

Differential genetic influences on competitive effect and response in *Arabidopsis thaliana*

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Summary

1 Competition plays an important role in structuring populations and communities, but our understanding of the genetic basis of competitive ability is poor. This is further complicated by the fact that plants can express both competitive effect (target plant influence upon neighbour growth) and competitive response (target plant growth as a function of a neighbour) abilities, with these ecological characteristics potentially being independent.

2 Using the model plant species *Arabidopsis thaliana*, we investigated patterns of intraspecific variation in competitive effect and response abilities and their relationships to other plant traits and resource supply rates.

3 Both competitive effect and response were measured for 11 genotypes, including the Columbia ecotype and 10 derived mutant genotypes. Plants were grown alone, with intragenotypic competition, and with intergenotypic competition in a replicated blocked design with high nutrient and low nutrient soil nutrient treatments. We quantified competitive effect and response on absolute and per-gram bases.

4 Competitive effect and response varied among genotypes, with the relative competitive abilities of genotypes consistent across fertilization treatments. Overall, high rates of fertilization increased competitive effect and competitive response abilities of all genotypes. Both competitive effect and response were correlated with neighbour biomass, though genotype-specific traits also influenced competitive response.

5 At the genotype level, there was no correlation between competitive effect and response in either fertilization treatment. Overall patterns in competitive response appeared consistent among inter- and intragenotypic competition treatments, indicating that a target genotype's response to competition was not driven by the genetic identity of the competitor.

6 These findings indicate that within *A. thaliana*, there is the potential for differential selection on competitive effect and response abilities, and that such selection may influence different sets of plant traits. The concept of a single competitive ability for a given plant is not supported by these data, and we suggest continued recognition of these dual competitive abilities is essential to understanding the potential role of competition in influencing intra- and interspecific processes.

Key-words: genes affecting competition, intra- and intergenotypic competition, molecular ecology, phenotypic plasticity

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Introduction

Substantial research effort has been devoted to understanding the mechanisms that generate variation in the

effects of competition on plant growth among locations and across species (Grime 2001; Keddy 2001). Identified factors include those external to the plant such as neighbour abundance (e.g. Reader *et al.* 1994), resource availability (e.g. Tilman 1982) and herbivory (e.g. Haag *et al.* 2004), as well as characteristics intrinsic to a plant itself, such as plant size (Keddy *et al.* 2002), architecture and morphology (Fitter *et al.* 2002; Keddy *et al.* 2002),

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phenotypic plasticity (Schmitt *et al.* 1995), and interactions among root and shoot competition (Cahill 1999, 2002). Though it is reasonable to believe that a plant's phenotype influences its competitive ability, we have a poor understanding of how or why.

Despite the general belief that below-ground competition is as strong as or stronger than competition above ground (Casper & Jackson 1997), the vast majority of our understanding comes from studies focused on plant shoots. Additionally, plants may vary independently in competitive effect and response abilities (Goldberg & Landa 1991), resulting in at least two independent forms of competitive ability. In exploitative (resource) competition, competitive effect represents a plant's influence on a shared resource pool and the resulting negative impact on the neighbouring plants. How a plant grows under low resource conditions (caused by neighbouring plants) is its competitive response (Goldberg 1990). Competitive effect and response are not necessarily correlated (Goldberg & Landa 1991), and thus the traits needed to cause harm to others may differ from those needed to not be harmed by others. The trait-centred empirical data demonstrating this are lacking.

Increased competitive ability can be selected for experimentally (Miller 1995), indicating a heritable component to this ecological process. Studies showing direct effects of specific genes on competition are limited (Schmitt *et al.* 1995; Bates & Lynch 2001; Fitter *et al.* 2002; Alwerdt *et al.* 2005), and genetic influences on competitive ability are likely to involve numerous genes and epistatic interactions. Root hairs and lateral branching, for example, can influence competition for phosphorus (Krannitz *et al.* 1991; Bates & Lynch 2001; Fitter *et al.* 2002), while root system biomass is unrelated to relative competitive ability (Cahill 2003). Traits outside the root system can influence below-ground competitive ability if root and shoot competition interact to affect plant growth (Cahill 1999, 2002), or if competitive ability is a characteristic of a plant (Grime 2001). For example, R:FR phytochrome systems and ethylene sensitivity are both important in allowing a plant to adjust its phenotype to improve its ability to compete for light (Schmitt & Wulff 1993; Pierik *et al.* 2003), with unknown consequences for root growth and competition. Additionally, a mutation in the SDD1 gene that alters stomatal density in *Arabidopsis thaliana* alters photosynthetic activity under low-light conditions (Schluter *et al.* 2003), as well as the severity of intraspecific competition (Alwerdt *et al.* in press). Finally, if size itself directly influences competitive ability (Schwinning & Weiner 1998), then any allele that alters plant size should also impact competitive ability. Because of the existence of trade-offs between competitive ability and other ecological processes (susceptibility to disease, Damgaard & Jensen 2002; tolerance of soil compaction, Nash Suding *et al.* 2003), traits associated with improved competitive ability may come at some ecological cost. As a result, the selection for strong competitive ability should only occur under specific conditions. For example, if the strength

of competition varies with resource availability, then the selective pressure itself should vary along that gradient.

To explore the mechanistic linkages between plant traits and competitive abilities (effect and response), we conducted an experiment using 10 mutants of *Arabidopsis thaliana*. Plants were grown alone or with a competitor of a known genotype at two levels of resource supply. Silique production was measured as an indicator of plant fitness. By varying resource conditions we are able to address the question of whether any observed trait-function linkages are contingent upon resource conditions, or if instead they are consistent regardless of external resource supply.

Materials and methods

There are two basic approaches to understanding relationships between plant traits and ecological processes. The first approach is to use comparative methodology involving large numbers of species (e.g. Gaudet & Keddy 1988; Keddy *et al.* 2002). This approach has the shortcoming that species vary simultaneously in numerous correlated traits (hence they are called different species), and thus it is impossible to demonstrate a causal link among resulting trait-competition correlations.

An alternative approach, and the one used here, is to compare differences in competitive effect and/or response between a wild-type genotype and a derived genetic mutant within a single species. This approach has provided amongst the most convincing arguments for the importance of shade avoidance strategies in response to light competition (Schmitt *et al.* 1995). A concern with this approach is that pleiotropic or epistatic interactions will result in a single genetic mutation altering more than just the trait of interest. Though this is certainly true, it is reasonable to believe that the number of correlated changes associated with this genetic approach will be small relative to the number of traits that vary among species in the comparative approach. An additional concern is that the deleterious effects of induced mutations may be more severe than natural allelic variation (e.g. gene inactivity instead of reduced activity), and thus the traits expressed by such mutants are outside the naturally occurring range of variation. However, it remains conceptually ambiguous as to whether it is better to use plants that have only minor variation in a trait (ecotypic variation), or use plants that have the maximal variation in a trait (mutation). To answer the question of trait-function relationship, using naturally occurring variation is not necessarily the ideal methodological choice. A further discussion of the relative merits of these different approaches is, however, beyond the scope of this paper.

FOCAL SPECIES

Arabidopsis thaliana (L.) Heynh. (Brassicaceae) is an annual plant native to Eurasia, naturalized throughout much of the world (Al-Shehbaz & O'Kane 2002).

Growth is initially as a vegetative rosette, with a flowering inflorescence appearing at bolting. Plants are generally small, with inflorescences generally ranging from 5 to 30 cm in height, and basal leaves generally less than 4 cm in length (Al-Shehbaz & O'Kane 2002). As with many/most other Brassicaceae species, *A. thaliana* does not form mycorrhizal associations, and thus soil resource uptake will be determined by the root system itself (Fitter *et al.* 2002; Alwerdt *et al.* 2005). Competition is apparent in growing populations, with its effects on plant growth influenced by planting density (Fitter *et al.* 2002), resource availability (Bates & Lynch 2001; Fitter *et al.* 2002) and interplant distances (Purves & Law 2002).

GENOTYPE SELECTION

Mutant selection was driven primarily by the desire to cast a wide net, selecting mutants with described phenotypes that we thought may influence competitive ability. We restricted our search to include only mutant lines derived from the Columbia (Col) ecotype, allowing direct comparisons of all mutants with the same genetic background. Mutant lines that possessed what we considered to be numerous obvious phenotypic changes (relative to Col), or (with one exception) that had described mutations at multiple loci, were not selected for this study. We acknowledge there are often going to be multiple genes and biochemical pathways responsible for the observed phenotypes; however, our goal was to determine whether a plant's genotype influenced its competitive ability, and not to imply that there was only a single gene that could cause such phenotypic change. Seeds were obtained from the *Arabidopsis* Biological Resource Center (Columbus, Ohio, USA).

Phenotypic differences among the mutants can roughly be broken down into root architecture, leaf architecture, plant size and nutrient use. Root architecture mutants were similar to Col above ground, but not below. The *spe-1* (CS3766) mutant has increased root mass and lateral root branching (Watson *et al.* 1998), while *axr4-2* (CS8019) has a reduced number of lateral roots and lacks the ability to proliferate roots in response to local nutrient patches (Fitter *et al.* 2002), although other studies have reported *axr4* to show wild-type root proliferation responses (Williamson *et al.* 2001; Linkohr *et al.* 2002). The *aux1-7* (CS3074) line, another auxin mutant, has increased root elongation (Pickett *et al.* 1990) and the double auxin mutant (*aux1-7, axr4-2*) (CS8040) has far fewer lateral roots than either of the parental lines (Hobbie & Estelle 1995). *Rhd1-1* (CS2257) has root hairs similar in length and distribution to Col, though bulbous in shape (Schiefelbein & Somerville 1990). The two leaf architecture mutants used were *phy-b* and *gll-1*: *phy-b* (CS6217) is a phytochrome B photoreceptor mutant that has elongated petioles, stems and root hairs (Reed *et al.* 1994), whereas *gll-1* (CS3126) lacks trichomes on stem and leaves, although a few may be located on leaf margins (Herman & Marks

1989). The two plant size mutants, *eto1-1* (CS3072) and *xv-1* (CS3133), produced plants generally smaller than Col: *eto1-1* plants are ethylene over-producers, and have an increased number of root hairs (Guzman & Ecker 1990), whereas *xv-1* plants are also characterized by their yellow-green leaves. The nutrient mutant, *pho-2* (CS8508), hyper-accumulates inorganic phosphate in the aerial portions of the plant (Delhaize & Randall 1995).

We have also conducted a related study measuring phenotypic plasticity in numerous plant traits (e.g. time to bolt, leaf area index, specific root length, SRL) in seven of the mutant lines above, as well as in seven ecotypes. A discriminant analysis failed to separate plants according to whether they were ecotypes or mutants (Wilks Lambda = 0.443, $P = 0.729$) indicating that, although mutants varied from ecotypes in single traits, there were no obvious multivariate differences between these two groups (S. W. Kembel *et al.*, unpublished data). These findings support our decision to use mutants in this study and suggest that any pleiotropic effects are not severe enough for these mutant plants to be fundamentally different from the phenotypic variation observed in nature.

EXPERIMENTAL TREATMENTS AND HARVEST

The experiment consisted of 14 replicate blocks, each containing two 32-cell flats. Each $6 \times 6 \times 6$ cm cell was filled with a 3 : 1 sand : topsoil mixture. Within each block, one flat was randomly assigned the high nutrient treatment, receiving 2 mL per cell of $1.0 \times$ Hoagland's solution twice weekly (Epstein 1972). The second flat in each block received the low nutrient treatment of 2 mL cell⁻¹ of $0.1 \times$ Hoagland's solution twice weekly. All plants were grown in a growth room within the Biotron facility at the University of Alberta (18 : 6 L : D; 24 °C).

Many experimental designs have been developed to study competition among plants, and there has been significant debate about which is most appropriate (Gibson *et al.* 1999; Connolly *et al.* 2001; McPhee & Aarssen 2001). As all the mutants used here are derived from the same Col ecotype, a 'target-neighbour' design was used, with each mutant line (= target) competing against Col. Advantages of this design include allowing comparisons of competitive abilities among genotypes without conducting all pairwise contests (45 would be needed).

Three target individuals of each of the 10 mutants were planted within each flat, one alone (control), one in a cell with a Col individual (intergenotypic competition) and one in combination with another individual of the same genotype (intra-genotypic competition). The remaining two cells in each flat contained Col grown alone and Col grown with intra-genotypic competition. The locations of each treatment were randomized for each flat.

Seeds of all genotypes were stratified in water at 4 °C for 2 weeks prior to planting, and then transferred into

Petri dishes lined with moist filter paper and germinated under ambient light and temperature conditions. Seedlings were planted into each cell 2 days later by using a Pasteur pipette to draw up several (1–5) seedlings and positioning them in the appropriate locations in each flat. The target plant was always placed in the cell centre, with the competitor (if present) located 1 cm to the west. This interplant distance is the same as the mid-distance treatment used in a different study of intraspecific competition in this species (Purves & Law 2002). After 6 days, all cells were thinned to one seedling per planting location, and cells were weeded as necessary for the duration of the experiment.

The experiment was harvested 49–52 days after planting, at which point all plants of all genotypes were senescing. Harvest consisted of cutting each plant at the soil surface, counting the number of siliques present and weighing the shoots after drying at 60 °C for 48 h. In the competition treatments, plants were harvested and scored only if both plants were alive at the end of the study. As a result, we are unable to estimate mortality as a function of competition. Final sample sizes of individually grown plants varied among genotypes from 4 to 14 (mean = 10.9) in the low nutrient treatment and from 6 to 13 (mean = 10.7) with fertilization. With competition, there were 3–11 (mean = 8.6) and 1–12 (mean = 7.9) replicates for each genotype in which both the target genotype and competitor were alive at the end of the study. Target shoot biomass and silique number were tightly correlated ($R^2 > 0.8$ in all data sets), and silique number is a good predictor of total seed set within a genotype (S. W. Kembel, unpublished data). As we found no qualitative differences between the analyses of shoot biomass and silique numbers, we present only the silique results here.

STATISTICAL ANALYSES

All analyses were performed using GLM procedures in SPSS v 13.0 (SPSS 2004). Shoot biomass and silique number were natural logarithm transformed prior to analysis to improve normality and homogeneity of variance. There were no block effects for any response variable in any initial analysis (all $P > 0.3$), and therefore blocks were not included in the final statistical models.

To determine if the genotypes varied in competitive response (CR), a separate ANCOVA was conducted for the inter- and intragenotypic data sets. In each analysis, fertilizer and genotype served as fixed effects. Target plant silique number when grown with competition (in a given block) served as the response variable, while target plant silique number when grown alone (within the same block) served as the covariate. Genotypic variation in CR would be indicated by either a significant genotype effect or a genotype–fertilizer interaction. This approach avoids the use of ratios, which have previously been identified to be problematic (Weigelt & Jolliffe 2003), while still controlling for genotypic differences in silique production. An additional advantage

of this approach is that a significant covariate \times genotype or a covariate \times genotype \times fertilizer interaction would indicate size-dependent variation in competition among genotypes, something that could not be tested through the use of ratios. However, there were no significant covariate \times fixed effect interactions in either analysis in this particular study.

A similar ANCOVA was conducted to determine whether competitive effect (CE) varied among genotypes, with CE measured as silique production of the Col competitor when grown with each of the target genotypes. Col silique number when grown with competition served as the response variable, genotype and fertilizer served as fixed effects, and Col silique number grown without competition (in the same block) served as a covariate. Intergenotypic variation in CE would be indicated by either a significant genotype effect or a genotype \times fertilizer interaction.

Per-gram neighbour effects on competitive effect and intergenotypic competitive response were conducted by including a second covariate to each of the models described above. Specifically, to determine per-gram neighbour effects on CR, the dry biomass of the Col neighbour of a given target plant served as a second covariate with target plant biomass as the response variable. In the analysis of per-gram CE for each target plant, the dry biomass of the target plant served as the second covariate, with Col biomass as the response variable. In the CR analysis, a significant genotype effect would indicate that competitive ability varied among genotypes, even after accounting for variation in Col neighbour size. In the CE analysis, significant genotype effect would indicate that genotype influences competitive ability in some way other than through solely size-mediated effects.

Average CE and CR were quantified as ratios for each genotype by calculating the proportional silique reduction of the target genotype when grown with Col relative to mean silique production when grown alone (CR) and the mean proportional silique reduction of Col when grown in competition relative to growth without competition (CE). A simple test for correlation was conducted to determine whether there was any relationship between intergenotypic competitive effect and response among the genotypes.

Results

We observed no shading among plants in the low nutrient treatment, and any competition that occurred was therefore exclusively below-ground. When grown alone, high nutrient plants produced nearly twice as many siliques as low nutrient plants (Fig. 1) and, as a consequence of this increased size, shading among neighbouring plants was apparent. Competition can occur simultaneously above and below ground (Cahill 2002), and while shading indicates that above-ground competition occurred in the high nutrient treatment, competition below ground is not necessarily abolished, or even decreased in strength, by fertilization.

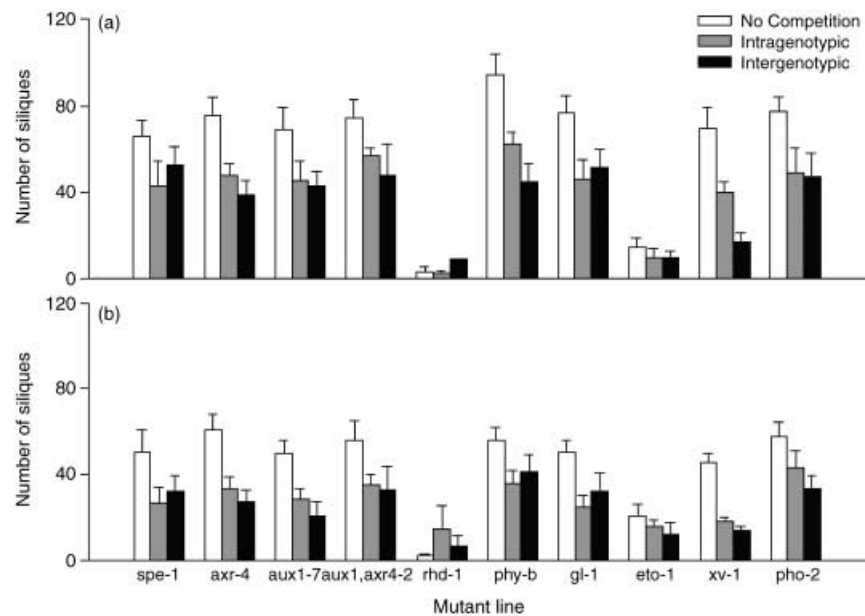


Fig. 1 Silique production (mean \pm 1 SE) of each genotype as a function of neighbour identity (none, intragenotypic, intergenotypic) in (a) high nutrient and (b) low nutrient soils. Competitive response would be represented as the relative difference in silique production between plants grown alone and those grown in either of the two competition treatments. There was only one surviving individual of *Rhd* in the intergenotypic competition treatment with fertilization, and thus no error bars are presented.

Table 1 Competitive response of each genotype measured as silique production in competition, as a function of silique production when grown alone ($Silique_{Alone}$), fertilization, and genotype. Subscripts under F ratio indicate the numerator and denominator degrees of freedom for each term in the fixed-effect ANCOVA. In the per-gram intergenotypic analysis, the biomass of the competitor plant (Col genotype) growing in the same pot as the target plant served as a second covariate. All variables were Ln transformed prior to analysis, and there were no significant covariate–fixed effect interactions in any of the analyses (results not presented).

	Intragenotypic CR			Intergenotypic CR			per-gram intergenotypic CR		
	MS	F_{DF}	P -value	MS	F_{DF}	P -value	MS	F_{DF}	P -value
Col biomass	–	–	–	–	–	–	8.418	13.321 _{1,115}	< 0.001
$Silique_{Alone}$	0.236	0.492 _{1,146}	0.484	0.669	0.956 _{1,116}	0.330	0.908	1.437 _{1,115}	0.233
Fertilization	6.123	12.745 _{1,146}	< 0.001	3.662	5.239 _{1,116}	0.024	7.907	12.512 _{1,115}	0.001
Genotype	1.985	4.131 _{10,146}	< 0.001	2.560	3.662 _{9,116}	< 0.001	1.925	3.047 _{9,115}	0.003
Fertilization \times Genotype	0.706	1.469 _{9,146}	0.165	0.392	0.560 _{9,116}	0.827	0.338	0.535 _{9,115}	0.846
Error	0.480	–	–	0.699	–	–	0.632	–	–

COMPETITIVE RESPONSE

Intra- and intergenotypic competition had similar effects on silique production (Fig. 1). In general, silique production decreased with either form of competition (Fig. 1), with the magnitude of competitive response varying among genotypes (Table 1; Fig. 1). Target plants were less suppressed by competition under high fertilization than low fertilization (increased CR, Table 1, Fig. 2). This fertilization effect on CR was consistent among genotypes as indicated by the lack of a significant genotype–fertilization interaction (Table 1).

Alternative method of analysis

Variation in competitive response among genotypes was also analysed using traditional three-way ANOVAS

with target silique number as the response variable, and competition (intra- vs. control, intergenotypic vs. control), genotype, fertilizer and all interactions as fixed effects. Although there are some discrepancies between the two approaches, we believe the ANCOVA method to be preferred, due both to its ability to detect size-dependent responses (should they occur), and the fact that the main hypothesis of interest is tested as a main effect rather than a higher-order interaction. The major finding, genotypic variation in competitive response among genotypes (as reported in Table 1 using the ANCOVA approach), was supported in the alternative analyses (intra- vs. control, genotype–competition interaction $F_{10,407} = 1.766$, $P = 0.065$; intergenotypic, genotype–competition interaction $F_{9,358} = 1.901$; $P = 0.051$). However, in neither the intra nor intergenotypic analysis was there support for the finding that competitive

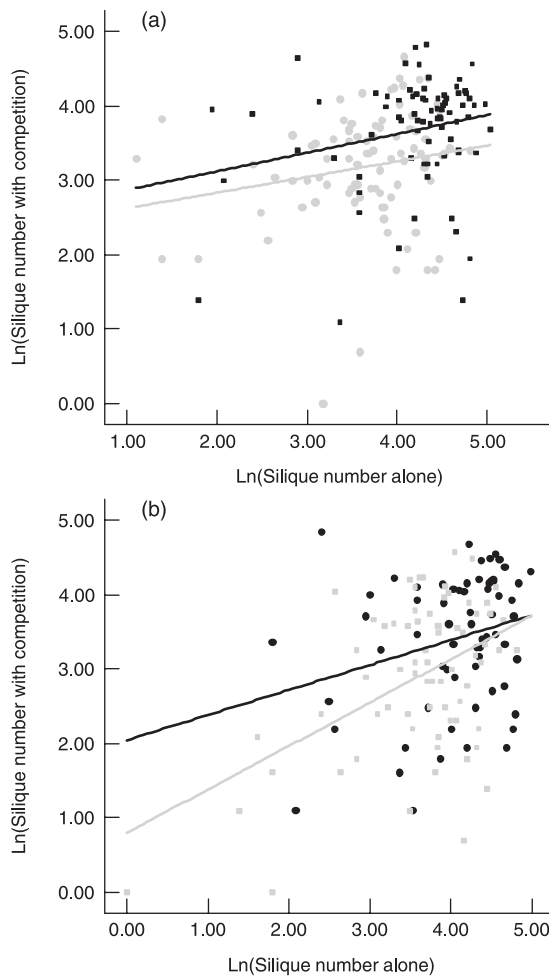


Fig. 2 Target plant silique production grown in competition as a function of silique production of the same genotype in the same block when grown without competition, and fertilization treatment, for both the (a) intragenotypic and (b) intergenotypic treatments. For ease of visualization of the main effect of the fertilization treatment on competitive response (plants were less suppressed by competition under high fertilization than with low fertilization), genotype is not represented on the figure. Black shading indicates high fertilization and grey shading corresponds to low fertilization. On both graphs, the high fertilization regression line is above the low fertilization regression line, indicating that for a given silique production of individually grown plants, plants will produce more siliques under competition in the high fertilization treatment.

response increased with fertilization (fertilization–competition interaction $P > 0.20$ for both data sets).

Per-gram effects

In the analysis per-gram competitive responses, Col biomass was negatively associated with target silique production (Table 1). Even when Col biomass was included in the model, however, fertilization and genotype were still significant, indicating that the effects of genotype on competitive response are not caused simply by variation in neighbour biomass. No interaction terms including the covariate analysis were significant (all $P > 0.05$), further indicating that the differences

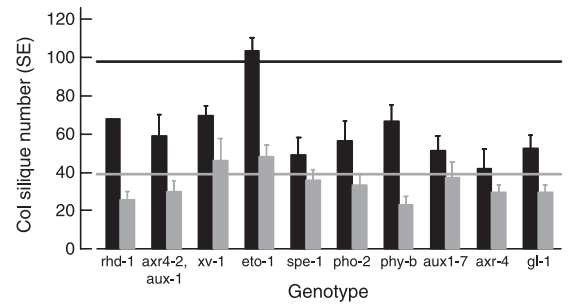


Fig. 3 Competitive effect as expressed as silique production (mean \pm 1 SE) of Col as a function of neighbour genotypic identity and fertilization treatment (grey = low fertilization, black = high fertilization). There was only one surviving individual of *Rhd* in the high nutrient treatment, and thus no error bars are presented. For reference, the horizontal lines represent the mean silique production of Col when grown without competition.

observed among genotypes in competitive response were not size dependent.

COMPETITIVE EFFECT

Competitive effect was affected by the target plant's genotype ($F_{9,144} = 2.52$, $P = 0.010$; Fig. 3) and fertilization ($F_{1,144} = 31.85$, $P < 0.0001$). The lack of a significant genotype–fertilization interaction term ($F_{9,144} = 1.16$, $P = 0.328$) indicates that the competitive effect abilities of the genotypes were consistent across fertilization levels. However, despite the significant genotype effect described above, Col performance appeared relatively consistent regardless of the identity of the competitor, with the one exception of the *eto-1* competitor against which Col silique production was increased relative to the other genotypes (Fig. 3).

In the per-gram analyses, Col silique production was negatively affected by increased neighbour biomass ($F_{1,125} = 16.38$, $P < 0.001$). The lack of a significant fertilization effect ($F_{1,125} = 0.765$, $P = 0.383$) indicates the effects of fertilization on enhancing competitive effect in the prior analysis were caused by a resulting increase in plant size, rather than some other effect. The lack of a significant genotype effect ($F_{9,125} = 1.499$, $P = 0.155$) or a genotype–fertilization interaction ($F_{8,125} = 1.244$, $P = 0.279$) indicates that the observed variation in competitive effect among genotypes in the first CE analysis can be attributed to differences in the size of the plants of the different genotypes, rather than any additional genotype-specific effects.

INTERGENOTYPIC EFFECT AND RESPONSE RATIOS

Competitive effect and response abilities were not correlated among genotypes in either the high ($r = 0.47$, $P = 0.90$) or low nutrient treatments ($r = -0.568$, $P = 0.09$, Fig. 4). Removing the apparent outlier (*Rhd*) did not alter the lack of correlation between CE and CR in either fertilization treatment.

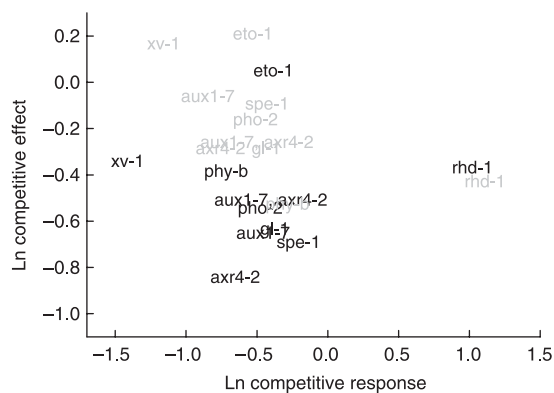


Fig. 4 Relationship between intergenotypic competitive effect and response as a function of fertilization treatment (black lettering = high nutrient, grey lettering = low nutrient). Letter codes correspond to each of the mutant genotypes. For both competitive effect and response, values of 0 (in Ln scale) indicate that neighbours had no effect on silique production, values < 0 indicate competition, and values > 0 indicate increased silique production in the presence of neighbours.

Discussion

Competitive effect and response varied among genotypes and with fertilization (Figs 1–3), yet the lack of any genotype by fertilization interactions indicates consistency among the genotypes in their relative competitive abilities, despite a 10-fold increase in resource supply (Table 1). Such a finding is particularly surprising given that competition was solely below ground in the low nutrient treatment and either both above and below ground or above ground only in the high nutrient treatment. Such a shift in the location of competition with increased fertilization might have been expected to alter the relative competitive abilities of these genotypes, and these results are counter to the prediction that there exists an inherent trade-off in a plant's ability to compete above and below ground (Tilman 1988). The data are, however, consistent with the idea that competitive ability itself is a plant trait (Turnbull *et al.* 2004) and that those plants that are strong competitors for one resource will also be strong competitors for other resources (Grime 2001).

Although genotypes varied in competitive effect and response, these two forms of competition were uncorrelated among genotypes in both fertilization treatments (Fig. 4). This absence, rather than a negative correlation, suggests that these two competitive strategies are not mutually exclusive and some genotypes can be strong (or weak) at both or either form of competition. This result is in agreement with prior studies demonstrating a lack of concordance between competitive effect and response among species (Goldberg & Landa 1991; Keddy *et al.* 1994), and further suggests that there are multiple ways in which a plant can be successful in the presence of competitors. We suggest that a better understanding of the role of competition in natural systems would be achieved through a more widespread

understanding that 'competition' is not a single process, but instead consists of at least two different processes, each of which appears to be wholly independent of the other.

One competitive strategy is to have high rates of resource capture and use, leading to rapid depletion of a shared resource pool. Such 'effect' competitors thereby have an indirect negative effect on their neighbours mediated through the resource pool (Goldberg 1990). The variation in competitive effect abilities among genotypes found here was attributable to differences in size, consistent with an interspecific comparative study (Gaudet & Keddy 1988). The classic trait associated with effect competition is plant height, where the taller plant can overtop its neighbour and be in a dominant position with respect to light capture and size-asymmetric competition (Harper 1977). However, a height (or depth) advantage is unlikely to be important below ground, where soil resources are more diffuse. Instead, soil resource capture will be a function of both the foraging area of the competing plants and uptake kinetics (Caldwell 1987; Fitter *et al.* 1991), and the strength of competition is related to root abundance (Cahill & Casper 2000). Other studies have found changes in competitive effect as a function of other mutations in *A. thaliana*, although these studies generally did not document whether there was also a change in plant size among their genotypes. They were also generally conducted in P-limited soils where, due to the relatively immobile nature of P in the soil, bulk flow becomes less important for P uptake and fine root extensions (root hairs) are very important. Some plant traits are thus likely to influence competition for some soil resources but not others (Fitter *et al.* 2002) and it is unclear whether physical traits such as root surface area are more important in competition in the N-limited soils used here (E. Lamb, unpublished data).

A second competitive strategy is to minimize the effects on one's own fitness of reduced nutrient availability due to competition. This 'response' strategy also varied among genotypes (Fig. 1), and was, in part, explained by variation in the size of the competing plants, although additional, unidentified, genotype-specific traits (see below) were important. These results suggest that there are more strategies for responding to competition than there are for harming one's neighbour. A variety of mechanisms can alter the impacts of competition on a plant. For example, morphological plasticity in root and shoot growth may minimize the effects of neighbours above (Schmitt & Dudley 1996) or below ground (Gersani *et al.* 2001). There also exist a variety of mechanisms available to alter one's nitrogen-use efficiency, which could further minimize the negative consequences of reduced N uptake, and thus increase competitive response ability. Keddy *et al.* (1998) suggested that, due to the diversity of potential mechanisms for altering competitive response ability, competitive response could be subdivided into escape, foraging and persistence responses. Numerous other

classification schemes have recognized life-history strategies similar to the competitive response strategies, e.g. 'competitors-stress tolerators-ruderals' (Grime 2001), and 'resource acquisition-conservation' (Chapin 1980; Reich *et al.* 1997). However, we only examined intraspecific variation, which is modest in comparison with differences among species, and thus we do not believe that our observed differences among genotypes were due to such coarse differences in strategy. Instead, we suggest that, even within a single response strategy, minor genetic changes can result in functionally important shifts in competitive response ability.

Such variation has important implications for the current large-scale efforts that relate variation in plant traits to ecological process (e.g. competition) and community composition (Lavorel & Garnier 2002; Nash Suding *et al.* 2003). The idea that even single locus variation within a species can have a significant impact on one well-studied ecological process (competition) suggests that developing a more general theory linking traits to function will be more difficult than previously imagined. Recent evidence that intraspecific genetic diversity has significant impacts on community diversity (Booth & Grime 2003) further suggests that important functional variation occurs at a level below that of species (but see Weltzin *et al.* 2003).

The competitive response of each genotype was consistent between inter- and intragenotypic treatments, indicating that competitive response is driven by the genetic identity of the target plant rather than that of its competitor (Fig. 1). Similarly, the lack of significant genotype-fertilization interactions for both CE and CR (Table 1) suggests that observed variation in competitive abilities is driven in part by intrinsic (genetic) factors. This finding is consistent with work on different species that has found variation in competitive ability among genotypes (Latta *et al.* 2004) and that genotype can be a better predictor of competitive interactions than neighbour identity (Gustafson *et al.* 2004). However, both CE and CR did change with increased fertilization, indicating that external factors (resources) also are important in determining the strength of competition. Interestingly, the lack of correlation between competitive response and competitive effect (Fig. 4) suggests that different internal factors (traits) operate for each of these two forms of competition. Despite decades of research on plant competition, a full understanding of the relative importance of intrinsic and extrinsic factors in determining the strength of competition still eludes us. We suggest that the genotype of the individual should not be ignored, nor should we assume that all individuals within a single population experience competition in the same way, due either to local variations in resources, or intrinsic differences in genotype.

It is worth noting that the results presented in this study are from a single species. Though single species studies are widespread in competition literature, their ability to extrapolate to other species is limited. Until similar research is conducted with a multitude of species,

it will remain unclear exactly how widespread genetic differentiation of competitive effect and response are among plant species (Fig. 4). That said, the ability of ecologists to easily exploit a variety of well-developed genetic models presents opportunities for advancement in many areas of research, particularly functional ecology.

GENOTYPE-SPECIFIC FINDINGS

There was no general pattern of differential competitive effect or response abilities among our four mutant groups (root architecture, shoot architecture, plant size and nutrient use), suggesting competitive ability can be influenced by a diverse array of traits. Although a full explanation of why each genotype responded the way it did is both beyond the scope of this paper, and not possible without a rigorous phenotypic screening of each genotype, some specific comments are warranted.

The ethylene overproducing mutant was a particularly poor effect competitor, with Col doing as well, or better, when grown with *eto* than when grown alone (Fig. 3). This variation could be attributed to difference in plant size, and this genotype was amongst the smallest. However, recent work with tobacco suggests an alternative explanation may be possible as well (Pierik *et al.* 2003). Specifically, although we have long known that the R:FR phytochrome system is essential for the expression of a shade avoidance response (Aphalo *et al.* 1999), it appears that ethylene is also involved in this behaviour. Low concentrations of ethylene can induce a shade avoidance response, as ethylene-insensitive tobacco plants exhibit a delayed shade avoidance response (Pierik *et al.* 2003). Ethylene is also involved in the developmental pathway responsible for root hair initiation and elongation (Lynch & Brown 1997), with the addition of exogenous ethylene to soil inducing root hair formation in *A. thaliana* (Ma *et al.* 2001). It is possible that the ethylene overproducing genotype used here 'primed' the Col competitor that competition was going to happen or induced a root growth response, even before there had been a shift in light quality or soil nutrients, allowing the Col neighbour to be in a more advantageous condition when competition was actually engaged. If this is true, it would appear to be one of the first cases of an actual cost (increasing competitive performance of neighbours) associated with plant-plant communication, with potentially important implications for the evolution and use of volatile signals in plants. Further studies investigating the hormonal control of competition and phenotypic plasticity are clearly needed.

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