). Other traits may be equally relevant for crop improvement but are more difficult to target. A well-known example is “shade avoidance” (SA), whereby sensing neighbouring plants through changes in light quality can trigger responses which increase individual competitive ability for light but reduce overall yield

(Weiner et al., 2010). In soybean (*Glycine max*), shade often increases petiole and internode elongation but reduces branching (Lyu et al., 2023), and ultimately leads to higher disease susceptibility and lower yield per plant (Green-Tracewicz et al., 2011; Lyu et al., 2023). From an agricultural perspective, shade avoidance is typically undesired within a field because it reallocates resources to shade avoidance responses that would otherwise be available for seed production (Pantazopoulou et al., 2021; Weiner et al., 2010). At the same time, it is evident that some aspects of light sensing and the resulting responses can also have beneficial effects on the organization of the canopy and light interception in crop stands (López Pereira et al., 2017; Zhou et al., 2024). Therefore, breeding progress by specifically targeting shade avoidance responses may be hampered by the existence of trade-offs.

Belowground competitive responses and their consequences for population-level functioning are comparably less well understood. Over two decades ago, two game theoretical modelling studies showed that the adaptation of individual plants to root competition can lead to a reallocation of resources towards increased root production, at the expense of overall group productivity (Gersani et al., 2001; Zhang et al., 1999). In these models, plants under competition invested more into foraging organs than they would if grown alone, i.e. the evolutionary stable strategy exhibited lower marginal gains from investments into foraging than the cooperative strategy that would optimize stand-level productivity. In experiments, Gersani et al. found that soybean plants that competed belowground increased allocation to roots and had a lower seed yield than plants that were separated belowground by a physical soil barrier. This seemingly confirmed game-theoretical considerations, and the notion of a root-competition induced tragedy if the commons. However, the interpretation of these results was later criticized: although the two owners did have the same overall soil nutrients available as the sharers, each individual had only access to half the soil volume, which itself could be regarded a resource (Hess & De Kroon, 2007; McNickle, 2020; Poorter & Sack, 2012; Semchenko et al., 2007). Several studies have since tried to correct for this bias (Chen et al., 2015; Maina et al., 2002), but controlling all three critical variables pot volume, total amount of nutrients per plant and soil nutrient

concentration simultaneously has proven to be challenging (see McNickle, 2020 for an in depth discussion). More recently, one solution to this problem has been to use nutrient-permeable but root-impermeable mesh dividers between competing plants, compared to using completely impermeable dividers for non-competing plants (Chen et al., 2021; Zhu et al., 2019). However, here the assumption is that root responses are caused by cues that pass the mesh divider but not the solid divider (Cabal, 2022; Chen et al., 2021; McNickle, 2020; Zhu et al., 2019). Overall, these studies indicate that the presence of neighbour plants can stimulate root growth in the zone in which plants compete. However, the opposite also has been observed: plants sometimes avoid root competition by producing spatially segregated root systems (Lepik et al., 2021; Schmid et al., 2015). Indeed, a recent meta-analysis showed that root responses in pea are inconsistent throughout published studies (Mobley et al., 2022).

Recently, Cabal et al., (2020) suggested that these apparently contradictory neighbour-effects on root growth occur because they are distance-dependent. They proposed that the costs of growing and maintaining roots increases with distance from the stem. Under these assumptions, a game-theoretical model predicted that plants respond to competition by producing more roots close to the plant's stem where the costs of maintaining roots are low, but producing less roots further away where costs are high. Therefore, the phenomenon emerging from such a model, termed "exploitative segregation of plant roots", is one where the very same resource foraging strategy leads to divergent neighbour responses depending on inter-plant distance (Cabal, 2022; Cabal et al., 2020).

Here, we investigated the influence of competition on biomass allocation patterns in soybean. We measured allocation to roots and shoots at flowering. This has two advantages as compared to quantifying biomass allocation at maturity. First, flowering is a growth stage when plants are highly responsive to competition (Sun et al., 2021). Effects on biomass allocation might thus be most apparent at this point and closely reflect the investment strategies that plants pursue under different competition treatments to maximize individual gains. Second, measuring root biomass after senescence can lead to confounding effects due to nutrient remobilization, whereas quantifying at flowering provides a more accurate assessment of biomass allocation during active growth (Liu et al.,

2019; Maillard et al., 2015). We isolated contributions from shoot- and root competition and their distance-dependency. For this, we conducted an experiment that combined the traditionally-used separation treatments (but both separately above and belowground) with a range of inter-plant distances (Fig. 1). With this design, we can separate effects of available soil volume from effects of interactions with the neighbour, because the competitive interaction decreases with distance, while the total soil volume remains constant. Hence, we focus on the statistical interaction of the separation treatment with the distance to the neighbour. For both the belowground and the aboveground treatments, we expect that neighbour-induced shifts in allocation only occur when plants are not separated and when the neighbour is close (c.f. Cabal, 2022; Cabal et al., 2020). Specifically, (1) when allowing belowground competition only, we expect that the relative allocation to roots will increase with increasing competition, i.e. root-to-shoot ratios will increase (Fig. 1a); (2) when allowing aboveground competition only, we expect that the relative allocation to shoots will increase with increasing competition, i.e. root-to-shoot ratios will decrease (Fig. 1b); (3). In the absence of any divider, plants will compete both above- and belowground, and these two components of competition will likely not be independent. We therefore expect that effects of belowground competition will differ depending on whether plants also compete aboveground or not (Fig. 1c).

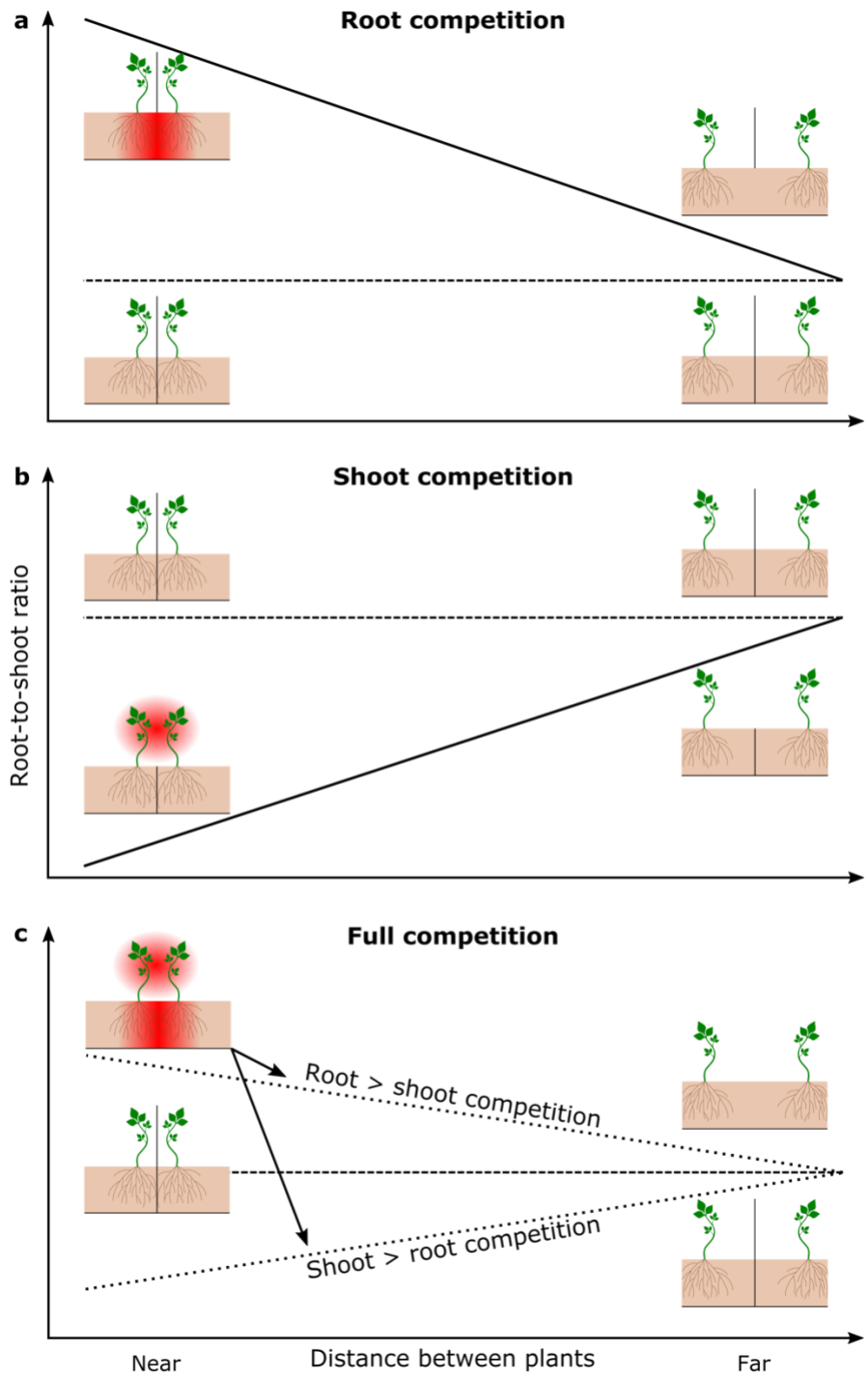

Figure 1: Expected outcome for plant biomass allocation depending on competition treatment and inter-plant distance. (a) Plants competing belowground and close together are expected to relatively allocate more towards their roots and to have a higher root-to-shoot ratio than non-competing plants. When the two plants are distant, both treatments are expected to show the same root-to-shoot ratio. (b) Plants competing aboveground and close together are expected to relatively allocate more towards their shoots and to have a lower root-to-shoot ratio than non-competing plants. When the two plants are distant, both treatments are expected to show the same root-to-shoot ratio. (c) Plants competing both below- and aboveground are expected to shift their root-to-shoot ratio according to

the strength of the competition in the respective domain. If root competition is stronger than shoot competition, root-to-shoot ratio is expected to increase when the plants are closer together. If shoot competition is stronger than root competition, root-to-shoot ratio is expected to decrease when the plants are closer together. If competition above- and belowground is equally strong, the root-to-shoot ratio is not expected to deviate from the no-competition scenario. When the two plants are distant, both treatments are expected to show the same root-to-shoot ratio.

Material and Methods

To study competition among soybean plants, we conducted an outdoor pot experiment in Wädenswil, Switzerland (47.222°N, 8.669°E, 509 m a.s.l.) in summer 2023. All pots contained two plants of the same genotype that were either separated aboveground by an 80x20 cm white polystyrene sheet to prevent light competition, separated belowground by a plastic sheet to provide the plants with isolated soil compartments, separated above- and belowground, or neither separated above- nor belowground. These divider combinations were replicated with inter-plant distance ranging from 3 to 24 cm in 3 cm steps (Fig. 1). We used four soybean genotypes obtained from the USDA soybean germplasm collection (Weber - PI 548524, Natsu Kurakake – PI 417187, Kanegawawase - PI 229330, and Kanagawa Wase - PI 506832), which form a gradient of competitive strategies ranging from "cooperative" (Weber) to "competitive" (Natsu Kurakake). These strategies were determined in a separate experiment (unpublished) using the methodology described in Wuest et al. (2022). Each separation treatment (n = 4) x distance (n = 8) x genotype (n = 4) combination was replicated three times, resulting in a total of 384 pots. Pots were protected from hail by a net and irrigated ad libitum (Supporting Fig. 1). Plants were germinated in propagator trays in the greenhouse for 14 days, and seedlings then transplanted to 7.5 l rectangular pots filled with lawn soil (Ökohum Art. 2633200) and moved outside.

Plant height was measured once a week, for a total of six measurements. Relative chlorophyll content was quantified one day before the end of the experiment with a MultispeQ V 2.0 device (Kuhlgert et al., 2016) by comparing the absorption of red light (absorbed by chlorophyll) to infrared

light (reference) . The plants were grown for 55 days until the majority of them had started to flower, then shoots were clipped at ground level, and roots washed. All biomass samples were dried at 60°C for 48 hours and weighed. Given that the two plants in each pot were in symmetric positions (i.e., the same distance from the opposite edges of the pots – see Fig. 1), and that not all roots could unequivocally be assigned to a particular plant individual, we analysed all data at the pot level.

Total plant biomass did not correlate significantly with root-to-shoot ratio ($R^2 = 0.001$, $p > 0.5$), and we therefore analysed root-to-shoot ratio without correcting for potential allometric effects. From the plant height measurements, we estimated linear growth rate by fitting the model $H = H_0 + r \cdot t$ (H: height of the plants, t: days since sowing of the height measurement) for each plant and extracting the linear growth rate r, which we averaged at the pot level. As we harvested the plants at flowering, height growth had not yet slowed, and a linear model fitted height better than a logistic one. Moreover, we calculated the shoot-biomass-to-height ratio as proxy of how much biomass were used per unit height growth.

We analysed shoot biomass, root biomass, total biomass, root-to-shoot ratio, height growth rate, relative chlorophyll content and shoot-biomass-to-height ratio in R with the function aov (R 4.3.1; R Core Team, 2021). In the model, we first corrected for spatial effects in the hail protection tunnels by fitting row and column terms (the pots were arranged in a rectangular grid pattern), and then added a full-factorial combination of genotype, distance between the pair of plants, aboveground divider treatment and belowground divider treatment. We were mostly interested in the dependence of the effect of the competition treatments on distance (two-way interaction of treatment with distance) and in the dependence of this relationship on genotype (three-way interactions of competition treatments, distance and genotype).

Results

Genotype had a statistically significant effect on all our response metrics (P<0.001 for main effect of genotype, Table 1, Fig. 2a). None of the other effects we tested depended on genotype, i.e. there was no statistical interaction of genotype with any of the other model terms.

The focus of our analysis was on effects of distance interactions, since distance moderates competition when dividers are absent. We found a significant three-way interaction between aboveground separation, belowground separation and inter-plant distance for final plant height, linear height growth rate, relative chlorophyll content, shoot biomass, and shoot-to-root ratio (p-values < 0.05; Table 1). For shoot-biomass-to-height ratio, root biomass and total plant biomass, there was a significant two-way interaction between aboveground separation and inter-plant distance.

Table 1: F statistic and p-value for linear models. Y was modelled in dependence of G (genotype), D (the distance between the pair of plants), C_A (the aboveground treatment) and C_B (the belowground treatment) and including all two- and three-way interactions between G, D, C_A and C_B.

Response	**Explanatory variable[1]**	**F (df_n, df_d)**	**p-value**
Total biomass	G	161.03 (3, 347)	**< 0.001 ***
	D	>0.001 (1, 347)	0.99
	D x C_A	6.845 (1, 347)	**0.009 ***
	D x C_B	0.02 (1, 347)	0.9
	G x D x C_A	1.784 (3, 347)	0.15
	G x D x C_B	0.122 (3, 347)	0.95
	D x C_A x C_B	2.62 (1, 347)	0.106
Shoot biomass	G	132.46 (3, 347)	**< 0.001 ***
	D	0.14 (1, 347)	0.71
	D x C_A	5.71 (1, 347)	**0.017 ***
	D x C_B	0.15 (1, 347)	0.7
	G x D x C_A	1.04 (3, 347)	0.37
	G x D x C_B	0.2 (3, 347)	0.9
	D x C_A x C_B	5.4 (1, 347)	**0.021 ***
Root biomass	G	187.11 (3, 347)	**< 0.001 ***
	D	2.66 (1, 347)	0.6
	D x C_A	5.49 (1, 347)	**0.02 ***
	D x C_B	0.69 (1, 347)	0.79
	G x D x C_A	2.2 (3, 347)	0.088
	G x D x C_B	0.05 (3, 347)	0.99
	D x C_A x C_B	0.09 (1, 347)	0.76

Root-to-shoot ratio	G	164.88 (3, 347)	**< 0.001 ***
	D	0.793 (1, 347)	0.37
	D x C_A	0.006 (1, 347)	0.94
	D x C_B	0.58 (1, 347)	0.45
	G x D x C_A	0.786 (3, 347)	0.5
	G x D x C_B	0.172 (3, 347)	0.92
	D x C_A x C_B	4.163 (1, 347)	**0.042 ***
Linear height growth rate	G	70.32 (3, 347)	**< 0.001 ***
	D	>0.001 (1, 347)	0.93
	D x C_A	2.692 (1, 347)	0.1
	D x C_B	0.912 (1, 347)	0.34
	G x D x C_A	0.32 (3, 347)	0.811
	G x D x C_B	0.323 (3, 347)	0.81
	D x C_A x C_B	6.993 (1, 347)	**0.009 ***
Final height	G	136.85 (3, 347)	**< 0.001 ***
	D	>0.001 (1, 347)	0.98
	D x C_A	2.24 (1, 347)	0.135
	D x C_B	0.611 (1, 347)	0.435
	G x D x C_A	0.113 (3, 347)	0.952
	G x D x C_B	0.3 (3, 347)	0.825
	D x C_A x C_B	4.774 (1, 347)	**0.03 ***
Shoot-biomass-to-height ratio	G	67.55 (3, 347)	**< 0.001 ***
	D	0.11 (1, 347)	0.74
	D x C_A	4.031 (1, 347)	**0.045 ***
	D x C_B	0.01 (1, 347)	0.908
	G x D x C_A	1.101 (3, 347)	0.349
	G x D x C_B	0.992 (3, 347)	0.397
	D x C_A x C_B	2.176 (1, 347)	0.141
Relative chlorophyll content	G	6.545 (3, 347)	**< 0.001 ***
	D	2.98 (1, 347)	0.085
	D x C_A	1.761 (1, 347)	0.185
	D x C_B	0.244 (1, 347)	0.621
	G x D x C_A	1.282 (3, 347)	0.28
	G x D x C_B	0.696 (3, 347)	0.555
	D x C_A x C_B	4.06 (1, 347)	**0.045 ***

[1]: To avoid confounding with pot volume, competition treatments can faithfully be interpreted only in interaction with inter-plant distance.

The shoot-biomass-to-height ratio, which is a proxy of the shade avoidance response, was lower in plants that competed aboveground, i.e. that were not separated aboveground and grew closely together ($F_{1,347} = 4.03$, $p < 0.05$; Fig. 2b). Thus, plants competing more strongly aboveground had a slenderer growth habit, in agreement with expectations.

We next assessed the extent to which plants competing with their neighbours (i.e. no dividers and close distance) increased relative allocation to roots. Indeed, we observed a consistent increase in the root-to-shoot ratio of soybean plants that grew closer together, but only when there was neither above- nor belowground competition, i.e. when there were no dividers ($F_{1,347} = 4.16$, $p < 0.05$; Fig. 3).

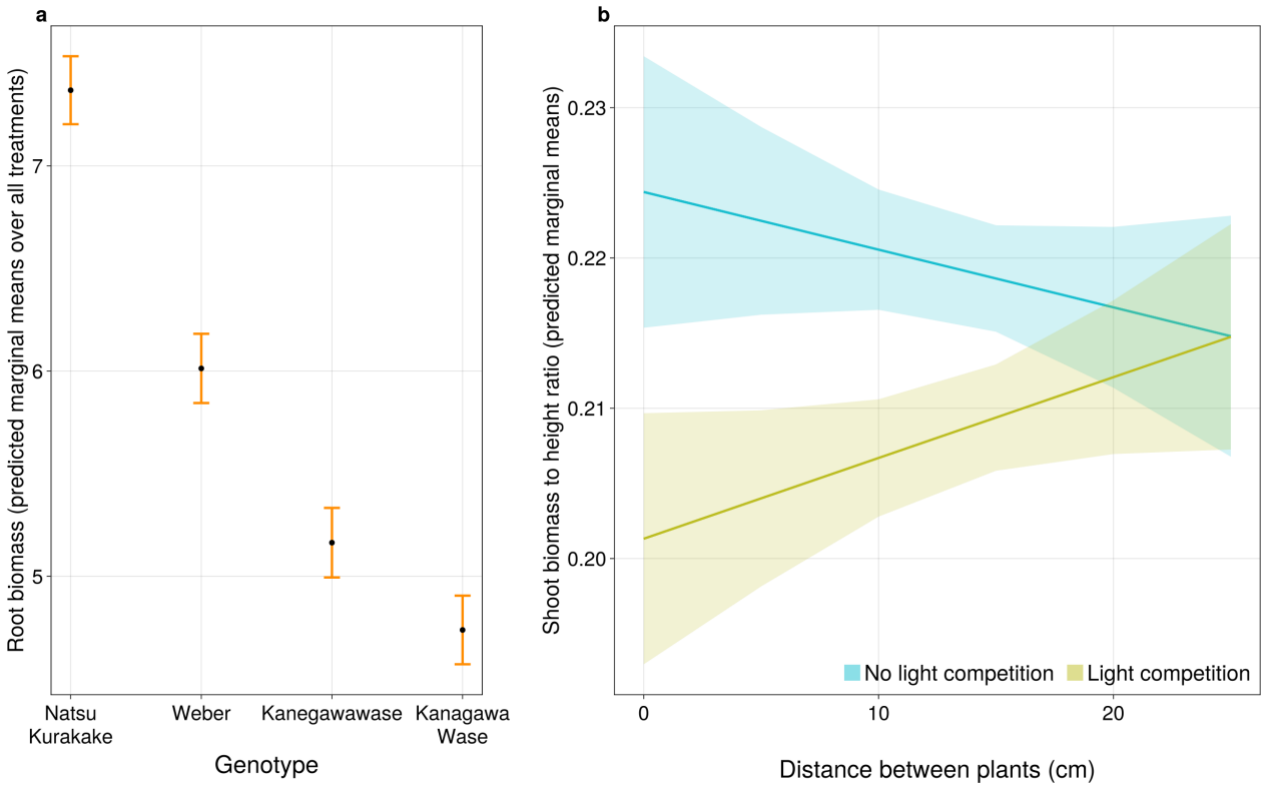

Figure 2: (a) The four genotypes strongly differed in all measured traits, as shown here for root biomass. (b) Plants which were competing aboveground and growing closer together invested less biomass per cm of height growth, in accordance with expectations based on known shade avoidance responses.

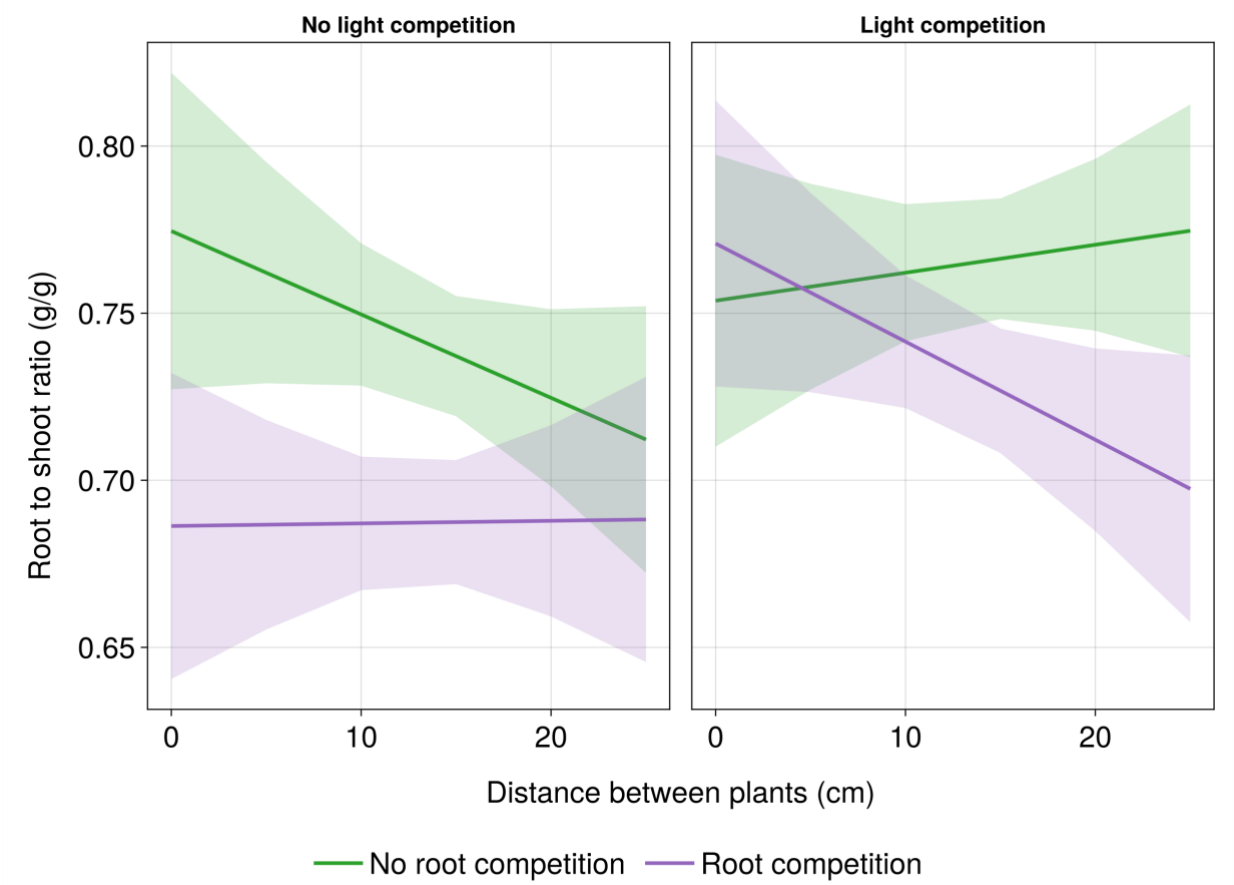

Figure 3: Predicted marginal means for root-to-shoot ratio. When facing no aboveground competition, the plants didn't increase their relative root production when exposed to belowground competition (left). When facing aboveground competition, plants increased their relative root production when simultaneously exposed to belowground competition and close together (right).

Shifts in root-to-shoot ratio may be caused by changes in root biomass, in shoot biomass, or in both. We found that plants competing aboveground had lower root biomass ($F_{1,347} = 5.49$, $p < 0.05$, Fig. 4a). Shoot biomass was reduced when plants competed both above- and belowground ($F_{1,347} = 5.4$, $p < 0.05$, Fig. 4b). On the other hand, plants competing belowground only had a higher shoot biomass (purple lines in Fig. 4b). Height growth and relative chlorophyll contents responded similarly ($F_{1,347} = 6.7$, $p < 0.01$ and $F_{1,347} = 4.06$, $p < 0.05$, respectively, Supporting Fig. 2): plants grew faster and had higher relative chlorophyll content when competing belowground but not aboveground. This was also evident in the final height of the plants, where plants competing above- and belowground were smaller than plants competing belowground only ($F_{1,347} = 4.77$, $p < 0.05$; Fig. 4c).

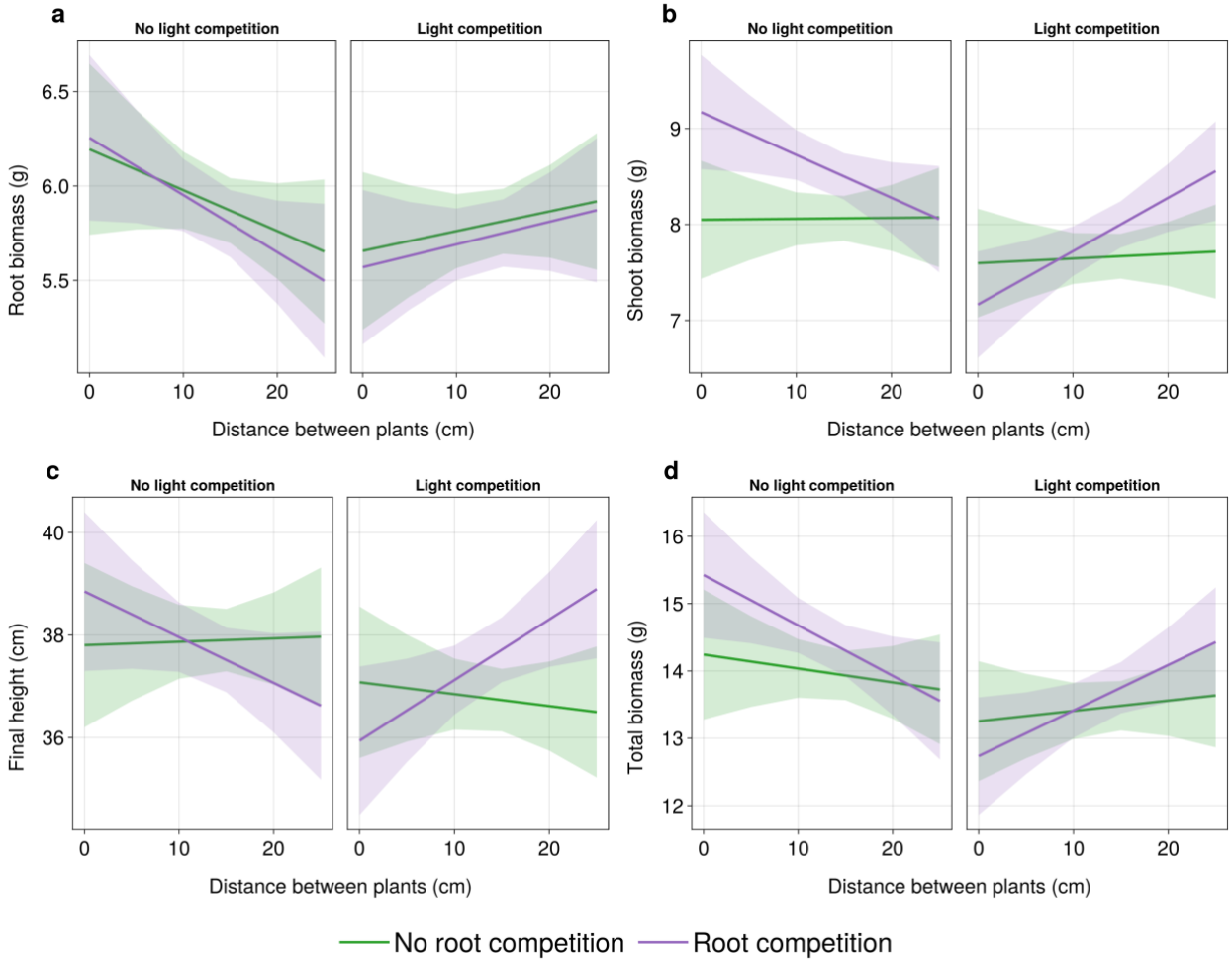

Figure 4: Predicted marginal means for (a) root biomass, (b) shoot biomass, (c) final plant height and (d) total biomass.

Finally, plants competing aboveground produced less total biomass ($F_{1,347} = 6.85$, $p < 0.01$, Fig. 4d), indicating a strong cost associated with aboveground competition.

Discussion

Aboveground and belowground signals are processed hierarchically

Competition between two plants ranges from fully symmetric to strongly asymmetric: depending on the extent to which larger plants acquire amounts of resources that are proportionately or disproportionately large relative to their size (Weiner, 1990). Light competition is usually asymmetric, because the taller plant can pre-empt light, as light is a largely directional resource.

Nutrient competition is more symmetric with nutrient acquisition largely proportional to the size of the root system (Schwinning & Weiner, 1998). From our study, we think that plants adjust their responses to different competition cues hierarchically. In this scenario aboveground signals would have precedence over belowground signals. Indeed, the interaction between aboveground competition and neighbour distance was significant for multiple measurements. However, the interaction between belowground competition and neighbour distance was never significant in absence of an interaction with aboveground competition. An integration of above- and belowground responses to competition on root growth could occur through various processes. For example, plants may "sense" the strength of a neighbouring competitor aboveground and adjust their belowground foraging strategy (Gottlieb & Gruntman, 2022). Alternatively, as predicted by game theoretical models for belowground interactions (Cabal et al., 2020), aboveground interactions with neighbours may also increase the costs of root production and maintenance. Certainly, extending the current game theoretical models to incorporate interactions in both above- and belowground domains would be revealing.

Concomitant above- and belowground competition leads to preferential biomass allocation to roots

In our experiment, we found increased relative allocation to roots and decreased total biomass when plants were closer to neighbours, but only when plants were simultaneously competing aboveground and belowground. While for the preferential biomass allocation to the root system both aboveground and belowground competition was necessary, the aboveground competition was sufficient to lead to a reduction of total biomass. Interestingly, aboveground competition also led to a reduction of final root biomass, not influenced by belowground competition. This was unexpected, as previous results showed final root biomass to increase under full competition, while we observed only an increased relative allocation to roots. We assume that at the beginning of our experiment, the plants competing both aboveground and belowground did in fact produce overall more roots, but that this led to a reduction in shoot production and a slower growth rate. Over time, this led to the observed

situation where competing plants show an increased relative allocation to roots without producing overall more root biomass.

Our results are in line with Gersani et al. (2001), who manipulated belowground competitive interactions using physical dividers and found evidence for the occurrence of a "tragedy of the commons" (TOC), i.e. a situation in which individual plants gain at the expense of the plant group (Hardin, 1968). It is interesting to note that Gersani et al. used a setup where competing plants were grown relatively close to each other, without aboveground dividers and in a greenhouse over the winter period requiring supporting artificial light – conditions that typically induce a shade avoidance response. This growth condition was similar to our close-proximity and no-aboveground-separator treatment. In our experiment, we decided to quantify plant biomass at flowering instead of final yield for two reasons. First, this allowed us to measure biomass allocation at a moment of high competition between the plants. Second, this ensured that no biomass was remobilized due to senescence. Nevertheless, our observations suggest that beyond neighbour distance, aboveground competition may also be important for the expression of a TOC. Indeed, it is plausible to assume that our experiment would have led to a tragedy of the commons if we quantified final yield. Additionally, this could indicate that discrepancies among past studies arose due to unanticipated yet important differences in experimental setups (i.e. the presence or absence of light competition due to light quality and quantity as well as neighbour-distance), instead of representing statistical sampling errors (Mobley et al., 2022)

Shade avoidance responses under aboveground competition lead to a stronger decrease in shoot than in root biomass

Responses to increased aboveground competition were consistent with the typical shade avoidance (SA) syndrome described previously (Ballaré & Pierik, 2017; Golan et al., 2023; Green-Tracewicz et al., 2011; Keuskamp et al., 2010; Lyu et al., 2023; Pantazopoulou et al., 2021; Wille et al., 2017), i.e. more slender plants and lower root production. At the same time, plants were smaller when close

together and competing aboveground. Plant height typically also increases under shade avoidance (Pierik & De Wit, 2014). Thus, this was likely a consequence of the negative effects of shade avoidance on overall plant performance expressed in terms of biomass. Indeed, SA exerted a strong negative effect on overall plant performance. We argue that this was not caused by a limitation of light per se (Supporting Fig. 1) but rather by the sensing of neighbours through light quality changes. Even though SA behaviour can increase the fitness of individuals at high densities, our results and those of others suggest that the light-foraging strategy invoked by the presence of neighbours is detrimental to the performance of plants overall (Pantazopoulou et al., 2021; Schmitt et al., 1995; Wille et al., 2017).

Neighbour response should be considered as breeding target in future

Our approach presents a novel and simple way to control for the confounding factors which have long dominated the debate about plant pair competition experiments. We strongly suggest to explicitly account for neighbour distance in future works investigating the effect of individual foraging strategies on plant group performance. While it was anticipated long ago, most famously by Donald (1968) that reducing competitive traits of crop plants may harbour much potential to increase yields (see also Duvick et al., 2003; Jennings & Herrera, 1968), this has recently become a renewed focus of the emerging research field of “crop evolutionary ecology” (Anten & Vermeulen, 2016; Denison, 2017; Weiner, 2019; Weiner et al., 2017). Interestingly, the four different genotypes included in the experiment were of different origin and improvement status (e.g. landrace Natsu Kurakake vs. elite breeding line Weber). However, despite strong absolute differences amongst genotypes in all allocation traits measured, there was no evidence that the responses to competition varied amongst them. This indicates that neighbour response has not been targeted by breeding so-far, and should be considered for future crop improvement.

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Competing interests

The authors declare no competing interests.

Author contributions

E.B.K., S.E.W. and P.A.N conceptualized and designed the research (with input from N.P.R.A.). E.B.K and S.E.W performed the experiments. E.B.K performed the analyses and wrote the manuscript. All authors revised and approved the final version of the manuscript.

Data availability

Data and essential scripts for analyses will be deposited on Zenodo.

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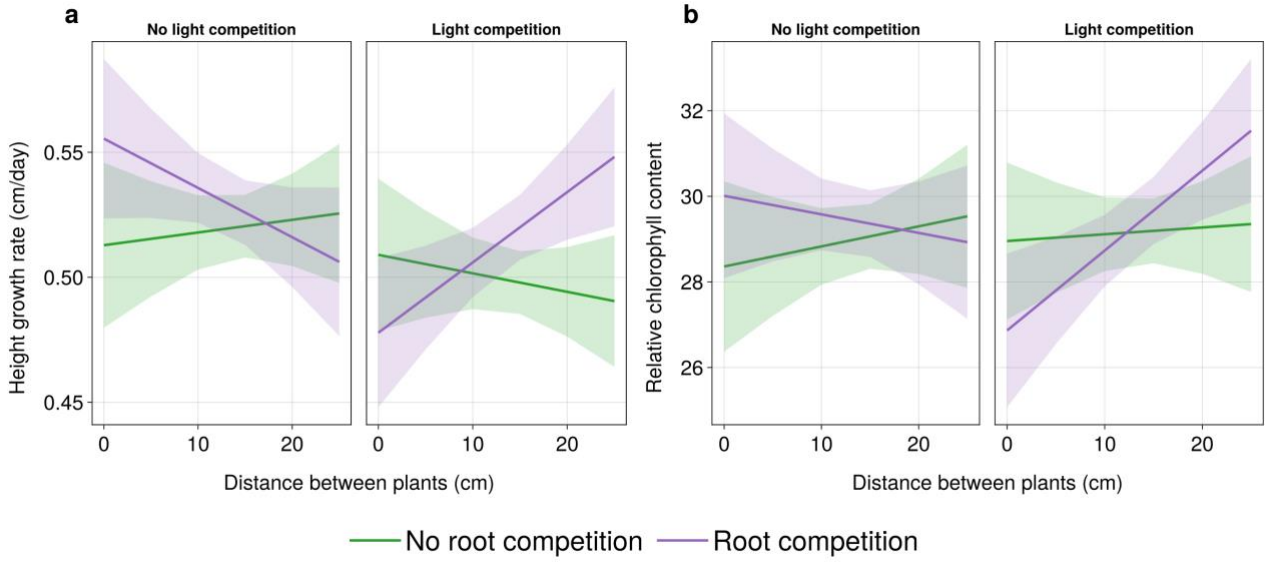
Supplementary Material

Supporting Figure 1: Experiment under hail protection net. The plants were clearly not light limited.



Supporting Figure 2: Predicted marginal means for (a) height growth rate and (b) chlorophyll content.