

THE EVOLUTIONARY POTENTIAL OF BAKER'S WEEDINESS
 TRAITS IN THE COMMON MORNING GLORY, *IPOMOEA PURPUREA*
 (CONVOLVULACEAE)¹

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- *Premise of the study:* Many reports have cited Baker's list of weediness traits, or those that exemplify the "ideal" weed, yet few have considered the evolutionary potential of such traits as a group. Thus, it is unknown whether constraints on the evolution of increased weediness, such as a lack of genetic variation or genetic correlations between the traits, are present. *Ipomoea purpurea*, the common morning glory, is a problematic weed that exhibits many of Baker's ideal weed traits.
- *Methods:* We used progeny from a half/full-sib breeding design in a series of three greenhouse experiments to assess the presence of genetic variation, narrow sense heritabilities, and genetic correlations in Baker's growth, competition, and fitness "weediness" traits in two populations of *I. purpurea*.
- *Key results:* We uncovered genetic variation underlying reproductive fitness traits and competitive ability in at least one population, but no evidence of genetic variation underlying growth rate in either population. Genetic correlations between many of the weediness characters differed significantly from zero; however, their direction and/or magnitude differed between populations.
- *Conclusions:* We found that increased weediness in the common morning glory is more likely to occur through selection on reproductive output and competitive ability rather than through selection on growth rate. Assessing Baker's traits in a quantitative genetics framework can provide a solid perspective on their evolutionary potential and a unique framework within which to determine how weeds will respond to different environmental stresses and/or scenarios of global climate change.

Key words: Baker's traits; Convolvulaceae; genetic correlations; genetic variation; heritability; *Ipomoea purpurea*; morning glory; weed.

In 1965, Baker produced a list of weediness traits, or those he thought defined the ideal weed (Table 1) (Baker, 1965, 1974). He compiled this list by comparing traits of weedy and nonweedy congeners; he considered species that exhibit many of these traits to be major weeds, whereas those that exhibit few are minor weeds. Baker's list is heavily cited in both the invasive plant (e.g., Sutherland, 2004; Richards et al., 2006; Muth and Pigliucci, 2006; Whitney and Gabler, 2008) and weed ecology literature (e.g., Young and Evans, 1976; Holt and Orcutt, 1991; Perrins et al., 1992; Chao et al., 2005) and has been used primarily to predict which weeds will become invasive (Mack, 1996; Daehler, 1998; Goodwin et al., 1999). Despite the focus on Baker's list, the processes that govern the evolution of multiple weediness traits have yet to be considered *within* a species. This omission is especially relevant since Baker himself stated that "weeds are excellent subjects for the study of *microevolution*" (our italics, Baker, 1974, p. 1).

The evolution of weediness traits may play an important role in the establishment and spread of weedy and invasive species (Sakai et al., 2001; Dlugosch and Parker, 2008). If weediness traits such as competitive ability or relative growth rate lack genetic variation, the potential for the species to evolve into a

more troublesome weed might be limited (Maynard Smith et al., 1985; Falconer and Mackay, 1996). While genetic variation has been found in floral and plant growth traits of some weedy plants (Conner and Via, 1993; O'Neil, 1997; Sahli et al., 2008), the evolutionary potential of multiple Baker's traits has yet to be explicitly considered within a single species. In addition, the possibility that such traits are correlated and thus potentially act as constraints on their respective or dual evolutionary trajectories has not previously been examined (Lande, 1979; Conner and Via, 1993; Stanton and Young, 1994; Agrawal and Stinchcombe, 2009). Assessing Baker's traits in a quantitative genetics framework can provide perspective on their evolutionary potential; such a view can also allow predictions to be made regarding how agricultural regimes may or may not select for more problematic weeds over time (De Wet and Harlan, 1975).

The common morning glory, *Ipomoea purpurea* (L.) Roth. (Convolvulaceae), a plant that exhibits at least nine of Baker's 12 ideal weed traits (see boldfaced sections of Table 1), is often found in agricultural fields and is a highly effective competitor that restricts crop productivity by climbing onto and up crop species (Cordes and Bauman, 1984). Plants of this species can grow as rapidly as 20 cm per day (R. S. Baucom, unpublished data) and will produce many flowers in a growing season (daily: 0–80). Flowers are pollinated by bumblebees and generalist species (Epperson and Clegg, 1987; Chang and Rausher, 1998) but are also capable of self-fertilization (Ennos, 1981). Each plant can produce around 10000 seeds each season (Crowley and Buchanan, 1982). Additionally, *I. purpurea* is tolerant of a variety of stressors including herbivores (Tiffin, 2002), pathogens (Simms, 1993), and herbicide (Baucom and Mauricio,

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TABLE 1. Baker’s ideal weed characteristics. The traits of *I. purpurea* are in boldface, and traits examined in the present work are underlined. Adapted from Baker (1974).

No.	Trait
1	Germinates in many environments
2	Great longevity of seed
3	<u>Rapid growth through vegetative phase to flowering</u>
4	<u>Continuous seed production</u>
5	Self-compatible
6	When cross-pollinated, unspecialized visitors or wind used
7	<u>Very high seed output</u>
8	Tolerant and plastic
9	Has adaptations for short- and long-distance dispersal
10	Vigorous vegetative reproduction or regeneration from fragments
11	Plant not easily drawn from the ground
12	<u>Ability to compete interspecifically by special means</u> (rosette, <u>choking growth</u> , allelochemicals)

2004). Thus, this species could be classified as one of Baker’s major weeds.

Here, we assessed the evolutionary potential of Baker’s ideal weed traits in *I. purpurea* using a common garden greenhouse study. Although this species exhibits the majority of Baker’s weediness traits, we focused our efforts on estimates of growth, competition, and reproductive fitness (Table 1, underlined and boldfaced). We asked: (1) Is there evidence of genetic variation underlying Baker’s weediness traits in *I. purpurea*? (2) Are the traits genetically correlated to one another such that selection on one trait could cause a constraint on the evolution of the other?

MATERIALS AND METHODS

Study species—The common morning glory, *Ipomoea purpurea* (L.) Roth. (Convolvulaceae), is a climbing annual vine native to central America and commonly found in disturbed sites in the United States. Germination occurs from mid-May to August and flowers are produced about 6 wk after emergence until the plant senesces or killed by frost (Brown and Clegg, 1984; Uva et al., 1997). Flowers open early in the morning and last a single day. In the United States, *I. purpurea* is often found in maize, soy, and cotton fields and can cause significant losses in crop yield (Cordes and Bauman, 1984; Defelice, 2001), which has led to its inclusion on the list of the top 10 troublesome weeds in agriculture in the southern United States (Webster and Coble, 1997).

Crossing design—A partial diallel crossing design was used to generate experimental individuals. Two populations with different collection and breeding histories were assessed so that a broad perspective of the variation within this species could be examined. One population (hereinafter NC), generously supplied by M. Rausher, was collected in 1985 in Durham, North Carolina and inbred in the greenhouse for about 15 generations. The other population (hereinafter GA) was originally collected from an agricultural field in Oconee Co., Georgia in 2001 and selfed once in the greenhouse. Crosses were performed for each of the two populations using a full/half-sibling breeding design, with two diallels per population and 10 maternal lines per diallel, yielding 40 maternal lines total. One seed from each of the 40 maternal lines was planted on 5 August 2010 in the University of Cincinnati greenhouse in a 4-inch pot with a general-purpose soil (Fafard 3B Mix, Agawam, Massachusetts, USA), and fertilized with a 20-4-8 NPK fertilizer (Scott’s Osmocote Pro, Marysville, Ohio, USA). Plants were exposed to supplementary sodium halide lights on a 16-h day schedule. Pollinations were performed by touching anthers of the parental plant to the stigma of the maternal parent. To prevent self-pollination, we emasculated all individuals the night before crosses were made. For this partial diallel crossing design (Simms and Rausher, 1987), each individual was crossed as a maternal plant to five paternal plants, and as a paternal plant with five maternal plants (Fig. 1). These crosses produced 200 families total. Replicate seeds from these families were then used for the three common-garden greenhouse

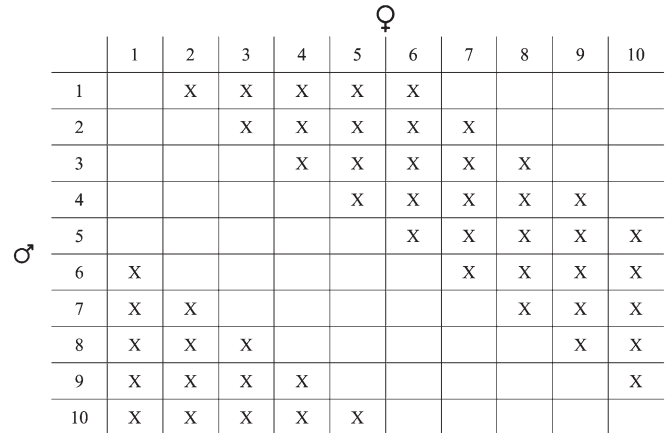


Fig. 1. Partial-diallel crossing design used to generate experimental individuals. Crosses were performed for each cell with an X. The same set of plants used as maternal parents was used as paternal parents. Two diallels were used for each of the two populations.

experiments described next. The destructive harvest in two of our response variables necessitated a series of three experiments. Due to greenhouse space and seed number limitations, not all 200 families were used in each experiment; however, the highest number possible of common families was used to provide uniformity across experiments.

Experimental procedure—Relative growth rate—In the first experiment, we assessed variation in the relative growth rate of *I. purpurea* to address Baker’s “rapid growth through vegetative phase to flowering” weediness trait. On 20 December 2010, we scarified and planted eight replicate seeds from 192 families for a total of 1536 individuals. Seeds were planted in supercell conetainers (164-mL capacity; Stuewe and Sons, Tangent, Oregon, USA) in general-purpose soil (Fafard 3B Mix) in a randomized design in the University of Cincinnati greenhouse and watered daily. After 4 wk of growth, shoots of half of the replicates were harvested. Fourteen days later, shoots of the remaining four replicates were harvested. All plants were in a vegetative phase at time of both harvests. All shoot mass was dried in a drying oven at 70°C for 3 d and weighed to measure dry biomass. Relative growth rate (RGR) for each family was calculated using the mean natural logarithm-transformed plant biomass (*W*) to avoid bias in the formula

$$RGR = \frac{\ln \overline{W}_2 - \ln \overline{W}_1}{t_2 - t_1}$$

where $\ln \overline{W}_t$ is the mean of the ln-transformed plant biomass at time *t* (Hoffmann and Poorter, 2002).

Competitive ability—A second experiment was used to examine Baker’s competitive ability (“the ability to compete interspecifically by special means such as choking growth”) in two ways: (1) as the date that plants “grabbed on” to a competitor maize plant or nearest object (such as a bamboo stake); (2) as an estimate of dry biomass of plants grown in competition with maize. A plant was considered to have “grabbed on” when the plant’s vining stem created a C-shaped hook around the maize plant or bamboo stake. Three replicates of 145 families were planted in two treatments—in the presence or absence of maize—for a total of 870 experimental plants. General-purpose soil (Fafard 3B Mix) was filled 5 cm deep in 15 cm deep square kordlok pots (Myers Industries, Middlefield, Ohio, USA). On 14 February 2011, one seed of Golden Cross Bantam sweet corn (Ferry Morse, Fulton, Kentucky, USA) was planted in half of the pots in a randomized design in the University of Cincinnati greenhouse and watered daily. After 2 wk, when the maize was ca. 20 cm tall, *I. purpurea* seeds were scarified with a razor blade and planted in every pot. We allowed maize to establish prior to planting the experimental *I. purpurea* seeds as this pattern is the general trend seen in agricultural crops. Additionally, we wished to follow the experimental design of Price and Wilcut (2007) who examined the climbing growth habit of *I. hederacea* toward different-colored stakes or maize. We provided the “no maize” treatment individuals with 60 cm tall bamboo stakes. All plants were harvested on 30 March and dried in a drying oven at 70°C for an estimate of dry biomass.

Flowering—On 23 February 2011, we planted three scarified replicate seeds of 196 families (588 individuals total) in supercell containers (164-mL capacity; Stuewe and Sons), with general-purpose soil (Fafard 3B Mix), in a completely randomized design in the University of Cincinnati greenhouse and watered daily. Plants were fertilized and treated with insecticide as needed throughout the duration of the experiment. The length of flowering and total number of flowers was collected once flowering began on 11 April. Every 2 d, the flowers and buds on each plant were counted. Counting the flowers and buds every other day leads to a good approximation of the total number of flowers produced by each individual plant since the flowers of *I. purpurea* are open for a single day and flower buds are present on plants the day prior to opening. Flowering data were collected until the end of the experiment on 5 July, 4 mo from the initial planting, which is approximately the length of time *I. purpurea* plants flower in field conditions. We used total number of flowers and length of flowering as a proxy for Baker's "very high seed output" and "continuous seed production" weediness characters since our studies were performed in the greenhouse without natural pollinators and since releasing natural pollinators in the greenhouse was not an option. Further, total number of flowers in this species is an excellent predictor of total number of seed ($r = 0.924$, $t = 13.23$, $N = 32$ (maternal lines), $P < 0.0001$; R. S. Baucom and R. Mauricio, unpublished data); thus, we can be reasonably certain that the length and total number of flowers produced provides a good approximation of reproductive fitness in this annual species.

Data analysis—Data proofing—Data were used only when the plants germinated, survived throughout the duration of the experiment, and in the flowering experiment, flowered. Examination of the data revealed that total number of flowers was nonnormal and exhibited positive skew; thus, we performed a log ($y + 1$) transformation, which improved normality upon examination of the residuals.

Genetic variation in Baker's weediness traits—We used a series of univariate mixed model REML analyses of variance to test for the presence of genetic variation in the following Baker's weediness traits: relative growth rate, total number of flowers, length of flowering, and two measures of competitive ability (see underlined sections of Table 1). The MIXED procedure of the SAS Statistical Software (version 9.2; SAS, Cary, North Carolina, USA) was used to perform separate analyses of each population. We analyzed models for the relative growth rate and flowering experiments with the model (1) trait = μ + diallel + maternal line (diallel) + paternal line (diallel) + ϵ and for the competitive ability experiment with the model: (2) trait = μ + treatment + diallel + maternal line (diallel) + paternal line (diallel) + treatment \times maternal line (diallel) + treatment \times paternal line (diallel) + ϵ , where μ is the intercept or mean of the model (fit by default), treatment and replicate diallel as fixed effects and terms involving pedigree (maternal and paternal line) as random effects. The significance of random effects was determined using the likelihood-ratio statistic. The difference between the $-2 \log$ likelihood of the full model and the model with the random effect removed was calculated, and the P -value was determined with a χ^2 test with one degree of freedom. Significant paternal effects would indicate the presence of additive genetic variation, whereas a significant maternal effect indicates the presence of additive and nonadditive genetic variation. The interaction effect of maternal and paternal line was not included in the final model as preliminary analysis indicated that it was not a significant effect, and further, its inclusion does not inform the main conclusions of this study.

To determine whether genetic variation was present for growth rate in the two *I. purpurea* populations, we used relative growth rate of each family as the dependent variable and diallel and maternal and paternal line nested within diallel as the independent variables. Maternal and paternal lines were random effects in the model, and diallel was considered a fixed effect.

Variation in competitive ability was tested using a mixed model with either biomass or the day that the vine grabbed on as the dependent variable, maternal and paternal line nested within diallel, diallel, the treatment effect (maize or no maize) and the interaction of maternal and paternal line with treatment as independent variables. Maternal and paternal lines were included as random effects in the model with treatment and diallel as fixed effects, and interaction effects were considered random.

Genetic variation underlying the total number of flowers and length of flowering was likewise tested using a series of mixed model analyses of variance with diallel and the maternal and paternal line nested within diallel as independent variables. Maternal and paternal lines were random effects in the model, and diallel was considered a fixed effect.

For each trait, narrow sense heritability (h^2) was estimated as four times the paternal variance component divided by the total phenotypic variance as

determined in the mixed model ANOVAs (Falconer and Mackay, 1996). Significance tests of individual heritabilities are from the likelihood-ratio tests of the paternal line variance component of the earlier PROC MIXED models (Conner et al., 2003). Population differences in the traits were tested by using the LSMEANS function in PROC MIXED with the effects as described already, this time including the term population as a fixed effect (Caruso, 2004).

Genetic correlations and covariances between Baker's weediness traits—We assessed the strength and direction of genetic correlations and covariances among paternal line means of weediness traits by performing the CORR COV procedure in SAS. Paternal line means were calculated by averaging trait values for each paternal line. The significance of genetic correlations and covariances was assessed by resampling the data using the jackknife procedure across each paternal line (Roff and Preziosi, 1994). A t -statistic was used to calculate a P -value for the confidence interval to determine whether the correlations between the two measures differed from zero. P -values were corrected for type I errors using the Bonferroni procedure.

RESULTS

Two of the five measures of Baker's weediness traits—total number of flowers and length of flowering—differed between the GA and NC populations ($F_{1,35} = 20.42$, $P < 0.0001$ and $F_{1,35} = 14.33$, $P = 0.001$, respectively). The NC population flowered 76% longer and had nearly three times more flowers compared to the GA population (GA 6.03 ± 0.76 , 18.10 ± 1.95 and NC 17.26 ± 1.67 , 31.84 ± 1.81 ; total number and length of flowering means ± 1 SE, respectively). The estimates of relative growth rate and competitive ability (biomass with maize and day of grabbing on to maize) did not differ significantly between the two populations ($F_{1,36} = 0.83$, $P = 0.370$; $F_{1,36} = 1.04$, $P = 0.314$; and $F_{1,35} = 0.94$, $P = 0.339$; respectively).

We detected additive genetic variation in two of the five traits studied in the NC population (Table 2: i.e., a significant paternal line effect): total number of flowers and length of flowering. One measure of competitive ability, the day that the vine grabbed on to the maize plant or stake, exhibited a trend for paternal line variation (Table 2, $P = 0.083$). In comparison, the GA population showed no significant additive genetic variance in the weediness traits we investigated; however, this population exhibited a significant maternal line effect of day of grabbing on (Table 2). These results provide evidence of genetic variation in weediness traits underlying the reproductive fitness and competition in at least one population of *I. purpurea*.

The heritability of these traits ranged from 0 to 0.716 in the NC population (Table 3) and 0 to 0.484 in the GA population (Table 4). Although the heritability for total number of flowers in the GA population was moderate, our mixed model REML analysis did not uncover significant genetic variation in this trait ($P = 0.129$) in the greenhouse environment.

For both populations, there was a significant treatment effect of maize in terms of competitive ability, i.e., both the day of grabbing on and biomass of plants were significantly impacted by the presence of maize. This competition resulted in a 21% reduction in biomass of *I. purpurea* plants, and, on average, a lag of 2 d for grabbing on when plants were grown with maize. The interaction effect between maize and the maternal and/or paternal line was not significant in either population, suggesting that the paternal and maternal lines responded similarly in the presence of maize as in the presence of stakes (Table 2).

All of the genetic correlations and covariances among Baker's weediness traits differed significantly from zero following Bonferroni corrections, with one noted exception in the GA population (Tables 3, 4). In both populations, the length of

TABLE 2. Results of mixed-model REML analysis demonstrating genetic variation for Baker's weediness traits in two populations. Models were fit separately for each trait. The variance estimate is given for each random effect, boldfaced if significant, with P -value given in parentheses (calculated from log-likelihood χ^2 value with $df = 1$). For fixed effects, the F -statistic is given with P -value given in parentheses.

Effect for each population	Relative growth rate (P)	Total no. of flowers (P)	Duration of flowering (P)	Biomass (P)	Day of grabbing on (P)
Population: North Carolina					
Random effects					
Maternal (Diallel)	0.000 (0.584)	0.000 (1.000)	0.000 (1.000)	0.000 (0.752)	0.000 (1.000)
Paternal (Diallel)	0.000 (1.000)	0.120 (0.048)	80.887 (0.003)	0.001 (0.439)	1.220 (0.083)
Mat \times Maize (Diallel)				0.000 (1.000)	0.000 (1.000)
Pat \times Maize (Diallel)				0.001 (0.655)	0.000 (1.000)
Fixed effects					
	$F_{1,18}$	$F_{1,18}$	$F_{1,18}$	$F_{1,18}$	$F_{1,18}$
Diallel	0.83 (0.374)	0.36 (0.557)	0.13 (0.724)	4.24 (0.054)	1.16 (0.296)
Maize				301.7 (<0.0001)	22.51 (0.0002)
Population: Georgia					
Random effects					
Maternal (Diallel)	0.000 (1.000)	0.000 (1.000)	0.000 (1.000)	0.001 (0.439)	1.371 (0.018)
Paternal (Diallel)	0.000 (1.000)	0.078 (0.129)	8.834 (0.752)	0.000 (1.000)	0.257 (0.403)
Mat \times Maize (Diallel)				0.002 (0.371)	0.000 (1.000)
Pat \times Maize (Diallel)				0.000 (1.000)	0.000 (1.000)
Fixed effects					
	$F_{1,18}$	$F_{1,17}$	$F_{1,17}$	$F_{1,18}$	$F_{1,18}$
Diallel	1.01 (0.328)	1.07 (0.315)	1.20 (0.288)	4.62 (0.046)	2.92 (0.105)
Maize				322.5 (<0.0001)	49.89 (<0.0001)

flowering was positively correlated with the total number of flowers produced, suggesting that plants that flower longer will exhibit higher fitness. In the NC population, we identified low but significant positive correlations between day of grabbing on to maize with the total number of flowers produced ($r = 0.188$). We also uncovered a low but significant negative correlation between the day of grabbing on and the length of flowering ($r = -0.111$); plants that grabbed on to their maize plant earlier flowered for a longer period compared to those that grabbed later. These relationships were different in the GA population. Day of grabbing on was positively correlated with length of flowering ($r = 0.132$); plants that grabbed on earlier flowered for a shorter period. In the GA population, the correlation of the day of grabbing on to maize and total number of flowers was not significant ($r = 0.004$, $P = 0.692$).

DISCUSSION

We detected the presence of genetic variation underlying some, but not all, of the investigated Baker's weediness traits. The reproductive fitness traits—total number of flowers and length of flowering—exhibited variation, with a trend for variation in competitive ability. Somewhat surprisingly, relative growth rate did not exhibit evidence of variation, suggesting that past natural selection has acted to increase the growth rate of the common morning glory, thus leading to a lack of detectable variation (Fisher, 1930; Wright, 1935; Lande, 1982). This

is consistent with the observation that *I. purpurea* plants are extremely fast growers, that can increase in height around 20 cm per day in ideal conditions (R. S. Baucom, unpublished data). Other interpretations are that variation in this trait has never been present in this species or that our power to detect it was low. Relative growth rate was calculated per family (see Methods) rather than for each individual, reducing our sample size (from $N = 15$ per paternal line to $N = 5$ per family line). To address the possibility that our power was too low to detect genetic variation in relative growth rate, we performed a post hoc power analysis using G*Power 3 (Faul et al., 2007), which showed that the power in this analysis was indeed low ($1 - \beta = 0.254$). As such, we considered other estimates of growth that would allow us to maintain a higher sample size, i.e., biomass, number of leaves, and plant height at the second time of sampling, as well as individual leaf relative growth rate (leaf number at t_2 - leaf number at t_1). Although both the sample size ($N = 15$ per paternal family) and the power for these analyses were much higher ($1 - \beta > 0.900$), mixed-model analyses of variance provided no evidence of genetic variation underlying these potential correlates of growth in either population. We tentatively suggest that our failure to detect variation is due to a real lack of genetic variation underlying relative growth rate in the common morning glory rather than low power.

Ipomoea purpurea is a vining weed species that climbs onto and up prostrate competitors, quickly overtopping them; thus this species exhibits Baker's weediness trait the "ability to compete interspecifically by special means such as choking growth."

TABLE 3. Narrow-sense heritabilities (in boldface on the diagonal) and paternal line mean correlations (above diagonal) and covariances (below diagonal) with jackknifed 95% CIs in parentheses, for Baker's weediness traits in the North Carolina population.

Trait	Relative growth rate	Total no. of flowers	Duration of flowering	Biomass with maize	Day of grabbing on to maize
Relative growth rate	0.000	-0.321 \pm 0.015	-0.188 \pm 0.025	-0.247 \pm 0.027	0.421 \pm 0.020
Total no. of flowers	-0.007 \pm 0.006	0.416*	0.710 \pm 0.012	0.048 \pm 0.029	0.188 \pm 0.030
Duration of flowering	-0.091 \pm 0.012	4.229 \pm 2.396	0.716**	0.205 \pm 0.018	-0.111 \pm 0.029
Biomass with maize	0.000 \pm 0.000	0.001 \pm 0.008	0.088 \pm 0.008	0.000	-0.575 \pm 0.019
Day of grabbing on to maize	0.037 \pm 0.002	0.201 \pm 0.474	-2.635 \pm 0.660	-0.045 \pm 0.002	0.171

Notes: All correlations and covariances are significant with Bonferroni corrected P -values. Significance tests of individual heritabilities are from log-likelihood test of the paternal variance component (see Methods) and are denoted with asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

TABLE 4. Narrow-sense heritabilities (in boldface on the diagonal) and paternal line mean correlations (above diagonal) and covariances (below diagonal) with jackknifed 95% CI's presented in parentheses, for Baker's weediness traits in the Georgia population.

Trait	Relative growth rate	Total no. of flowers	Duration of flowering	Biomass with maize	Day of grabbing on to maize
Relative growth rate	0.000	0.051 ± 0.027	0.271 ± 0.029	-0.523 ± 0.013	0.321 ± 0.020
Total no. of flowers	0.001 ± 0.000	0.484	0.670 ± 0.017	-0.067 ± 0.028	0.004 ± 0.021 NS
Duration of flowering	0.050 ± 0.005	2.802 ± 0.137	0.101	-0.193 ± 0.017	0.132 ± 0.028
Biomass with maize	0.000 ± 0.000	-0.001 ± 0.000	-0.038 ± 0.003	0.000	-0.730 ± 0.009
Day of grabbing on to maize	0.015 ± 0.001	0.004 ± 0.019 NS	1.797 ± 0.356	-0.046 ± 0.002	0.000

Notes: All correlations and covariances are significant with Bonferroni corrected *P*-values, with two noted exceptions (NS). Although reported, heritabilities in this population do not differ significantly from zero.

To address competitive ability by choking growth, we recorded the day of grabbing on to a stake or plant competitor because we hypothesized that those plants that grab on earliest are likely the ones that also produce the most biomass in the presence of competition. We uncovered a trend for paternal line variation in the day of grabbing on in the NC population ($P = 0.083$), such that some paternal lines began to vine onto their nearest neighbor earlier than others. Furthermore, the GA population exhibited maternal line variation in this trait ($P = 0.026$), an effect that includes both additive and nonadditive components of genetic variance.

The presence of variation underlying this trait would be of little consequence if there were no size and/or fitness benefit of producing choking or vining growth early in the growing season. As such, we investigated the relationship between date of grabbing on and biomass while in the presence of maize competition, and we found a significant negative genetic correlation in both populations (GA: $r = -0.730$, $P < 0.001$; NC: $r = -0.575$, $P < 0.001$), suggesting that plants that vine onto competitors earlier are also larger and thus putatively better competitors. The present series of experiments cannot address whether vining capability is simply due to being larger or to an innately different plant sensory and/or climbing ability. Previous work with *I. hederacea*, sister to *I. purpurea*, found that plants of this species appear to respond to reflectance of nearby objects and to project stems toward neighboring structures such as differently colored bamboo stakes. Further, plants that were successful in climbing weighed more and produced more seeds than morning glories that did not climb (Price and Wilcut, 2007). Thus, it is possible that competitive "vining" capability could be due to more than size in *I. purpurea*.

The relationship between competitive ability and reproductive fitness differed in the two populations. *Ipomoea purpurea* plants from the NC population had a negative correlation between date of grabbing on and length of flowering ($r = -0.111$), suggesting that those that climbed onto their competitor earlier also flowered longer. There was a significant positive correlation between the date of grabbing on to a competitor and the total number of flowers produced ($r = 0.188$), suggesting that earlier vining would not necessarily produce a greater fitness return. Individuals from the GA population had the opposite relationship: there was a positive correlation between date of grabbing on and duration of flowering ($r = 0.132$). These results suggest a trade off between competitive growth and reproductive fitness in this population—those that grab on earlier will flower for a shorter duration, whereas if they grab on later, they flower longer. Despite this potential trade off, there was no detectable correlation in this population between the total number of flowers produced and day of grabbing on to the competitor. Although it is interesting that the two populations differ regarding presence/absence of genetic variation and the pattern of some genetic

correlations, we do not know whether historical, geographic, collection time, or other differences such as breeding history are responsible for the differences. Further studies are required to parse out these differences in populations. We chose to assess these traits in more than one population in an effort to include a wider range of the potential variation in this species.

Our findings of significant genetic variation in reproductive fitness traits—total number of flowers and length of flowering—and a trend for variation in competitive ability suggests that selection on these traits could lead to the evolution of increased/decreased weediness. That we uncovered genetic correlations among such traits suggests that weediness should be considered in a multivariate context (Lande 1979; Agrawal and Stinchcombe, 2009). For example, if, in the NC population, either the total number of flowers or length of flowering were under positive selection, we would predict an increase in the overall reproductive fitness of the plant through the production of more flowers and over a longer period. If, however, selection favored a simultaneous increase in one trait and a decrease in the other, the positive correlation detected here may function as a constraint on the evolution of either trait (Lande, 1979; Lande and Arnold, 1983). Likewise, in the NC population, a trade off potentially exists between being a grabbing competitor and overall fitness return in that there was a weak positive relationship between the total number of flowers produced and the time in which a plant grabbed on to a nearby object. This relationship might reflect a fitness cost of early grabbing in the absence of intense competition, a highly likely scenario for this species because it is often found vining up agricultural competitor crops. Although most of our genetic correlation values were significant, many of them were low; thus, the extent to which the correlations identified here represent evolutionary constraints is currently unknown. An assessment of these traits in a natural setting would provide insight on the pattern of natural selection on weediness traits.

Although our study explicitly assesses the evolutionary potential of the traits that exemplify Baker's ideal weed, others have examined the evolutionary potential of some of these traits but in wholly different contexts. For example, additive genetic variation underlies flowering duration and seed number in purple loosestrife (*Lythrum salicaria*), a noxious semiaquatic perennial weed of North America (O'Neil, 1997). The work of Conner and colleagues finds significant genetic variation in many floral (Conner et al., 2003; Sahli et al., 2008) and plant growth traits (Conner and Via, 1993) of wild radish (*Raphanus raphanistrum*). Beyond these two examples in weedy plants, genetic variation underlying floral traits is widely supported (Shore and Barrett, 1990; Mazer and Schick, 1991; Caruso, 2004; Conner, 2006), and across many organisms fitness traits in general are often reported to exhibit higher levels of additive

genetic variance than nonfitness traits (Houle, 1992; Merilä and Sheldon, 1999). Furthermore, the relationship between estimates of plant growth and fitness has been considered by others but yet again in different contexts than Baker's weediness traits. In general, studies show that plants that flower later in the season exhibit greater biomass and/or size (Conner and Via, 1993; Mitchell-Olds, 1996; Latta and Gardner, 2009). While we find a significant negative correlation between relative growth rate and total number of flowers in one population (NC: $r = -0.321$), thus supporting the general finding of a trade off between growth and fitness, we find a significant but weak positive correlation between the total number of flowers and plant biomass in the same population ($r = 0.048$). However in the other population, we find a significant but weak positive correlation between relative growth rate and total number of flowers (GA: $r = 0.051$) and a significant but weak negative correlation between total number of flowers and plant biomass ($r = -0.067$). Since neither of the two investigated populations displayed evidence of genetic variation in relative growth rate and/or biomass, yet displayed evidence of variation in reproductive fitness, it is likely that selection for increased weediness in this species would be apparent through selection on fitness traits rather than growth rate and/or biomass traits. Evidence of genetic variation in both reproductive fitness and competitive ability suggests the relationship between the two traits deserves increased attention in this species.

Baker was the first to compile a list of traits that defined the ideal weed (Baker, 1965, 1974), and since then other lists have followed (De Wet and Harlan, 1975; Patterson, 1985; Roy, 1990). Although the ability to capture weediness in a well-defined and applicable way has appealed to many (Rejmanek, 2000), Baker's list has been criticized as lacking predictive power (Perrins et al., 1992; Williamson and Fitter, 1996; Mack, 1996; Reichard, 1997). Despite this, surprisingly few reports have explicitly tested for the presence of genetic variation underlying Baker's weediness traits as a group (Neve et al., 2009), and none have assessed the way in which the traits may be correlated, another oversight as these traits are likely to evolve together (Lande and Arnold, 1983). Addressing the evolutionary potential of traits thought to underlie plant weediness has the potential to help us determine which minor weeds may evolve into major weeds (Baker, 1974; Baker, 1991) and can provide a unique framework within which to determine how major and minor weeds will respond to different environmental stresses (Stanton et al., 2000) and/or scenarios of global climate change (Strauss et al., 2006).

LITERATURE CITED

- AGRAWAL, A. F., AND J. R. STINCHCOMBE. 2009. How much do genetic covariances alter the rate of adaptation? *Proceedings of the Royal Society, B, Biological Sciences* 276: 1183–1192.
- BAKER, H. G. 1965. Characteristics and mode of origin of weeds. In H. G. Baker and G. L. Stebbins [eds.], *The genetics of colonizing species*, 147–172. Academic Press, New York, New York, USA.
- BAKER, H. G. 1974. The evolution of weeds. *Annual Review of Ecology and Systematics* 5: 1–24.
- BAKER, H. G. 1991. The continuing evolution of weeds. *Economic Botany* 45: 445–449.
- BAUCOM, R. S., AND R. MAURICIO. 2004. Fitness costs and benefits of novel herbicide tolerance in a noxious weed. *Proceedings of the National Academy of Sciences, USA* 101: 13386–13390.
- BROWN, B. A., AND M. T. CLEGG. 1984. Influence of flower color polymorphism on genetic transmission in a natural population of the common morning glory, *Ipomoea purpurea*. *Evolution* 38: 796–803.
- CARUSO, C. M. 2004. The quantitative genetics of floral trait variation in *Lobelia*: Potential constraints on adaptive evolution. *Evolution* 58: 732–740.
- CHANG, S. M., AND M. D. RAUSHER. 1998. Frequency-dependent pollen discounting contributes to maintenance of a mixed mating system in the common morning glory *Ipomoea purpurea*. *American Naturalist* 152: 671–683.
- CHAO, W. S., D. P. HORVATH, J. V. ANDERSON, AND M. E. FOLEY. 2005. Potential model weeds to study genomics, ecology, and physiology in the 21st century. *Weed Science* 53: 929–937.
- CONNER, J., AND S. VIA. 1993. Patterns of phenotypic and genetic correlations among morphological and life-history traits in wild radish, *Raphanus raphanistrum*. *Evolution* 47: 704–711.
- CONNER, J. K. 2006. Ecological genetics of floral evolution. In L. D. Harder and S. C. H. Barrett [eds.], *Ecology and evolution of flowers*, 260–277. Oxford University Press, New York, New York, USA.
- CONNER, J. K., R. FRANKS, AND C. STEWART. 2003. Expression of additive genetic variances and covariances for wild radish floral traits: Comparison between field and greenhouse environments. *Evolution* 57: 487–495.
- CORDES, R. C., AND T. T. BAUMAN. 1984. Field competition between ivyleaf morningglory (*Ipomoea hederacea*) and soybeans (*Glycine max*). *Weed Science* 32: 364–370.
- CROWLEY, R. H., AND G. A. BUCHANAN. 1982. Variations in seed production and the response to pests of morningglory (*Ipomoea*) species and smallflower morningglory (*Jacquemontia tamnifolia*). *Weed Science* 30: 187–190.
- DAEHLER, C. C. 1998. The taxonomic distribution of invasive angiosperm plants: Ecological insights and comparison to agricultural weeds. *Biological Conservation* 84: 167–180.
- DE WET, J. M. J., AND J. R. HARLAN. 1975. Weeds and domesticates: Evolution in the man-made habitat. *Economic Botany* 29: 99–108.
- DEFELICE, M. S. 2001. Tall morningglory, *Ipomoea purpurea* (L.) Roth—Flower of foe? *Weed Technology* 15: 601–606.
- DLUGOSCH, K., AND I. PARKER. 2008. Founding events in species invasions: Genetic variation, adaptive evolution, and the role of multiple introductions. *Molecular Ecology* 17: 431–449.
- ENNOS, R. A. 1981. Quantitative studies of the mating system in two sympatric species of *Ipomoea* (Convolvulaceae). *Genetica* 57: 93–98.
- EPPERSON, B. K., AND M. T. CLEGG. 1987. Frequency-dependent variation for outcrossing rate among flower-color morphs of *Ipomoea purpurea*. *Evolution* 41: 1302–1311.
- FALCONER, D. S., AND T. F. C. MACKAY. 1996. *Introduction to quantitative genetics*. Longman, Essex, UK.
- FAUL, F., E. ERDFELDER, A. LANG, AND A. BUCHNER. 2007. G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods* 39: 175–191.
- FISHER, R. A. 1930. *The genetical theory of natural selection*. Clarendon Press, Oxford, UK.
- GOODWIN, B. J., A. J. McALLISTER, AND L. FAHRIG. 1999. Predicting invasiveness of plant species based on biological information. *Conservation Biology* 13: 422–426.
- HOFFMANN, W. A., AND H. POORTER. 2002. Avoiding bias in calculations of relative growth rate. *Annals of Botany* 90: 37–42.
- HOLT, J. S., AND D. R. ORCUTT. 1991. Functional relationships of growth and competitiveness in perennial weeds and cotton (*Gossypium hirsutum*). *Weed Science* 39: 575–584.
- HOULE, D. 1992. Comparing evolvability and variability of quantitative traits. *Genetics* 130: 195–204.
- LANDE, R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain: Body size allometry. *Evolution* 33: 402–416.
- LANDE, R. 1982. A quantitative genetic theory of life history evolution. *Ecology* 63: 607–615.
- LANDE, R., AND S. J. ARNOLD. 1983. The measurement of selection on correlated characters. *Evolution* 37: 1210–1226.
- LATTA, R. G., AND K. M. GARDNER. 2009. Natural selection on pleiotropic quantitative trait loci affecting a life-history trade-off in *Avena barbata*. *Evolution* 63: 2153–2163.
- MACK, R. N. 1996. Predicting the identity and fate of plant invaders: Emergent and emerging approaches. *Biological Conservation* 78: 107–121.

- MAYNARD SMITH, J., R. BURIAN, S. KAUFFMAN, P. ALBERCH, J. CAMPBELL, B. GOODWIN, R. LANDE, D. RAUP, AND L. WOLPERT. 1985. Developmental constraints and evolution: A perspective from the Mountain Lake Conference on Development and Evolution. *Quarterly Review of Biology* 60: 265–287.
- MAZER, S. J., AND C. T. SCHICK. 1991. Constancy of population parameters for life-history and floral traits in *Raphanus sativus* L. II. Effects of planting density on phenotype and heritability estimates. *Evolution* 45: 1888–1907.
- MERILÄ, J., AND B. C. SHELDON. 1999. Genetic architecture of fitness and nonfitness traits: Empirical patterns and development of ideas. *Heredity* 83: 103–109.
- MITCHELL-OLDS, T. 1996. Genetic constraints on life-history evolution: Quantitative-trait loci influencing growth and flowering in *Arabidopsis thaliana*. *Evolution* 50: 140–145.
- MUTH, N. Z., AND M. PIGLIUCCI. 2006. Traits of invasives reconsidered: Phenotypic comparisons of introduced invasive and introduced noninvasive plant species within two closely related clades. *American Journal of Botany* 93: 188–196.
- NEVE, P., M. VILA AIUB, AND F. ROUX. 2009. Evolutionary-thinking in agricultural weed management. *New Phytologist* 184: 783–793.
- O'NEIL, P. 1997. Natural selection on genetically correlated phenological characters in *Lythrum salicaria* L. (Lythraceae). *Evolution* 51: 267–274.
- PATTERSON, D. T. 1985. Comparative ecophysiology of weeds and crops. In S. O. Duke [ed.], *Weed physiology*, vol. 1, Reproduction and ecophysiology, 101–129. CRC Press, Boca Raton, Florida, USA.
- PERRINS, J., M. WILLIAMSON, AND A. FITTER. 1992. A survey of differing views of weed classification: implications for regulation of introductions. *Biological Conservation* 60: 47–56.
- PRICE, A. J., AND J. W. WILCUT. 2007. Response of ivyleaf morning-glory (*Ipomoea hederacea*) to neighboring plants and objects. *Weed Technology* 21: 922–927.
- REICHARD, S. E. 1997. Prevention of invasive plant introductions on national and local levels. In J. Luken and J. Thieret [eds.], *Assessment and management of plant invasions*, 215–227. Springer, New York, New York, USA.
- REJMANEK, M. 2000. Invasive plants: Approaches and predictions. *Austral Ecology* 25: 497–506.
- RICHARDS, C. L., O. BOSSDORF, N. Z. MUTH, J. GUREVITCH, AND M. PIGLIUCCI. 2006. Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology Letters* 9: 981–993.
- ROFF, D. A., AND R. PREZIOSI. 1994. The estimation of the genetic correlation: The use of the jackknife. *Heredity* 73: 544–548.
- ROY, J. 1990. In search of the characteristics of plant invaders. In A. diCastri, J. Hansen, and M. Debussche [eds.], *Biological invasions in Europe and the Mediterranean basin*, vol. 65, 335–352. Kluwer, Dordrecht, Netherlands.
- SAHLI, H. F., J. K. CONNER, F. H. SHAW, S. HOWE, AND A. LALE. 2008. Adaptive differentiation of quantitative traits in the globally distributed weed, wild radish (*Raphanus raphanistrum*). *Genetics* 180: 945.
- SAKAI, A. K., F. W. ALLENDORF, J. S. HOLT, D. M. LODGE, J. MOLOFSKY, K. A. WITH, S. BAUGHMAN, R. J. CABIN, J. E. COHEN, AND N. C. ELLSTRAND. 2001. The population biology of invasive species. *Annual Review of Ecology and Systematics* 35: 305–332.
- SHORE, J. S., AND S. C. H. BARRETT. 1990. Quantitative genetics of floral characters in homostylous *Turnera ulmifolia* var. *angustifolia* Willd. (Turneraceae). *Heredity* 64: 105–112.
- SIMMS, E. 1993. Genetic variation for pathogen resistance in tall morning-glory. *Plant Disease* 77: 901–904.
- SIMMS, E. L., AND M. D. RAUSHER. 1987. Costs and benefits of plant resistance to herbivory. *American Naturalist* 130: 570–581.
- STANTON, M., B. ROY, AND D. THIEDE. 2000. Evolution in stressful environments. I. Phenotypic variability, phenotypic selection, and response to selection in five distinct environmental stresses. *Evolution* 54: 93–111.
- STANTON, M., AND H. J. YOUNG. 1994. Selecting for floral character associations in wild radish, *Raphanus sativus* L. *Journal of Evolutionary Biology* 7: 271–285.
- STRAUSS, S. Y., J. A. LAU, AND S. P. CARROLL. 2006. Evolutionary responses of natives to introduced species: What do introductions tell us about natural communities? *Ecology Letters* 9: 357–374.
- SUTHERLAND, S. 2004. What makes a weed a weed: Life history traits of native and exotic plants in the USA. *Oecologia* 141: 24–39.
- TIFFIN, P. 2002. Competition and time of damage affect the pattern of selection acting on plant defense against herbivores. *Ecology* 83: 1981–1990.
- UVA, R. H., J. C. NEAL, AND J. M. DiTOMASO. 1997. *Weeds of the north-east*. Cornell University Press, Ithaca, New York, USA.
- WEBSTER, T. M., AND H. D. COBLE. 1997. Changes in the weed species composition of the southern United States: 1974 to 1995. *Weed Technology* 11: 308–317.
- WHITNEY, K. D., AND C. A. GABLER. 2008. Rapid evolution in introduced species, 'invasive traits' and recipient communities: challenges for predicting invasive potential. *Diversity & Distributions* 14: 569–580.
- WILLIAMSON, M. H., AND A. FITTER. 1996. The characters of successful invaders. *Biological Conservation* 78: 163–170.
- WRIGHT, S. 1935. The analysis of variance and the correlations between relatives with respect to deviations from an optimum. *Journal of Genetics* 30: 243–256.
- YOUNG, J. A., AND R. A. EVANS. 1976. Responses of weed populations to human manipulations of the natural environment. *Weed Science* 24: 186–190.