ORIGINAL ARTICLE

THE COSTS AND BENEFITS OF TOLERANCE TO COMPETITION IN *IPOMOEA PURPUREA*, THE COMMON MORNING GLORY

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Tolerance to competition has been hypothesized to reduce the negative impact of plant–plant competition on fitness. Although competitive interactions are a strong selective force, an analysis of net selection on tolerance to competition is absent in the literature. Using 55 full/half-sibling families from 18 maternal lines in the crop weed *Ipomoea purpurea*, we measured fitness and putative tolerance traits when grown with and without competition in an agricultural field. We tested for the presence of genetic variation for tolerance to competition and determined if there were costs and benefits of this trait. We also assessed correlations between tolerance and potential tolerance traits. We uncovered a fitness benefit of tolerance in the presence of competition and a cost in its absence. We failed to detect evidence of additive genetic variation underlying tolerance, but did uncover the presence of a significant maternal-line effect for tolerance, which suggests its evolutionary trajectory is not easily predicted. The cost of tolerance is likely due to later initiation of flowering of tolerant individuals in the absence of competition, whereas relative growth rate was found to positively covary with tolerance in the presence of competition, and can thus be considered a tolerance trait.

Darwin (1859) hypothesized that interspecific competitive interactions could impact fitness trajectories as much or even more than an organism's physical environment. Since that time, ecologists have determined that competitive interactions can play a fundamental role in structuring natural communities (Wilbur 1972; Grime 1977; Holt 1977; Fowler 1986; Goldberg 1996; Fridley et al. 2007), and influence ecosystem functioning (Grace 1990) and the productivity of agricultural fields (Pierik et al. 2012). Competitive interactions are of particular importance to plants due to their sessile nature (Tilman 1994)—such interactions may limit important resources such as the availability of nutrients, water, and light (Schmitt and Wulff 1993) and ultimately lead to adverse effects on plant fitness (Reichenberger and Pyke 1990; Goldberg and Barton 1992). In turn, a plant may exhibit a variety of traits to reduce the negative impact of competition (Cipollini 2004;

Boege 2010; Pierik et al. 2012), such as shade avoidance through stem elongation (Dudley and Schmitt 1996), and reduced branching and leaf production (Dorn et al. 2000; Schmitt et al. 2003).

Plants may also employ competitive strategies that mitigate the impact of competition on fitness. Two such strategies—competitive response, the ability of a species to tolerate competition, and competitive effect, the ability of a species to suppress its neighbor—were clarified in the ecological literature approximately 20 years ago (Goldberg 1990). These competitive strategies have since been studied largely with the aim of understanding the role of interspecific competition on community assembly (Aarssen 1983; Goldberg and Landa 1991; Keddy et al. 1994) and/or the role that genotypic variation in competitive ability may play in the outcome of interspecific competitive interactions (Taylor and Aarssen 1990; Fridley et al. 2007; Lankau and

Strauss 2007). Surprisingly, the evolutionary dynamic of these competitive traits—that is, their potential cost and/or benefit—has gone largely unexamined in the plant evolutionary ecology literature. For example, it is unknown if competitive ability incurs a fitness cost, and if any potential costs may outweigh the benefits. Such a scenario would constrain the evolution of maximal levels of competitive ability, which may in turn affect patterns of community assembly.

Tolerance to competition—a type of competitive response trait—can reduce the negative impact of plant–plant competition on fitness (Willis et al. 2010). Tolerance is a term generally used across plant subdisciplines as the ability to "cope" with various stresses, but in the evolutionary ecology literature it is defined more precisely as an organism's ability to maintain fitness while sustaining damage (reviewed in Baucom and de Roode 2011). Tolerance has mainly been studied in the context of herbivory (Mauricio et al. 1997; Strauss and Agrawal 1999; Hochwender et al. 2000; Pilson 2000; Stowe et al. 2000; Stinchcombe 2002; Fornoni et al. 2004), and although some studies have looked at the role of tolerance to herbivory in a competitive environment (Tiffin 2002; Uriarte et al. 2002; Siemens et al. 2003; McNutt et al. 2012), tolerance to competitive interactions themselves, as measured in the currency of plant fitness, have received little examination. Of studies that have examined tolerance to competition, one uncovered the presence of genetic variation for tolerance among inbred lines of *Arabidopsis thaliana* (Willis et al. 2010) and another detected genetic variation for tolerance in *Ipomoea purpurea*, the common morning glory (Tiffin 2002). However, it is not clear if this genetic variation, in either species, has an additive genetic component, which would allow for predictable responses to natural selection. It is also unknown if fitness costs of tolerance to competition may outweigh any potential benefit, thus constraining the evolution of increased levels of tolerance. Furthermore, although the identification of traits that underlie competitive ability has been a major goal in both plant ecology (Goldberg 1996) and studies of plant tolerance evolution (Strauss and Agrawal 1999; Juenger and Bergelson 2000; Tiffin 2000; Weinig et al. 2003), the influence of putative tolerance traits on the evolution of tolerance to competition remains unexamined.

Here, we investigate tolerance to competition in the crop weed *I. purpurea* and determine if the requirements for the evolution of increased competitive tolerance are present in this species. We asked the following questions: (1) Is there genetic variation for tolerance to competition? (2) Do the patterns of selection on tolerance to competition differ in the presence of competition in contrast to its absence? (3) Is there evidence that tolerance is genetically correlated with tolerance traits? We perform this study in the context of an agricultural landscape and our design uses a focal individual—the agricultural weed *I. purpurea*—grown in interspecific competition with maize.

Methods
EXPERIMENTAL SYSTEM
Study species
The common morning glory, *I. purpurea* (L.) Roth. (Convolvulaceae), is a climbing annual vine that is commonly found in disturbed sites and agricultural fields in the United States. It can lead to significant crop yield losses in maize, soy, and cotton fields (Cordes and Bauman 1984; Defelice 2001) and is included in the top 10 troublesome weeds in agriculture in the southern United States (Webster and Coble 1997). Germination occurs between mid-May and August. Six weeks after emergence, plants begin to flower; flowering lasts until the plant senesces or is killed by frost (Brown and Clegg 1984; Uva et al. 1997). Plants bear multiple showy flowers daily (upwards of 80) that open for a single morning. Flowers are pollinated by bumblebees and other generalist species but are also capable of self-fertilization (Brown and Clegg 1984; Epperson and Clegg 1987; Chang and Rausher 1998). Fruits are dehiscent capsules, which mature four weeks after pollination and contain one to six seeds (Mojonnier and Rausher 1997).

Crossing design
Seeds of *I. purpurea* were originally collected from an agricultural field in Oconee Co., Georgia, and selfed once in the greenhouse. Experimental individuals were then generated using the partial diallel crossing design initially described in Chaney and Baucom (2012; Supporting Information Fig. S1). Briefly, we crossed 20 plants such that each individual was crossed as a maternal plant to five paternal plants, and as a paternal plant with five maternal plants, producing one hundred full/half-sibling families total. Due to limitations in seed number and field space, replicate seeds from 55 full-sib families (hereafter "families") from 18 maternal-half-sib families (hereafter "maternal lines") were used for the experiment described below.

Field experiment
The field experiment was planted in a fenced and tilled agricultural field and protected from herbivory by a 12-foot deer fence at the University of Cincinnati's Center for Field Studies in Harrison, Ohio. We planted four replicates of *I. purpurea* from 55 full-sib families in each of two treatments—the absence and presence of interspecific competition—for a total of 440 experimental individuals. To prevent competitive effects (e.g., shading, root competition) on control plants, we used a completely randomized split-plot design with three spatial blocks; each block consisted of a competition and control plot. Because we first randomized within our whole-plot factor (competition, no competition), our design was not completely balanced for each family line; however, each spatial block had on average 8.148 plants per each of the representative 18 maternal lines (range: 2–18). The statistical

methods we outline below are robust when modeling unbalanced data, and the split-plot design is statistically powerful for detecting genotype-by-environment interactions, which are needed to detect genetic variation in tolerance (Siemens et al. 2003). Prior to planting our experimental seeds, we planted 220 pairs of Golden Cross Bantam Sweet Corn (Ferry Morse, Fulton, KY) spaced 1 m^2 apart on 16th June 2011, in the competition treatment. After the maize germinated, we removed one germinant per plot so that our experiment could examine the effects of competition at a 1:1 ratio. Eleven days later, we planted replicate nicked *I. purpurea* seeds in both treatments. We kept the distance between the focal *I. purpurea* and competitor maize plant consistent at approximately 0.10 m apart and we allowed the maize to establish (approx. 0.25 m tall) prior to planting the morning glory, as this is the general trend seen in agricultural fields. Seedlings grown in the absence of competition were provided 1.20-m-high bamboo stakes. Each *I. purpurea* seed was clearly marked with a straw to facilitate distinguishing experimental plants and the plots were kept relatively weed free by a combination of hoeing and hand weeding throughout the experiment. Germination and survival were high, with 92% germination success rate (403/440) and 90% survival to flowering (398/440), leaving $n = 398$ for analysis. Likelihood ratio tests revealed no significant genetic effect ($P > 0.999$; for maternal and paternal lines) or treatment effect ($P = 0.412$) on the likelihood of individuals to survive. We elected to keep competition of the *I. purpurea* with its crop competitor maize at a 1:1 ratio because we wanted to perform a relatively simple experiment for this initial test of the costs and benefits of tolerance to competition. This design reflects real scenarios of how morning glories grow in agricultural fields. Many observations in U.S. agricultural land find a single morning glory individual vining up a single maize plant, and most often on the edge of the maize crop, rather than within the crop itself, where competition is likely more intense (R. S. Baucom, pers. obs.). This design does, however, exclude the combination of intra- and interspecific competition on a focal experimental individual, which has also been observed in nature.

Phenotypic measurements

For this experiment, we examined plant tolerance to competition, defined as the ability to maintain fitness across competitive treatments, as well as three candidate traits that may contribute to tolerance in *I. purpurea*. These candidate traits were chosen because they have previously been considered important weedy characteristics in this species (Chaney and Baucom 2012). Specifically, we focused on relative growth rate, the day that the vine "grabbed on" to its competitor maize plant or its stake, and the day of first flower (hereafter, phenology). For simplicity, these traits will be called our focal traits.

To estimate relative growth rate in *I. purpurea*, the length of all true, fully expanded leaves were measured four weeks after planting and again nine days later. Forty-three nonexperimental *I. purpurea* plants were harvested at this time, and using the ImageJ software (National Institute of Health, http://imagej.nih.gov/ij/) and methods described by O'Neal et al. (2002), we measured the length of each leaf from the harvested nonexperimental plants, and thereafter dried the shoot material in a drying oven at 37°C. A linear regression of summed leaf length and dry shoot biomass showed leaf length to be an excellent predictor of plant biomass ($n = 43$, $R^2 = 0.891$, $y = 0.039x - 0.337$, $P < 0.001$). We thus calculated relative growth rate (*rgr*) for each individual with the following formula: $rgr = (\Sigma L_2 - \Sigma L_1)/t_2 - t_1$, where ΣL_t is the sum of leaf length at time *t*. One individual did not have any fully emerged leaves at the time of the first measurement; this plant is recorded as not available (NA) for data analysis. Relative growth rate was examined because it has been previously shown to have an important relationship with tolerance (Weis et al. 2000).

We recorded the day of grabbing on for each plant as a measure of the day when the vining stem of *I. purpurea* creates a "C-shaped" hook around either the adjacent maize plant or stake. Due to the vining growth habit of this species, and to prevent individuals from becoming tangled, all plants that had not "grabbed on" by 3rd August were manually vined on to their respective corn or bamboo stake. These individuals ($n = 164$) were treated as NAs for that data point during data analysis. Likelihood ratio tests revealed no significant genetic effect on the likelihood of individuals to "grab on" ($P = 0.717$ and $P = 0.160$; paternal and maternal lines, respectively). We previously determined that individuals that grabbed on earlier to its competitor are also larger and thus putatively better competitors (genetic correlation between day of grabbing on and biomass in competition: $r = -0.730$, $P < 0.001$; Chaney and Baucom 2012).

Ipomoea purpurea plants began to flower on 8th August. Phenology, defined here as day of first flower, was recorded throughout the experiment for a total of 28 census dates. Seeds were collected from all plants upon maturation. The first killing frost occurred on October 29 and two weeks later plants were harvested and bagged for further seed collection. All fruits were removed from the plants and seeds were shucked and free of chaff prior to being counted. To estimate plant fitness, total number of viable seeds was counted using the 750–2 Total Count System seed counter (International Marketing and Design Co., San Antonio, TX). Precision and accuracy of the seed counter was verified by hand-counting 189 samples ($n = 189$, $R^2 = 0.999$, $y = 1.008x + 1.313$, $P < 0.001$). Relative fitness was then calculated for each individual as observed fitness divided by the mean fitness in the population. All the data files used in this analysis, as well as the *R* code, were uploaded for public access to the

online data repository Dryad (http://www.datadryad.org, Dryad doi: 10.5061/dryad.v2b8t).

DATA ANALYSIS

Impact of competition and genetic variation for tolerance

All statistical analysis was conducted in *R* (version 2.15.2; R Development Core Team). To test for the presence of genetic variation for tolerance to competition we used the *lmer* function from the *lme4* package (Bates et al. 2011). We fit the following mixed linear model:

$$y = \mu + \text{treatment} + \text{block} + (\text{block} \times \text{treatment})$$
$$+ \text{maternal line} + \text{paternal line} + (\text{maternal line} \times \text{treatment})$$
$$+ (\text{paternal line} \times \text{treatment}) + \varepsilon,$$

where *y*, the response variable, is relative fitness, μ is the intercept or mean of the model (fit by default), treatment and block are fixed-effect terms, terms involving pedigree (maternal and paternal line and their interactions) are random effects, and ε is the error term (fit by default). The interaction effect of maternal and paternal line, and the three-way interaction effect of maternal and paternal line and treatment were not included in the final model as preliminary analysis indicated they were not significant—further, their inclusion does not inform the main conclusions of this study. To meet the assumptions of normality for this analysis, relative fitness was $\log(1+y)$-transformed. To determine the significance of each random effect in the model, a likelihood ratio test (LRT) was used to compare the full model and the reduced model with the effect removed. The *P*-value for random effects was determined with a chi-squared test with one degree of freedom. Because the competition treatment was implemented in a split-plot design, we tested the treatment effect in our ANOVA's over the block $\times$ treatment interaction to obtain *F*-statistics. A significant effect of treatment would demonstrate that growing alone versus in competition impacts fitness. A significant paternal or maternal-line effect would indicate the presence of genetic variation for relative fitness, or differences in vigor by paternal or maternal line. The term of interest is a significant interaction between paternal line and treatment, which indicates that the fitness of genotypes responded differently to competition and provides evidence of additive genetic variation for tolerance to competition. Furthermore, a significant interaction between maternal line and treatment would indicate the presence of potential additive and nonadditive components of genetic variation. To determine if competition with maize impacted our focal traits (relative growth rate, grabbing on, and phenology), we performed similar analyses of variance, as above, using each trait as the response variable in separate models. To meet the assumptions of normality, relative growth rate and grab-

bing on were square root-transformed, and significance of each effect in the model was once again determined using an LRT.

Costs and benefits of tolerance

Tolerance to competition was operationally defined as the mean relative fitness of maternal lines grown in the presence of competition minus the mean relative fitness of replicates of the same maternal line when grown in the absence of competition ($W_\text{P} - W_\text{A}$; Tiffin and Rausher 1999; Willis et al. 2010). We elected to perform these and subsequent analyses utilizing maternal half-sibling lines ($n = 18$) and for comparison in some places with full-sib family lines ($n = 55$) because we did not detect paternal-line genetic variation for tolerance to competition—we did, however, uncover evidence of maternal-line genetic variation for tolerance (see Results). We determined if tolerance to competition incurred a cost and/or a benefit among maternal lines by estimating the covariance between tolerance and the untransformed maternal line mean of relative fitness in both the absence and presence of competition. This test is inherently confounded due to the fact that fitness and tolerance are correlated. We removed this artifactual covariance using standard methods (Mauricio et al. 1997; Tiffin and Rausher 1999). An artifactual covariance was calculated for each maternal line and was subtracted from the calculated covariance to obtain an unbiased estimate of the relationship between tolerance and fitness in each environment. Confidence intervals were estimated by jackknifing maternal line corrected estimates and a one-tailed *t*-test was used to calculate if this corrected covariance was significantly different from zero.

Selection acting on tolerance to competition

We used the regression method described by Rausher (1992) to perform a joint selection analysis acting on tolerance to competition and tolerance traits separately for each competitive environment. Rausher's method is similar to the analysis described by Lande and Arnold (1983) but eliminates environmentally induced biases (Stinchcombe et al. 2002). Further, it is relevant here because tolerance cannot be measured on a single individual, and this analysis is based on genotypic maternal-line values rather than individual phenotypic values (Tiffin and Rausher 1999). Each selection analysis regressed maternal line means of untransformed relative fitness on standardized values of four traits: relative growth rate, grabbing on, phenology, and tolerance to competition. Linear selection gradients were estimated in models containing only the linear terms. Quadratic selection gradients were estimated in a full model that contained linear terms, quadratic terms, and cross-product terms of focal traits. The strength of total selection for each trait was estimated by calculating genetic correlations as Pearson product moment correlations between maternal-line mean values of each trait and relative fitness. Total selection includes both direct selection and indirect selection caused by genetic correlations.

Genetic correlations

The strength and direction of genetic correlations were calculated among tolerance to competition and our three focal traits in each environment separately using maternal-line means. We hypothesized that relative growth rate, grabbing on, and phenology might contribute to *I. purpurea's* ability to tolerate competition. One maternal line in the absence of competition was missing data for grabbing on, resulting in a reduced sample size for genetic correlations with this trait ($n = 17$). We also evaluated the potential for correlations between tolerance to competition and the plasticity of candidate tolerance traits, because tolerance to competition is the plastic response of fitness in competition (Abrahamson and Weis 1997). Plasticity to competition was examined for each focal trait that exhibited differential expression across competitive treatment (i.e., significant treatment effect). Plasticity to competition was calculated as the maternal-line mean values grown in the presence of competition minus the maternal-line mean values grown in the absence of competition ($X_P - X_A$), following the analysis of Weinig et al. (2003). For comparative purposes, we also performed selection analyses and assessed correlations using the full-sib families ($n = 55$), similar to Tiffin (2002). For these analyses, tolerance was calculated for each of the 55 families, and family-line mean values of each trait were used.

The statistical analyses used for these data are standard for this type of experiment. Despite the strengths of these methods, they do have some weaknesses. For example, using maternal-line or family-line means greatly reduces variation compared with the phenotypic data from which they are calculated, there is potentially less power due to the reduction in sample size, and there may be biases introduced from dominance and environmental effects. Additionally, the genetic correlations presented here do not take into consideration error in the estimation of the maternal- or family-line mean. We elected not to use best linear unbiased predictors (BLUPs) because of their poor properties in regression-based analyses and estimation of selection gradients (Hadfield et al. 2010).

Results

IMPACT OF COMPETITION AND GENETIC VARIATION FOR TOLERANCE

Interspecific competition significantly affected phenotypic expression in *I. purpurea* for two of the three focal traits—relative growth rate and the competitive measure "grabbing on" (Table 1, significant treatment effect; Table 2). We found that *I. purpurea* grown in the presence of competition had on average 6.54 cm/day (315%) decline in relative growth rate compared to those grown alone. When grown in the presence of competition, *I. purpurea* "grabbed on" to its adjacent maize plant on average 2.2 days (9%) faster than plants "grabbing on" to adjacent stakes in the absence of competition. A significant maternal-line effect in relative growth rate and phenology was uncovered (Table 1). However, we found no evidence for either a maternal- or paternal-line effect in day of grabbing on, or evidence of genetic variation for plasticity in the three putative tolerance traits (i.e., no significant treatment × paternal- or maternal-line interaction for relative growth rate, grabbing on, or phenology; Table 1). This indicates the presence of at least nonadditive genetic variation in relative growth rate and phenology, but no evidence for additive genetic variation for plastic responses in these putative tolerance traits.

Competition significantly impacted fitness (Table 2); plants grown in the presence of competition produced 1550 fewer seeds (216% lower relative fitness) on average than those grown alone. We found a significant interaction of maternal line and treatment for relative fitness (Table 1; Fig. 1), providing evidence that this species exhibits genetic variation for tolerance to competition. However, we uncovered no evidence of a paternal line by treatment interaction (Table 1), suggesting that the genetic variation in tolerance observed in this study population is due to genetic

Table 1. Results from mixed-model ANOVA demonstrating variation in *I. purpurea* traits.

Trait	Growth	Grabbing on	Phenology	Relative fitness
Random effects:				
Maternal line	**4.035 (0.045)**[*]	0.000 (1.000)	**4.657 (0.031)**[*]	0.000 (1.000)
Paternal line	0.000 (1.000)	0.000 (1.000)	0.360 (0.549)	0.419 (0.518)
Mat × Trt	0.000 (1.000)	0.000 (1.000)	0.400 (0.528)	**9.084 (0.003)**[*]
Pat × Trt	0.047 (0.828)	0.000 (0.998)	0.750 (0.387)	0.668 (0.414)
Fixed effect:				
Treatment	**43.686 (0.022)**[*]	**158.900 (0.006)**[**]	0.163 (0.726)	**107.433 (0.009)**[**]
Block	**5.935 (0.003)**[*]	0.577 (0.563)	1.722 (0.180)	0.904 (0.406)
Block × Trt	**7.471 (0.001)**[***]	0.190 (0.827)	0.631 (0.533)	0.869 (0.420)

Each model was fit separately for each trait listed along the top. Values for random effects correspond to χ^2 taken from likelihood ratio tests and fixed effects show *F*-statistic with *P*-value in parenthesis. Significance of treatment was tested using the block × treatment term as the denominator in the *F*-test. Significant effects are in bold and indicated with asterisks: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Table 2. Impact of interspecific competition on *I. purpurea* traits.

Trait	Growth (cm/day)	Grabbing on (day)	Phenology (day)	Relative fitness (no. of seeds)
Presence of competition				
Mean	**3.043**	**27.229**	60.183	**0.632**
Standard error	**(0.128)**	**(0.230)**	(0.358)	**(0.029)**
Absence of competition				
Mean	**9.587**	**25.000**	60.323	**1.361**
Standard error	**(0.363)**	**(0.375)**	(0.217)	**(0.045)**

Shown are means and standard errors of three focal traits and tolerance both in the presence of competition and the absence of competition. Numbers in bold are significantly different between treatments (see Table 1 treatment effect).
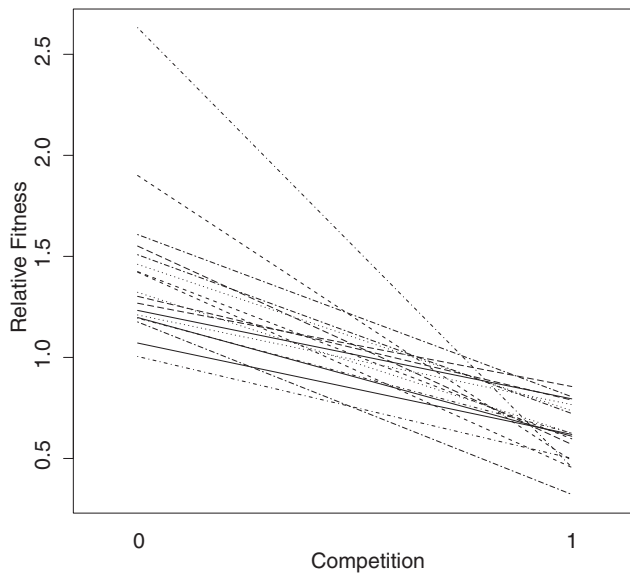

Figure 1. Relationship between relative fitness and competitive treatment for 18 maternal lines of *I. purpurea*. Different lines denote maternal-line means within the absence (0) and presence (1) of interspecific competition with maize. Evidence for genetic variation for tolerance to competition was found as seen by the heterogeneity of slopes. A slope of zero indicates complete tolerance whereas a steeper slope a less tolerant genotype.

differences among maternal lines, which can reflect an additive and nonadditive genetic basis as well as any potential lingering environmental maternal effects. Operationally defined tolerance for maternal lines indicated incomplete tolerance for all genotypes (genotypes grown in competition have lower relative fitness than genotypes grown alone). Tolerance values ranged from −2.1750 to −0.412 (mean = −0.786, SD = 0.430).

Costs and benefits of tolerance

Our analysis of the relationship between tolerance and fitness in the presence of competition found a benefit of being tolerant to competition (Fig. 2A). The corrected covariance between tolerance to competition and fitness in the presence of competition
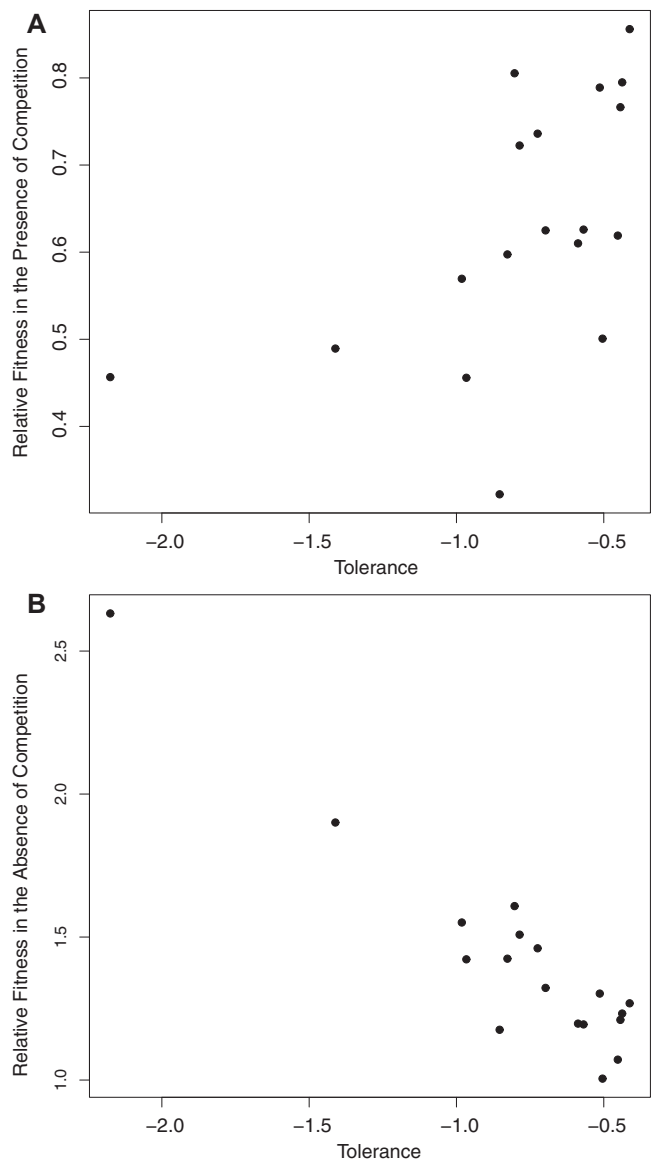

Figure 2. Relationship between relative fitness and tolerance in (A) presence and in the (B) absence of interspecific competition with maize. Maternal-line means of 18 *I. purpurea* plants are shown.

was equal to 0.025 (0.020, 0.029; 95% confidence interval) and is significantly different from zero ($t = 10.549$, $P < 0.001$). We further found that in the absence of competition, tolerance imposes a cost—the relationship between tolerance to competition and fitness was negative (Fig. 2B). The corrected covariance was equal to -0.082 (-0.133, -0.032; 95% confidence interval) and is significantly different from zero ($t = -3.178$, $P = 0.003$).

Selection acting on tolerance to competition and genetic correlations

In line with our cost/benefit analysis, the genotypic linear regression supports the notion that tolerance to competition is impacted by natural selection in *I. purpurea*. The regression of fitness on tolerance in the presence of competition indicates that tolerance is under positive directional selection (Table 3; $r = 0.542$, $P = 0.020$); however, a joint analysis of selection found that this relationship is mediated through direct linear selection on relative growth rate (Table 3; $\beta = 0.079$, $P = 0.008$) and a near significant positive correlation between tolerance and relative growth rate (Fig. 3A; $r = 0.452$, $P = 0.060$). We also uncovered a negative correlation between relative growth rate and date of "grabbing on" to a maize plant (Fig. 3A; $r = -0.597$, $P = 0.009$) in the presence of competition such that genotypes that grew faster also grabbed on earlier. Likewise, there was a negative correlation between date of "grabbing on" to a maize plant and tolerance—those that grabbed on to a maize plant were also more tolerant to competition (Fig. 3A; $r = -0.528$, $P = 0.024$). Most likely due to this correlation, we found negative directional selection on date of "grabbing on" (Table 3; $r = -0.728$, $P < 0.001$) in the presence of competition indicating that genotypes that grabbed on earlier are at a fitness advantage compared to those that grabbed on later in the season. Because date of "grabbing on" does not exhibit genetic variation of any kind (Table 1) selection is unlikely to act on this trait, and earlier "grabbing on" is likely due to the increased relative growth rate of those individuals.

In the absence of competition, there was strong negative directional selection on tolerance and phenology as indicated by significant negative correlations between each trait and fitness (Table 3; $r = -0.943$, $P < 0.001$ and $r = -0.770$, $P < 0.001$, respectively). Examination of the linear selection gradients uncovered negative direct selection on tolerance (Table 3; $\beta = -0.315$, $P < 0.001$)—likely due to flowering patterns in this species. We uncovered no evidence that phenology was phenotypically plastic (Table 1; treatment effect: $F_{1,2} = 0.163$, $P = 0.726$), and we found that tolerance was significantly positively correlated to phenology (Fig. 3; $r = 0.720$, $P < 0.001$), that is, maternal lines that are more tolerant flowered later in the season in the absence of competition. Taken together, these patterns suggest that early flowering is not a mechanism of tolerance to competition in *I. purpurea* and, in fact,

the cost of tolerance to competition is likely due to the later flowering time of more tolerant individuals compared to less tolerant individuals. Similarly, the analysis using full-sibling family lines ($n = 55$) revealed positive linear selection on relative growth rate and tolerance in the presence of competition; and as well, negative linear selection on tolerance in the absence of competition (Supporting Information Table S1). Furthermore, an analysis of correlations between traits based on family-line averages show that tolerance is positively correlated with relative growth rate in the presence of competition ($r = 0.415$, $P = 0.002$; Supporting Information Fig. S2) and phenology in the absence of competition ($r = 0.518$, $P < 0.001$; Supporting Information Fig. S2).

Quadratic selection gradients did not uncover evidence for nonlinear or correlated selection in any of our investigated traits (Table 3). We found no evidence for genetic correlations between tolerance to competition and the plasticity values of grabbing on ($r = -0.365$, $P = 0.150$) or relative growth rate ($r = 0.311$, $P = 0.209$). The same artifactual covariance between fitness and tolerance that was accounted for in the fitness cost/benefit analysis will also bias our selection analyses. Unfortunately, a procedure for removing this artifact with multiple regression has not been developed. However, in our cost/benefit analysis, we find this bias to be small and that it only marginally impacts our conclusions from the no-competition environment; the artifact does not significantly influence the covariance between fitness and tolerance in the presence of competition.

Discussion

Here, we present empirical evidence that tolerance to competition confers both a benefit and a cost in the agricultural weed, *I. purpurea*, and, correspondingly, that tolerance to competition is under positive selection in the presence of competition and negative selection in the absence of competition. However, our analysis does not find evidence for additive genetic variation underlying tolerance through paternal-line variation but rather finds significant maternal-line variation for this trait. This suggests that although natural selection favored lines that were more tolerant in the presence of competition, selection on this trait might not result in evolutionary change—or, alternatively, natural selection *could* result in evolutionary change, but predicting the response to such selection will be complicated by nonadditive genetic factors. Maternal effects can include additive and nonadditive genetic effects (e.g., dominance, epistasis) as well as inherited environmental influences; such effects originate from cytoplasmic genetic, endosperm nuclear, and maternal phenotypic sources (Roach and Wulff 1987). We grew parents in a common greenhouse environment for one generation prior to performing crosses, which should lessen, but perhaps not completely ameliorate the potential for field-derived maternal effects in our study population.

Table 3. Selection analysis showing direct and indirect selection on tolerance to competition and focal traits.

Trait	β	SE	P	γ	SE	P	r	P
Presence of competition								
Growth	**0.079**	**0.025**	**0.008**	−0.042	0.075	0.595	**0.807**	**<0.001**
Grabbing on	−0.039	0.028	0.194	0.034	0.096	0.732	**−0.728**	**<0.001**
Phenology	−0.024	0.023	0.322	0.036	0.083	0.680	−0.260	0.298
Tolerance	0.030	0.027	0.279	0.016	0.125	0.902	**0.542**	**0.020**
Growth × grab				−0.038	0.134	0.787		
Growth × phen				0.005	0.121	0.967		
Phen × grab				−0.070	0.117	0.571		
Absence of competition								
Growth	0.069	0.027	0.057	0.174	0.155	0.313	0.268	0.282
Grabbing on	0.005	0.032	0.869	−0.008	0.102	0.938	−0.084	0.749
Phenology	−0.042	0.044	0.367	−0.067	0.208	0.834	**−0.770**	**<0.001**
Tolerance	**−0.315**	**0.042**	**<0.001**	0.066	0.208	0.764	**−0.943**	**<0.001**
Growth × grab				0.197	0.230	0.432		
Growth × phen				−0.032	0.110	0.785		
Phen × grab				0.051	0.233	0.837		

Linear (β) and quadratic (γ) selection gradients, and total selection (r) with associated standard errors (SE) and P-values (P).

Linear coefficients were determined in each treatment from the first-order model only ($R^2 = 0.774$, $P < 0.001$ and $R^2 = 0.934$, $P < 0.001$; presence and absence of competition, respectively), whereas the second-order coefficients were determined from the full model with the linear, squared and cross-product terms ($R^2 = 0.904$, $P = 0.028$ and $R^2 = 0.959$, $P = 0.009$; presence and absence of competition, respectively). Quadratic regression coefficients were converted to selection gradients by doubling them and their respective standard errors. The r column represents the genetic correlations between the trait and fitness, estimated as Pearson product–moment correlations between maternal line means. Significant selection gradients and correlation coefficients are shown in boldface.

Furthermore, preliminary analyses indicated that there were no significant paternal × maternal effects (no effect of specific cross) for fitness or any other trait, and, analysis of reciprocal family effects was also not significant ($F_{4,55} = 1.131$, $P = 0.352$), indicating that offspring from the same full-sibling family did not differ depending on the identity of their seed parent. The absence of reciprocal effects but the presence of a maternal-line main effect indicates the presence of heritable genetic variation in tolerance (sensu Simms and Rausher 1989); however, because our breeding design generated a low number of reciprocal crosses (four reciprocal pairs) we are unable to draw this conclusion with a high degree of confidence.

Maternal effects underlying tolerance to competition may likewise be important in other plant species and/or experimental populations—previous work found a strong maternal effect responsible for competitive ability in *Desmodium paniculatum* (Wulff 1986), and Tiffin (2002) uncovered a significant family effect for tolerance to competition in *I. purpurea* grown in competition with crabgrass, *Digitaria sanguinalis*. Although the family-line variation identified in the Tiffin (2002) study was likely due to maternal variation, the crossing design employed did not allow for assessing the influence of paternal versus maternal-line variation, as did the design presented here. Although crossing designs that partition variation in traits into maternal environmental and maternal genetic effects are still relatively rare, based on the

results from our study, we suggest future studies of tolerance to competition should consider taking a multigenerational approach as well as one that uses a complete diallel design so that maternal environmental effects can be disentangled from maternal genetic effects.

Furthermore, we examined the potential that relative growth rate, phenology, and the date on which plants grabbed on to their competitor maize plant were tolerance traits. We found a trend for a positive correlation between tolerance and relative growth rate in the presence of competition using maternal-line means; analysis of family lines found a highly significant relationship between tolerance and relative growth rate. Our selection analysis on tolerance, which also included our putative tolerance traits, indicated that selection on competitive tolerance was *indirect* and mediated through direct, linear selection on relative growth rate and the positive correlation between tolerance and relative growth rate. Thus, relative growth rate contributes to tolerance to interspecific competition in the common morning glory and can be considered a tolerance trait—because it is both positively correlated to tolerance and increases plant fitness when in competitive stress (as per the definition of tolerance trait, Juenger and Bergelson 2000). Although this is the first study to show that relative growth rate is a tolerance trait when in interspecific competition, this result is broadly in line with our expectations. Another study in a sister species, *I. hederacea,* similarly found positive directional
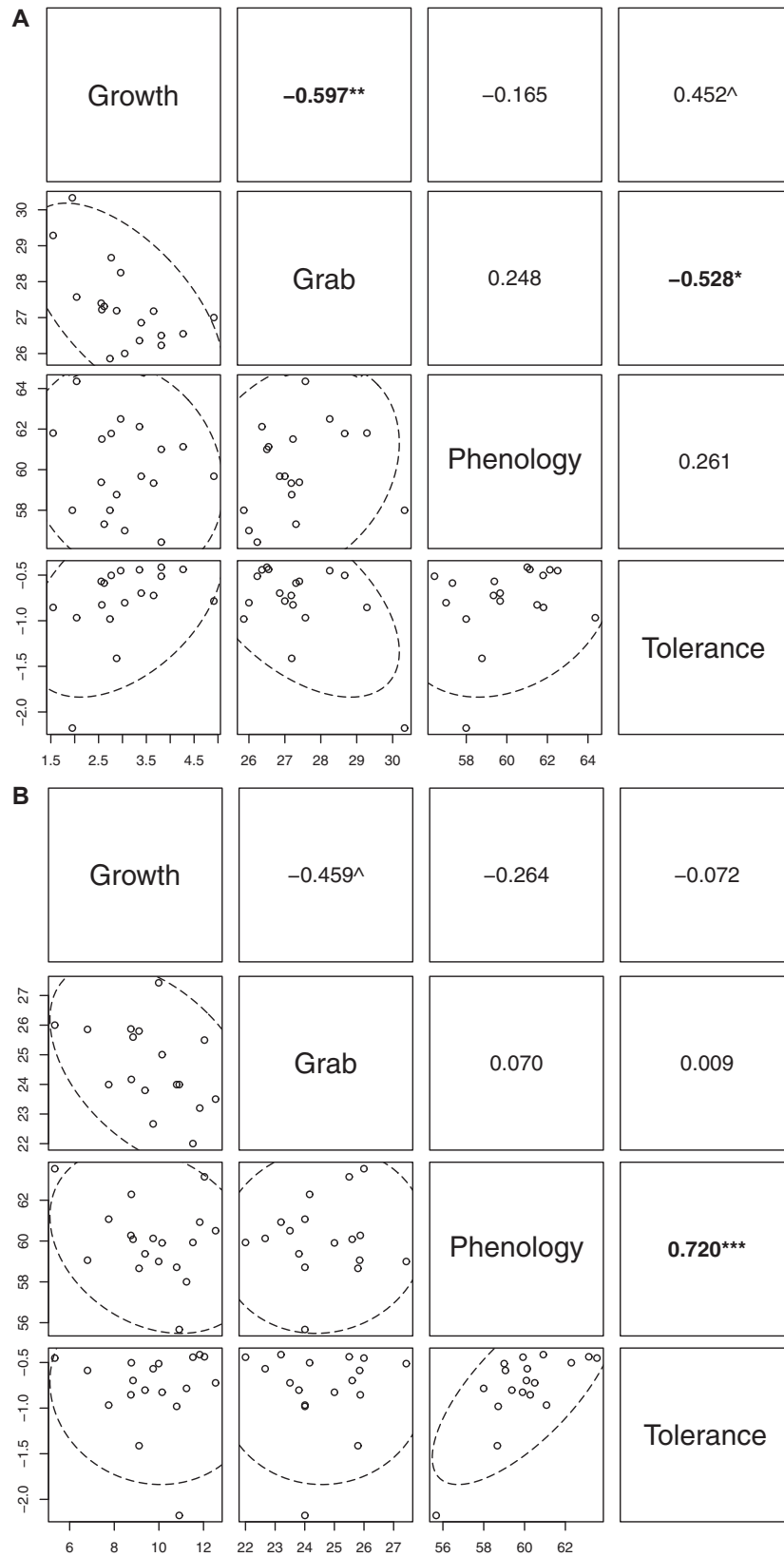
Figure 3. Genetic correlations among tolerance to competition and focus traits in the (A) presence and (B) absence of competition. Pearson's correlations coefficients (upper diagonal) were calculated using maternal line means. Scatter plots with 95% confidence region ellipsoids for each pairwise trait combination is displayed in the lower diagonal. Significant values are in bold and indicated with asterisks: ˆ$P < 0.10$, *$P < 0.05$, **$P < 0.01$, and ***$P < 0.001$. Growth, relative growth rate; grab, day of grabbing on; phenology, day of first flower; tolerance, tolerance to competition.

selection on growth when in interspecific competition (Simonsen and Stinchcombe 2010). Compensatory regrowth has previously been found as a tolerance to herbivory trait (Juenger and Bergelson 2000; Tiffin 2000); however, more recently, it was found that growth can be a defense trait itself (Turley et al. 2013). Additionally, plant growth has previously been found as a key trait for plant competitive success, particularly in agriculture (Radosevich and Roush 1990) and in *Impatiens capensis* and *Arabidopsis thaliana* grown in inter- and intraspecific competition, respectively (McGoey and Stinchcombe 2009; Willis et al. 2010).

In comparison, we found no relationship between tolerance to competition and relative growth rate in the absence of competition; instead, we found evidence that tolerance is positively correlated to phenology. The cost of tolerance is likely due to this correlation—maternal lines that are more tolerant initiated flowering later in the absence of competition in comparison to lines that were less tolerant, putting them at a fitness disadvantage. In line with this result, our selection analysis uncovered strong negative, *direct* linear selection on tolerance in the absence of competition. These patterns of selection indicate that tolerance should decrease in the absence of competition. Unlike relative growth rate and time to grabbing on the competitor plant, we uncovered no indication that phenology was phenotypically plastic. These results together suggest that phenology, although genetically correlated with tolerance, does not contribute to tolerance in *I. purpurea*. Such findings are counter to expectations—other studies have found that earlier flowering following stress is related to tolerance (Juenger and Bergelson 2000; Tiffin 2000; Willis et al. 2010), and, early flowering has long been hypothesized to be correlated to tolerance because plants that exhibit the shortest delay in reproduction following damage or stress will likely be able to maintain their fitness (Tiffin 2000).

Interestingly, and similar to tolerance to competition, both traits—relative growth rate and phenology—did not exhibit additive genetic variation in our breeding population but did exhibit maternal-line variation. Thus, the evolutionary dynamic of tolerance to competition, relative growth rate, and flowering time are each under maternal genetic and/or maternal non-genetic influences. Although maternal effects can strongly affect evolutionary processes (McGlothlin and Galloway 2013), this may come in unexpected and counterintuitive ways due to cross-generation effects of both the current previous generations. Maternal effects in a population may result in enhanced or reduced responses to selection, reversals in the direction of the response, or oscillatory dynamics (Galloway et al. 2009). Because direct and indirect components underlying genetic variation alter our usual predictions about changes in genetic values associated with selection (Wolf et al. 1998), the response to selection reported on the traits in our study should be viewed as an upper limit to responses that are possible.

Taken together, these results provide a broad view of tolerance to competition as a competitive response trait. *Ipomoea purpurea* plants that grow faster are at an advantage in the presence of competition, because faster growing plants can emerge from vegetation to access photosynthetic resources. However, genotypes that are more tolerant will flower later and thus be at a disadvantage when grown in the absence of competition compared to those that are less tolerant. Our results show that tolerance to competition can likely increase in natural populations of this weed species (assuming the maternal-line variation we uncovered is heritable), and, relative growth rate of individuals contribute to this tolerance. The evolution of increased tolerance is constrained by a fitness cost—and the source of this cost appears to be driven by day of first flowering. However, the presence of maternal-line variation underlying tolerance and the traits correlated to tolerance suggest that their evolutionary dynamics may in fact be more complicated, especially because maternal effects can either hinder or enhance adaptive evolution (McGlothlin and Galloway 2013).

Conclusion

Variation among species' competitive abilities has long been recognized (Goldberg 1996), as have fitness declines due to plant–plant competition (Reichenberger and Pyke 1990; Goldberg and Barton 1992; Schmitt and Wulff 1993). However, the potential that competitive tolerance exhibits either a benefit or a cost has not previously been reported. Weedy plants are known to undergo rapid adaptive evolution on short ecological time scales (Vigueira et al. 2013) and are confronted with powerful and fluctuating selection pressures that result from changes in cropping systems (Clements et al. 2004). Studying competition in an agriculture system offers a simplified plant community that provides links to the mechanisms and implications of competition in plant communities, as well as provides an ecological and evolutionary basis for crop–weed management (Radosevich and Roush 1990).

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table S1: Selection analysis showing direct and indirect selection on tolerance to competition and focal traits for family line means.
Figure S1: Partial-diallel crossing design used to generate experimental individuals.
Figure S2: Family line mean correlations among tolerance to competition and focus traits in the (A) presence and (B) absence of competition.