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Reviewed work(s):

Source: *The American Naturalist*, Vol. 179, No. 2 (February 2012), pp. 192-203

Published by: [The University of Chicago Press](#) for [The American Society of Naturalists](#)

Stable URL: <http://www.jstor.org/stable/10.1086/663684>

Accessed: 09/01/2012 12:34

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Hybridization Alters Early Life-History Traits and Increases Plant Colonization Success in a Novel Region

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Submitted November 14, 2010; Accepted October 3, 2011; Electronically published December 17, 2011

Online enhancement: appendix. Dryad data: <http://dx.doi.org/10.5061/dryad.d8mq37r7>.

ABSTRACT: Hybridization is hypothesized to promote invasiveness, but empirical tests comparing the performance of hybrid taxa versus parental taxa in novel regions are lacking. We experimentally compared colonization ability of populations of wild radish (*Raphanus raphanistrum*) with populations of advanced-generation hybrids between wild radish and cultivated radish (*Raphanus sativus*) in a southeast Texas pasture, well beyond the known invasive range of hybrid radish. We also manipulated the strength of interspecific competition to better generalize across variable environments. In both competitive environments, hybrid populations produced at least three times more seeds than did wild radish populations, a distinction that was driven by greater hybrid seedling emergence, earlier hybrid emergence, and more hybrid seedlings surviving to flower, rather than by greater individual fecundity. Flowering duration in hybrids was less negatively affected by competition than it was in wild radish, while early emergence was associated with subsequent high seed output in both biotypes. Our data show that hybridization can enhance colonization success in a novel region and, by comparison with previous studies, that the life-history traits enhancing hybrid success can differ across regions, even for lineages originating from the same hybridization event. These results imply a much larger arena for hybrid success than previously appreciated.

Keywords: seedling emergence, flowering phenology, biological invasions, adaptive introgression, life history, germination.

Introduction

Interspecific hybridization is widespread in both animals and plants (Schwenk et al. 2008; Whitney et al. 2010b). Recently, hybridization has been associated with the invasion process, in the context of either genetic swamping of native taxa (e.g., Rhymer and Simberloff 1996; Riley et al. 2003) or a link between hybridization and increased invasiveness (Ellstrand and Schierenbeck 2000; Vilà et al.

2000; Schierenbeck and Ellstrand 2009; Whitney et al. 2009). Hybridization might increase invasiveness if hybrid populations harbor increased genetic variation (e.g., Lewontin and Birch 1966; Campbell et al. 2009), if they contain novel and beneficial allelic combinations (e.g., Whitney et al. 2006; Latta et al. 2007), or if they experience fixed heterosis (e.g., Moody and Les 2002; Facon et al. 2005). Putative cases of hybrid-derived invasive species have accumulated rapidly, particularly since Ellstrand and Schierenbeck's (2000) influential article drew substantial attention to the topic. In the past decade, the number of studies published annually that address hybridization in the context of biological invasions has increased from nine in 2000 to more than 60 in 2010 (ISI Web of Knowledge search for "inva*" and "hybrid*" within the subjects of ecology and evolutionary biology). However, few empirical examples have been studied thoroughly enough to verify that hybridization is causally linked to increased invasiveness.

Common-garden experiments have demonstrated that hybrids can outperform their parental species, lending support to the idea that hybridization facilitates invasion and/or range expansion (e.g., *Carpobrotus* spp. [Vilà and D'Antonio 1998], *Raphanus* spp. [Campbell et al. 2006; Ridley and Ellstrand 2009], *Helianthus* spp. [Whitney et al. 2006, 2010a]). However, one might expect superior hybrid performance in these experiments, given that they were all conducted within the hybrid taxon's region of origin and spread. If the persistence and spread of a natural hybrid lineage were enhanced by region-specific conditions, then one might also expect experimentally planted hybrids to outperform parental taxa there. A distinct question is whether and how often hybridization can produce invasive phenotypes in completely novel regions (i.e., in locations where naturally occurring hybrids are absent). Empirical comparisons of hybrid performance and parental performance in novel regions are needed to address this question directly and to better understand the im-

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Am. Nat. 2012. Vol. 179, pp. 192–203. © 2011 by The University of Chicago. 0003-0147/2012/17902-52613\$15.00. All rights reserved.

DOI: 10.1086/663684

portance of hybridization in colonization and invasion dynamics.

Hybrid performance relative to parental taxa is also likely to depend on local biotic and abiotic factors such as competition, herbivory, and environmental stress (Campbell and Snow 2007; Mercer et al. 2007). For example, although wild radish (*Raphanus raphanistrum*) were more fecund than crop-wild hybrid radish grown in a Michigan common garden under noncompetitive conditions, hybrids were less negatively affected by intense competition (Campbell and Snow 2007). Similarly, although hybrid *Carpobrotus* was more resistant to herbivory than its parental taxa across three common gardens, total biomass of hybrids was greater only in certain habitats (Vilà and D'Antonio 1998). Such genotype \times environment interactions often impact hybrid success (Arnold et al. 1999; Mercer et al. 2006; Arnold and Martin 2010); thus, experiments manipulating putatively important local conditions are necessary to broaden our understanding of the link between hybridization and invasiveness.

In this article we assess the hypothesis that hybridization can facilitate invasiveness in a novel region by testing three predictions related to the performance of wild radish (*R. raphanistrum*) versus that of hybrids between wild and cultivated radish (*Raphanus sativus*). Hybrid radish is found throughout much of California, where it is considered invasive (see "Material and Methods"). First, we predicted that populations of hybrid radish would outperform populations of wild radish in a novel region (the coastal plain of Texas). Second, we predicted that interspecific competition would negatively affect wild radish to a greater extent than hybrid radish (see also Campbell and Snow 2007). Third, we predicted that performance differences in hybrid lineages versus wild lineages could be traced to traits influenced by the cultivated parent *R. sativus*, including seedling emergence and flowering phenology. In addition, by comparing hybrid life-history traits in our populations with those in previous studies, we could ask whether the traits explaining hybrid success were similar or different across regions.

Although important differences may exist between hybridization events involving crop taxa and those involving wild taxa only (see "Discussion"), our results represent the first experimental evidence from any system that hybridization promotes colonization beyond the hybrid's known invasive range. Further, we provide evidence that the key traits underlying hybrid colonization success can vary across regions, even for the same source genetic material. Our results indicate that hybridization may spark colonization/invasion success across a wider array of habitats and via a greater diversity of pathways than previously anticipated.

Material and Methods

Study System

The crop-wild complex of cultivated radish (*Raphanus sativus*) and its weedy relative wild radish (*Raphanus raphanistrum*, also known as jointed charlock) has been used widely to address questions in plant evolutionary ecology and to assess the ecological consequences of crop-to-wild gene flow (e.g., Mazer 1987; Stanton 1987; Conner and Via 1993; Klinger and Ellstrand 1994; Conner et al. 2003). Cultivated radish is a diploid, self-incompatible, late-flowering annual selected for its swollen hypocotyl and root (Snow and Campbell 2005). It is an ancient crop that was derived from several species, including wild radish (Yamagishi and Terachi 2003). Wild radish is a diploid, self-incompatible, early-flowering annual Eurasian weed with narrow, branching taproots that colonizes agricultural systems, disturbed sites, and coastal beaches in temperate and warm-temperate zones worldwide (Holm et al. 1997; Warwick and Francis 2005). Wild radish seeds are widely dispersed by people, often as contaminants of crop seeds (e.g., Michael et al. 2010). Both cultivated radish and wild radish were introduced to California from Europe by the nineteenth century (Panetos and Baker 1968). Since that time, the diploid crop-wild hybrid (known as California wild radish or feral *R. sativus*; referred to here as "hybrid radish" for clarity) has displaced all known populations of *R. raphanistrum* in California, becoming a regionally important weed (Ball et al. 2000; Hegde et al. 2006). To our knowledge, invasive populations of hybrid radish have been reported only in California. Putative natural hybrids have been observed in Michigan, but they are not common (Snow et al. 2001).

Generation of the Wild and Hybrid Biotypes

Detailed descriptions of the wild (*R. raphanistrum*) and hybrid (*R. raphanistrum* \times *R. sativus*) populations used here are available in Campbell et al. (2006). Briefly, two seed pools (F_1 wild and hybrid radish) were generated by hand-pollinating 100 wild *R. raphanistrum* plants from Pellston, Michigan, either with pollen from conspecifics or from 100 *R. sativus* var. "Red Silk" plants (Harris-Moran Seed, Modesto, CA). Hereafter, we refer to these lines as wild and hybrid "biotypes" (instead of "taxa") to avoid any implication of reproductive isolation. Note that we focus on this comparison only (and not that of hybrid radish versus cultivated radish) because nonhybrid *R. sativus* does not commonly occur outside of cultivation in North America (Snow and Campbell 2005; Campbell and Snow 2009) and has significantly lower reproductive output than either hybrid radish or wild radish (Ridley and Ellstrand 2009).

In 2002, four F_1 wild populations (W_1 – W_4) and four F_1 hybrid populations (H_1 – H_4) were established in pastures or agricultural fields in Emmett and Cheboygan counties, Michigan. To restrict unintended gene flow, all eight populations were isolated from each other and from local wild radish populations by at least 1 km. Each population was started by planting 50–60 F_1 seedlings in a tilled 15 × 15-m fertilized plot. For each biotype, all four populations were drawn from the same pool of seeds. We used no more than two seedlings per maternal plant for each population in order to provide genetic variation on which selection could act. Each spring, plots were tilled, fertilized, and hand-weeded to promote population persistence. Otherwise, populations were exposed to naturally occurring pollinators, herbivores, pathogens, competition, weather, and overwintering conditions in situ. Because maladapted gene combinations often hinder performance in early-generation hybrids (Arnold et al. 1999), each population was then exposed to three generations of natural selection before performance comparisons between the hybrid and wild biotypes.

In 2004, mature fruits were collected from plants in the wild and hybrid populations; these seeds served as starting material for the experiment reported here, as well as earlier common-garden experiments that we conducted in Michigan and California (Campbell et al. 2006). Because *R. raphanistrum* seeds may remain dormant in the soil for several years (Roberts and Boddrell 1983; Chancellor 1986), we cannot assume that the 2004 seeds were composed of only one generation (i.e., all F_4). Thus, we instead refer to this collection as G_4 , recognizing that it may represent a mixture of generations G_2 – G_4 (see Campbell et al. 2006). Seeds from wild and hybrid radish biotypes remain viable for many years when stored in a laboratory (A. A. Snow and L. G. Campbell, personal observations); percent germination of G_4 seeds in a greenhouse trial at the start of this study (February 2010) was 90% for wild biotypes and 85% for hybrids (see “Discussion”).

Colonization Experiment

We established a set of common-garden colonization trials in a pasture in Waller County, southeast Texas. We chose this location to determine whether hybrids would be more successful than nonhybrids in a novel location beyond the hybrid’s known range of origin and spread. Although *R. raphanistrum* and *R. sativus* are not known to co-occur in Waller County, they have been collected only 33 and 100 km, respectively, from our study site. All *R. sativus* herbarium collections in Texas with unambiguous locality information were collected from gardens, suggesting that naturalized *R. sativus* is exceedingly rare or nonexistent in the state (University of Texas–Austin [[.biosci.utexas.edu/prc/tex.html\] and Texas A&M University \[<http://www.bio.tamu.edu/courses/biol328/herbarium/tamuhome.htm>\] herbaria online; Sul Ross State College herbarium, M. Powell, personal communication; Botanical Research Institute of Texas herbarium, A. Neill, personal communication\). That both parents can survive and reproduce in the region suggests that hybrids could potentially occur and invade; however, we have not found records of hybrid radish occurring in Texas. Thus, we consider Texas to be a novel region that is potentially available for colonization and invasion by hybrid radish.](http://www</p>
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The pasture was disked on January 27, 2010, to expose the soil and break up extant vegetation, and 156 plots (0.5 m × 0.5 m) were established at ≥2-m spacing. On February 10, half the plots were sprayed with glyphosate herbicide (Roundup, 2% concentration; Monsanto, St. Louis, MO) to reduce competition from neighboring vegetation. On February 12–13 we initiated colonization by planting nine seeds at 1-cm depth and at 25-cm intervals (a 3 × 3 grid) in each plot (a “population”). In our region, this timing generally coincides with spring emergence of weedy annuals. Each seed planted within a plot was selected from a different maternal family. Because of limited seed availability, the original wild and hybrid source lineages were unequally represented in our experiment; in total, we established 72 wild ($n = 16, 22, 22,$ and 12 for W_1 – W_4 , respectively) and 84 hybrid ($n = 18, 22, 22,$ and 22 for H_1 – H_4) populations in a completely randomized experimental design. Thus, our reduced- and ambient-competition treatments each contained 36 wild and 42 hybrid populations. We did not apply fertilizer, insecticides, or supplemental water to the plots. The first seedlings emerged on February 24.

We quantified the degree to which competition was reduced by the herbicide treatment by assessing percent cover in each plot, using digitally analyzed photos taken on March 3 and April 16, 2010. We recorded percent vegetation cover by using the green leaf algorithm in VegMeasure2 (Johnson et al. 2003). On May 3, above-ground vegetation was clipped from the reduced-competition plots and in a 1-m perimeter surrounding the plots to ensure that competition treatment differences were retained well into the growing season.

Colonization Surveys and Response Measures

Plots were censused weekly for seedling emergence, survival, growth, and reproduction from February 24 until all plants senesced in mid-August. Twice weekly, all pre-flowering individuals were checked to record the date of first flowering and plant size at flowering. Plant size at flowering was measured as the stem diameter at the base

of the plant and the length of the longest leaf, using digital calipers (Mitutoyo, Aurora, IL).

To estimate reproductive effort and lifetime fecundity, we recorded flower number, fruit number, and seeds per fruit. Seed number can be counted nondestructively by examining the external swellings of ripened radish fruits (siliques). On plants with 10 or fewer fruits, we recorded seed numbers for each fruit; otherwise, we did so for 10 haphazardly chosen fruits per plant. Total per-plant fecundity was estimated by multiplying the average number of seeds per fruit by total fruit number. We used these data to quantify five components of population (plot-level) seed production: the proportion of seeds emerging, the proportion of emerged seedlings that flowered, the number of flowers per flowering plant, the proportion of flowers that matured into fruit, and the number of seeds per fruit. Overall population fecundity was assessed as the total estimated number of seeds per plot (the product of the above five components multiplied by the nine initial colonist seeds).

To assess phenological differences between hybrid and wild biotypes in our treatments, we calculated the time to emergence (date of seedling emergence minus planting date), age at reproduction (date of flowering minus date of seedling emergence), and flowering duration (last flowering date minus first flowering date). For these three measures, we averaged across all individuals within a given plot before conducting analyses at the plot level.

Statistical Analyses

We conducted most analyses by using generalized linear mixed models with PROC GLIMMIX in SAS, version 9.2 (SAS Institute, Cary, NC). We used a statistical model that tested for three fixed effects: biotype (hybrid or wild), competition (reduced or ambient), and the biotype \times competition interaction. We included source population from the natural selection phase of the experiment (i.e., W_1 – W_4 and H_1 – H_4 , nested within biotype) as a random effect, although when the variance-covariance matrix could not be estimated because the parameter estimate for population was nearly zero, that term was dropped from the model (Littell et al. 2006). Inferences regarding significance of the population term were tested using the ratio of likelihoods or pseudolikelihoods for models with and without the random effect included (the COVTEST command). This (pseudo)likelihood ratio was tested against a χ^2 distribution (with $df = 1$), whereas traditional F statistics were used to assess fixed effects.

Because generalized linear models specify the underlying distribution and link function appropriate for each response, data transformations were largely unnecessary. The single exception was for lognormally distributed responses

that included raw values between 0 and 1 (proportion of flowers maturing to fruit, population fecundity, and stem diameter); for these variables we added a constant before running the analysis to avoid unrealistic negative least squares mean values. Residuals were approximately normally distributed in all cases. We used sequential Bonferroni adjustments (with $\alpha = 0.05$) to make pairwise comparisons following a significant biotype \times competition interaction effect and to illustrate treatment differences in the figures. We conducted all analyses at the population (=plot) level ($n \leq 156$), except for post hoc tests in which we assessed the relationship between individual fecundity and time to emergence by fitting an exponential decay model ($Y = ae^{-bx}$) to the data, using nonlinear regression (PROC NLIN). Unless otherwise noted, we report least squares mean values (± 1 SE) throughout.

Results

Biotype Differences in Population-Level Seed Production and Plant Size

Hybrid populations produced nearly three times more seeds than did wild radish populations (fig. 1f), a distinction that was ultimately the result of earlier seedling emergence, greater seedling emergence, and an increased proportion of hybrid seedlings that flowered (fig. 1a, 1b; table A1, available online). Biotype differences in seedling emergence are unlikely to have resulted from inherently greater seed dormancy or lower seed viability in the wild biotype, based on greenhouse trials we conducted shortly after seeds were sown in the field and drawing from the same set of seeds (90% vs. 85% seedling emergence out of 20 wild and hybrid seeds, respectively). Hybrid and wild biotypes produced similar numbers of flowers per flowering plant, matured a similar proportion of flowers to fruits, and yielded similar numbers of seeds per fruit (fig. 1c–1e; table A1). Average plant size at flowering (as measured by stem diameter and leaf length) also did not differ for hybrid populations versus wild populations (fig. A1, available online; table A1).

Effects of Competition on Seed Production and Plant Size

The percent cover of neighboring vegetation 18 days after planting was low in all colonization plots and did not differ by treatment (ambient competition: $3.8\% \pm 0.2\%$; reduced competition: $4.1\% \pm 0.2\%$; $F_{1,154} = 3.46$, $P = .065$). However, by mid-April (62 days after planting) the single February herbicide application in reduced-competition plots had decreased nonradish cover by 27.3% relative to that in ambient-competition plots (ambient com-

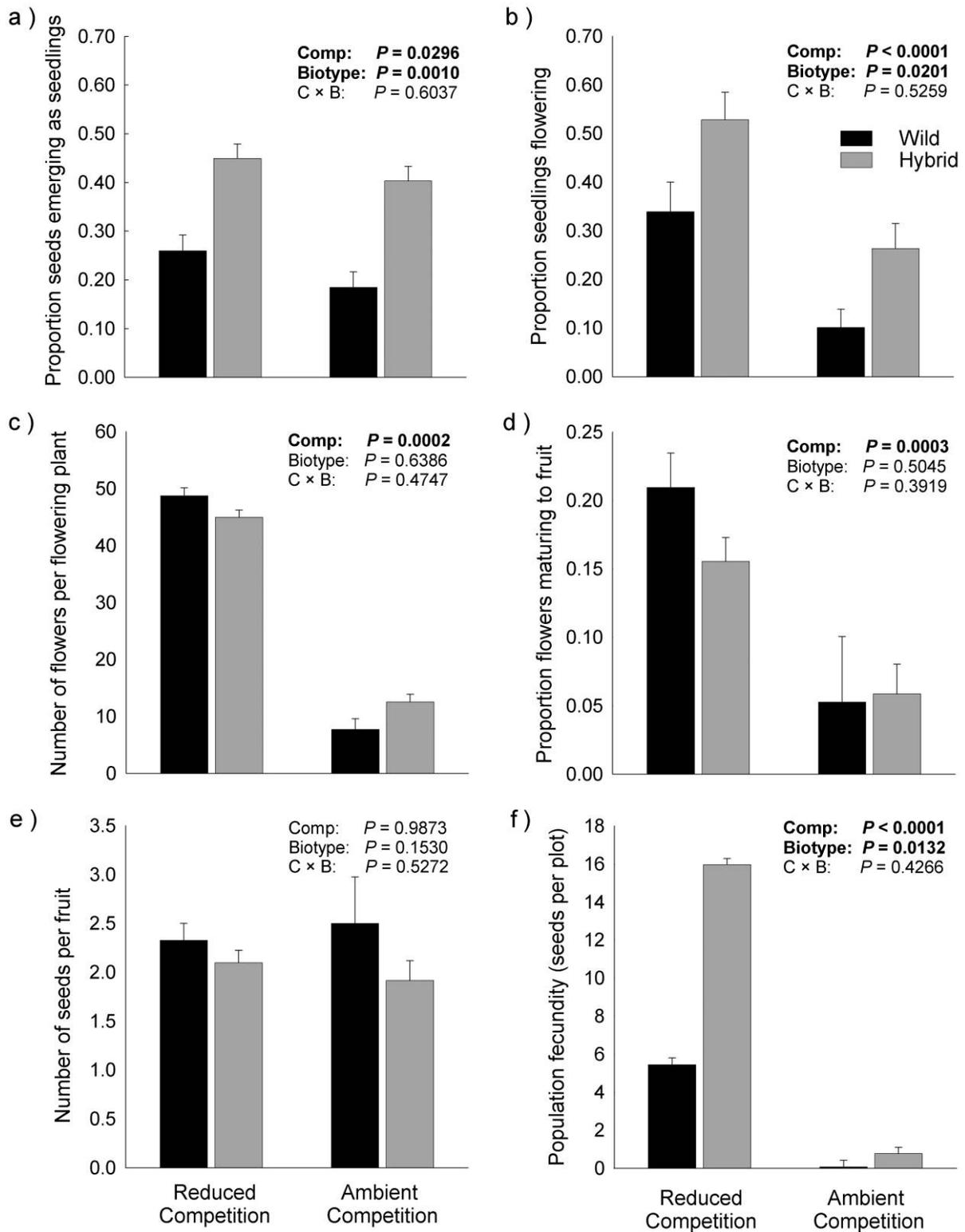
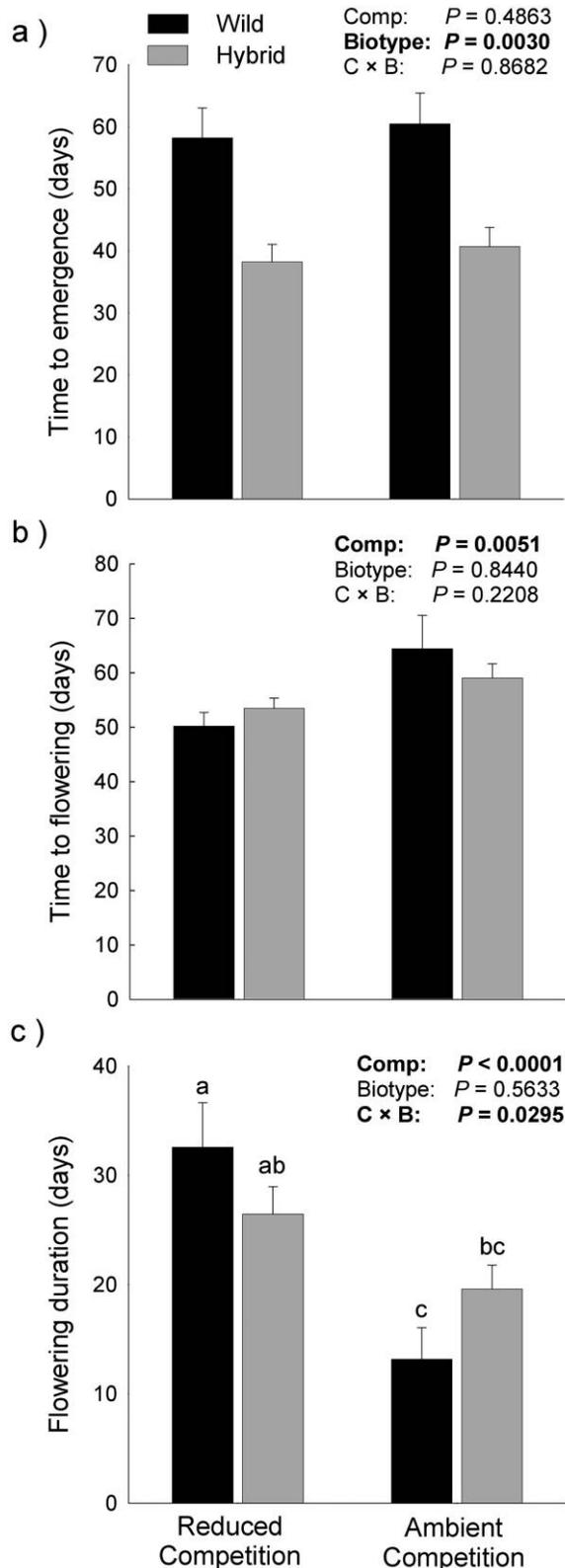


Figure 1: Biotype differences in population-level seed production (f) and its components ($a-e$). Significant fixed effects are in bold (see also table A1, available online). Note that because these are least squares means (+1 SE), the values in f cannot be directly obtained from values in $a-e$.



petition: $53.2\% \pm 3.4\%$; reduced competition: $38.7\% \pm 3.5\%$; $F_{1,154} = 34.77$, $P < .0001$). Estimates of percent cover from digital photographs were highly correlated with non-radish biomass (based on biomass clipped from reduced-competition plots on May 3; $r = 0.74$, $P < .0001$, $n = 77$).

Hybrid and wild biotypes saw similar increases in seed production and its components when neighbor biomass was reduced (significant competition effects but no significant competition × biotype interactions; table A1). Only the number of seeds per fruit was unaffected by the competition treatment, and this was the case for both biotypes (table A1). Increases in average plant size were also similar for hybrid and wild biotypes in response to reduced competition (fig. A1; table A1).

Seedling Emergence and Flowering Phenology

Phenological differences between hybrid radish and wild radish were striking and contributed to population-level differences in reproductive output. Hybrids emerged significantly earlier than wild radish (least squares means: ~40 vs. 60 days; figs. 2a, 3b; table A1), and across plots of both biotypes, average emergence time was negatively correlated with seedling emergence ($r = -0.21$, $P = .011$, $n = 146$) and survival to flowering ($r = -0.49$, $P < .0001$). At the individual level, fecundity dropped exponentially with increased time to emergence for both biotypes (fig. 3a; nonlinear regression for hybrid: $F_{2,320} = 18.58$, $P < .0001$; nonlinear regression for wild: $F_{2,140} = 5.22$, $P = .0065$). Wild and hybrid biotypes had marginally different values for the exponential decay function parameter describing the slope, indicating that the decline in fecundity as time to emergence increased was somewhat more pronounced for hybrid individuals than for wild individuals (90% confidence intervals [CIs] for hybrid: [0.132, 0.273]; 90% CIs for wild: [-0.027, 0.116]). Estimates of maximum fecundity (the y -intercept) did not differ significantly for individuals of both biotypes, largely because of substantial error surrounding these parameter estimates (90% CIs for hybrid: [-135, 3,387]; 90% CIs for wild: [-210, 928]).

Although competition did not affect average time to seedling emergence, the reduced-competition treatment was associated with decreased time from emergence to

Figure 2: Biotype differences in phenology. Significant fixed effects are in bold (see also table A1, available online). Values are least squares means (+1 SE). Shared letters in *c* indicate statistically indistinguishable means based on sequential Bonferroni adjustments (with $\alpha = 0.05$).

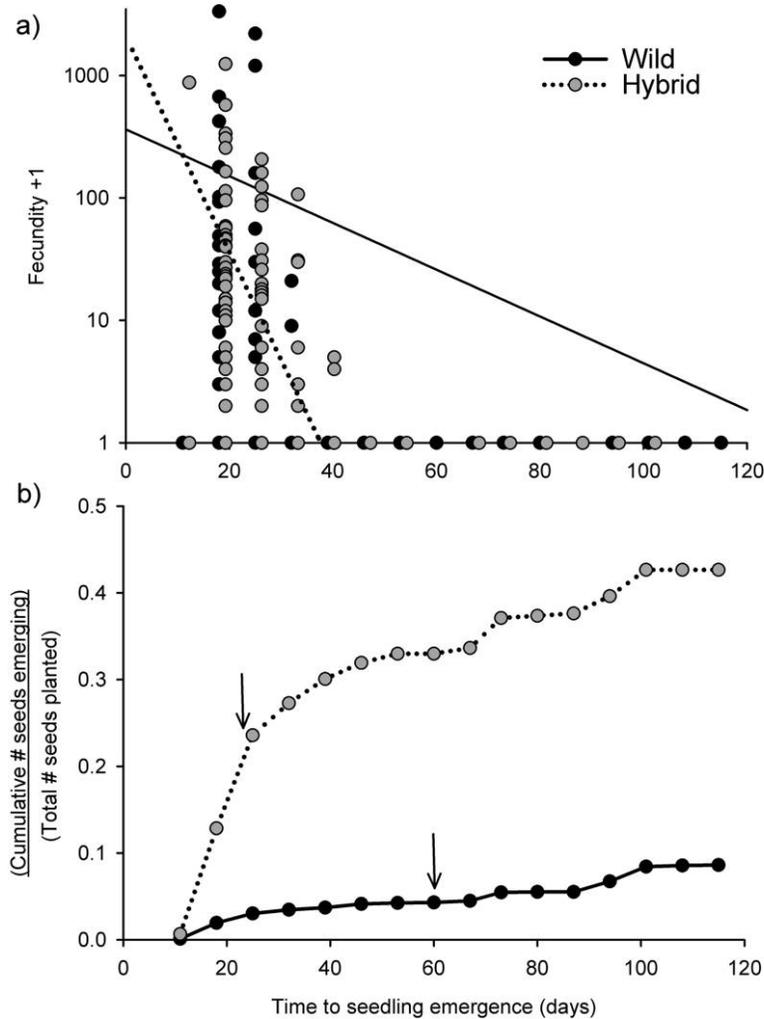


Figure 3: Seedling emergence phenology and fecundity. *a*, Relationship between time to emergence and subsequent individual fecundity. Lines represent the negative exponential relationship between time to emergence and fecundity for wild and hybrid radish, calculated separately for each biotype. Note that fecundity is plotted on a log scale. Most points on the X-axis represent multiple individuals with fecundity equal to 0. Data points for hybrids are slightly offset to the right for better visualization. *b*, Cumulative proportion of seeds emerging as seedlings over time. Arrows indicate the number of days after planting when half of all seedlings had emerged (= 23 days for hybrids and 60 days for wild radish).

flowering in both biotypes (fig. 2*b*; table A1). Because the herbicide treatment was conducted only 2–3 days before sowing seeds, the benefits of reduced neighbor biomass may not have been realized until after most seedlings had already emerged. When both the time to emergence and the time to flowering were summed, hybrids began flowering roughly 90–100 days after planting (mid-May), 2–3 weeks before flowering by wild radish. Reduced competition increased flowering duration for both biotypes, but the response for wild radish was significantly stronger (competition \times biotype: $P = .0295$; table A1). Hybrid

flowering duration was thus more stable in the face of different competitive environments (fig. 2*c*).

Discussion

Hybrid radish populations in a novel environment produced significantly more seeds than did those of *R. raphanistrum*, their weedy parental biotype, indicating enhanced colonization success. In our study site, this distinction can be clearly traced to three trait differences: increased seedling emergence, earlier emergence, and an

increased proportion of seedlings surviving to flower. Furthermore, the fecundity difference between biotypes was most pronounced in reduced-competition plots. Overall, these results suggest that hybrid radish is more likely to colonize novel habitats than its wild parental biotype in at least some locations, particularly in disturbed sites where competition from neighboring vegetation is reduced.

*Comparisons with Radish Performance in California:
Different Routes to Hybrid Success*

Two previous studies have experimentally examined the role of hybridization in performance of advanced-generation hybrid radish in California, where hybrids have evolved naturally (Campbell et al. 2006; Ridley and Ellstrand 2009). These studies started with greenhouse-grown seedlings transplanted to the field and showed that hybrid individuals usually outperform wild radish individuals. This pattern held in cases where hybrid lineages were experimentally derived (Campbell et al. 2006) and when they were collected from natural hybrid populations (Ridley and Ellstrand 2009). Hybrid advantage in these studies was often large: hybrid survival was up to 22% greater, and hybrid plants were up to 2.5 times larger, producing two or three times more flowers and two to four times more seeds than wild plants (Campbell et al. 2006; Ridley and Ellstrand 2009).

We expected that southeast Texas would represent a novel environment relative to the invasive range of hybrid radish, and indeed, mean temperatures at our site were higher throughout most of the growing season than they were in the California gardens (fig. A2, available online); presumably the sites differ in many other environmental characteristics as well. Despite these environmental differences, hybrid populations also outperformed wild radish in Texas, producing 2.5 times more seeds. However, the seed production components underlying that difference contrasted with those in the California gardens—despite our use of seeds from the same source pool and generation used by Campbell et al. (2006). In Texas, hybrids produced slightly fewer flowers per flowering plant, fruits per flower, and seeds per fruit than did wild radish (though not significantly so; fig. 1), and there were no biotype differences in plant size (fig. A1). Instead, superior performance of our hybrid populations was linked to greater seedling emergence, earlier emergence, and greater survival.

The presence of individual-level biotype differences in size and fecundity in California but not Texas might be explained by plants in Texas being more stressed. In contrast to the watered, fertilized, and weeded California common gardens (Campbell et al. 2006; Ridley and Ellstrand 2009), our populations received no supplemental water or

fertilizer, and even our reduced-competition treatments were approximately 40% vegetated with nonradish biomass by mid-April. Relative to our most favorable conditions (reduced-competition plots), hybrid survival in the California gardens was thus more than four times greater, and California hybrids produced between 60 and 240 times more seeds per plant (Campbell et al. 2006; Ridley and Ellstrand 2009). Because plants in our common garden were small, there simply may have been too little variation in plant size and individual fecundity to generate biotype differences similar to those found in California gardens.

We note that our experiment represents a single hybridization event and colonization in a single location; thus, outcomes could be quite different if repeated using different genetic material or in a different site. In fact, tests conducted in Michigan that used the same genetic material as in our study found that hybrid radish did not outperform wild radish in that location (Campbell et al. 2006). Therefore, although hybrid radish have shown better performance than parentals in two locations, this is not a universal outcome.

Hybridization and the Response to Competition

We found weak support for our second prediction, that hybrids would be less negatively impacted by competition than wild radish (as in Campbell and Snow 2007). Consistent with this prediction, wild (but not hybrid) radish populations experienced a significant decrease in flowering duration in response to increased competition (fig. 2c). Although the same trend can be seen for other responses (e.g., see figs. 1c, 1d, 2b), in all other cases wild and hybrid radish were affected similarly by competition (no significant competition \times biotype effects). The significant competition \times biotype interaction for flowering duration is probably due to the combined effect of hybrids emerging earlier than wild radish and vegetation cover becoming a significant impediment to radish performance in midseason and beyond. Later-emerging seedlings (which were primarily wild radish) would have been suppressed the most by interspecific competition. If there had been a strong early-season difference in vegetation cover between ambient- and reduced-competition plots, we suspect that we would have found significant competition \times biotype effects for additional responses and stronger overall support for our prediction.

We were surprised to find that hybrid and wild radish populations in our experiment did not differ in their time from emergence to flowering. Because cultivated *R. sativus* bolts and flowers later than wild *R. raphanistrum* (Snow and Campbell 2005), we expected hybrids to have delayed flowering relative to wild radish, as demonstrated in California common gardens (Campbell et al. 2006; Ridley and

Ellstrand 2009). We detected a trend in this direction (fig. 2*b*), but the difference was slight, nonsignificant, and present only in reduced-competition plots. We suspect that emerging earlier, when competition was less pronounced, may have allowed hybrids to flower relatively more quickly following emergence, minimizing any biotype differences that otherwise would have been observed.

The Effect of Seedling Emergence Phenology

The fecundity differences we observed in hybrid radish versus wild radish can be traced in part to biotype differences in their time to emergence. In our study, 50% of all hybrid seedlings had emerged by 23 days after planting, whereas the same fraction of wild radish seedlings did not emerge until 60 days after planting (fig. 3*b*). This time difference apparently allowed a larger number of hybrids to produce flowers and seeds before the summer heat set in, competition intensity increased, and plants began senescing, because we found a strong seed production advantage for earlier-emerging seedlings of both biotypes (fig. 3*a*). Early seedling emergence often benefits plant populations (Mack and Pyke 1983; Kelly and Levin 1997; Verdú and Traveset 2005), and it may be a key trait that promotes biological invasions more broadly (O'Donnell and Pigliucci 2010; Schlaepfer et al. 2010).

Rapid seedling emergence is also particularly interesting as an example of a domestication trait that may promote invasiveness in hybrids involving wild radish, an already-weedy taxon. Domestication traits, such as synchronized rapid seed germination, are often assumed to reduce weed fitness in variable environments (Stewart et al. 2003; Snow and Campbell 2005). However, in this case we have shown that early germination (and associated relatively synchronous emergence) may be associated with increased invasiveness. We hypothesize that these differences in emergence phenology between wild radish and hybrid radish resulted from crop radish alleles in the hybrids, based on greenhouse germination trials from 2005 showing that seedlings of "Red Silk" crop radish emerged significantly earlier than did either hybrid radish or wild radish (crop: 3.5 ± 0.1 days; hybrid: 11.2 ± 0.1 days; wild: 11.5 ± 0.1 days; biotype: $P < .001$, $n = 118, 398$, and 195 , respectively; L. G. Campbell and A. A. Snow, unpublished data).

Comparison with Hybrid Performance in Other Systems

To our knowledge, this is the first experiment to show that invasive hybrids can outperform their parental taxa in a novel habitat, perhaps because all other experimental parent-hybrid comparisons have been located within the region where hybrids naturally occur. Yet an additional, crucial distinction is that nearly all previous parent-hybrid

comparisons have examined early-generation hybrids (i.e., F_1 or F_2) rather than advanced-generation hybrids (e.g., Arriola and Ellstrand 1997; Song et al. 2004). This distinction is important because performance of early-generation hybrids is often extremely variable and may differ from performance in later generations. In some cases, mean early-generation hybrid performance is poor, but performance can rapidly improve in later generations as natural selection removes maladaptive combinations of alleles (Arnold 1997; Arnold et al. 1999). In other cases, early-generation hybrids have high fitness due to heterosis, but later-generation hybrids experience hybrid breakdown (Rieseberg and Carney 1998; Barton 2001). Thus, parent-hybrid comparisons using only early-generation hybrids may be poorly predictive of relative hybrid performance over the longer term.

The importance of considering hybrid class in the context of invasiveness is elegantly illustrated by performance comparisons conducted in *Lactuca*, the only genus besides *Raphanus* for which advanced-generation hybrids have been examined. First-generation hybrids between cultivated lettuce (*Lactuca sativa*) and weedy prickly lettuce (*Lactuca serriola*) have higher germination, survival, and seed output than do both parents (Hooftman et al. 2007). However, in contrast to patterns in *Raphanus*, third- and fourth-generation *Lactuca* hybrids outperform weedy *L. serriola* only in regard to percent germination, and this difference does not lead to increased population-level performance in hybrids relative to parents (Hooftman et al. 2007). Thus, the relative performance benefits realized by early-generation *Lactuca* hybrids apparently do not persist over time.

We recognize that important differences may distinguish our crop-wild hybrids from systems where neither parental taxon has been domesticated. However, we note that crop-wild hybrids are common (Ellstrand et al. 2010), accounting for many of our best-studied hybrid invaders (e.g., Arriola and Ellstrand 1997; Song et al. 2004; Hooftman et al. 2007). We also note that hybrid performance advantages in year 1 could be negated if seed bank survival and second-year germination is sufficiently reduced in hybrids relative to wild radish. However, this scenario is unlikely. For each experimental population, we examined marked locations of seeds that were planted but did not emerge in 2010 and found no biotype differences in the proportion of seeds that survived to emerge in 2011 (hybrid: 0.031 ± 0.01 , $n = 84$ populations; wild: 0.041 ± 0.01 , $n = 72$ populations; t -test: $P = .51$).

Implications for Our Understanding of Hybrid Evolution and Invasion

Our results provide a new perspective on the contribution of hybridization to colonization/invasion success, one that

challenges several paradigms of hybrid evolution and enlarges the range of conditions under which hybrids are expected to be successful. First, superior performance of hybrid *Raphanus* populations in a novel habitat contradicts models (e.g., the mosaic model and the tension zone model [Harrison 1986 and Barton and Hewitt 1985, respectively]) that assume all hybrids (including advanced-generation hybrids) are less fit than their parental taxa and thus that continued gene flow is the key to hybrid persistence.

Second, our results also conflict with models that envision hybrids as successful only under a restrictive set of conditions. The bounded hybrid superiority model (Moore 1977) posits that hybrids may outperform parents but only in narrow ecotonal regions. Similarly, Anderson's (1948, 1949) model posits that post-F₁ hybrids recombine parental physiological tolerances and therefore that hybrids are most likely to persist only where strong habitat disturbance in the zone of parental contact generates a variety of intermediate niches. Our data are not in accord with these views, since hybrid success took place far outside a contact zone in a region unlikely to contain niche space intermediate to that occupied by the parental taxa in their regions of origin. These considerations suggest that the traditional view of hybrids as intermediates (or simple recombinants) is inadequate; instead, hybrids may be able to exploit a much wider range of novel habitats than previously appreciated.

Third, our comparisons of hybrid life histories in Texas and California document a previously unknown phenomenon: that genetically similar hybrids (drawn from the same hybridization event and same selective history) may utilize different routes to success in different regions. While it has long been understood that successful hybrid populations can vary widely with respect to the traits that promote colonization, establishment, and population growth (Latta et al. 2007; Ridley and Ellstrand 2010), it has been presumed that these differences arise due to differing genetic histories, for example, independent hybridization events and/or unique episodes of selection and drift (Bleeker and Matthies 2005). The finding that genetically similar hybrids can harbor more than one set of "winning" traits that are appropriate for different environments indicates that hybridization may be an even more potent force driving colonization and invasion than previously suggested (Stebbins 1959; Ellstrand and Schierenbeck 2000).

Acknowledgments

Sincere thanks to L. Albert, E. Siefert, M. Stansberry, P. Sweeney, and E. Yin for field and laboratory assistance. Many thanks also to W. Newman (Katy Prairie Conser-

vancy) for coordinating site selection and to J. Stahman for allowing the use of his land. This article benefitted greatly from comments by three anonymous reviewers. Funding was provided by a Rice University Huxley Fellowship to L.G.C. and a National Science Foundation grant (DEB-0716868) to K.D.W.

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Associate Editor: Tia-Lynn R. Ashman
Editor: Ruth G. Shaw



Top, study site where the colonization experiment was conducted, soon after seed additions occurred (mid-February). Bottom, top view of a plot that was sown with hybrid radish seeds (white flowers on two flowering radish plants). Photographs by S. Hovick.

Appendix from S. M. Hovick et al., “Hybridization Alters Early Life-History Traits and Increases Plant Colonization Success in a Novel Region”

(Am. Nat., vol. 179, no. 2, p. 192)

Supporting Information

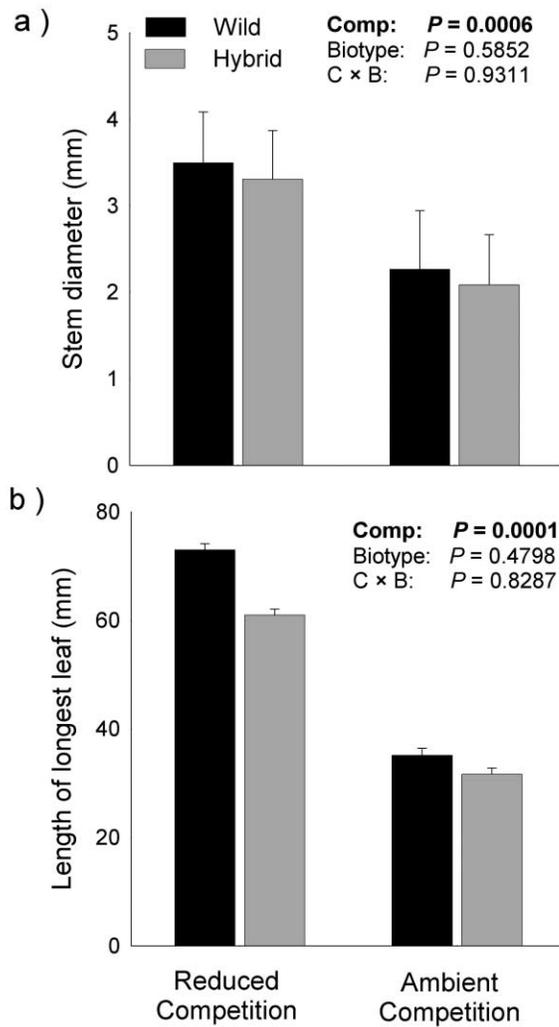


Figure A1: Plant size at flowering. Significant fixed effects are in bold (see also table A1). Values are least squares means (+1 SE).

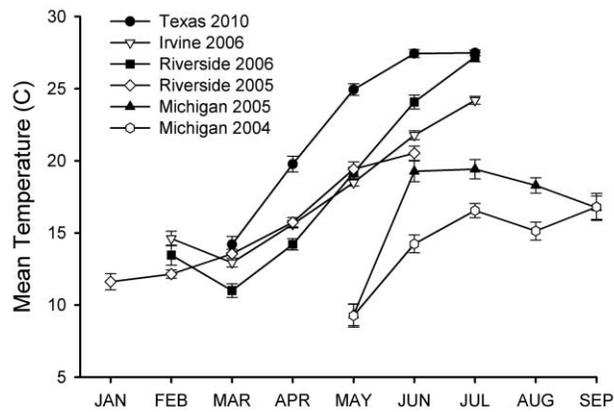


Figure A2: Mean daily temperatures, averaged by month (± 1 SE), for site-year combinations in which common gardens have been used to compare hybrid radish performance and wild radish performance. Temperature data are shown only for the time between planting and senescence within a given common garden. Radish performance has been assessed from gardens in Texas (this study); Irvine and Riverside, California, in 2005 and 2006 (three gardens with natural hybrids; Ridley and Ellstrand 2009); Riverside, California, and Pellston, Michigan, in 2005 (two gardens with experimentally derived hybrids; Campbell et al. 2006); and Pellston, Michigan, in 2004 (one garden with experimentally derived hybrids; Campbell and Snow 2007). The eight field populations used as seed sources in this study originate from and then experienced 3 years of natural selection near Pellston, Michigan. Weather stations from which data were collected are located in Katy, Texas (KTME); Irvine, California (KSNA); Riverside, California (KRAL); and Pellston, Michigan (KPLN).

Table A1. Statistical tests of biotype (hybrid vs. wild) and competition (reduced vs. ambient) effects for all response measures, using PROC GLIMMIX

Response and parameter	df	F	χ^2	P
Seed production components:				
Proportion of seeds emerging as seedlings (normal, identity; $n = 156$):				
Competition	1, 146	4.83		.0296
Biotype	1, 6	36.04		.0010
Competition \times biotype	1, 146	.27		.6037
Population(biotype)	1		.55	.2286
Proportion of seedlings flowering (beta, logit; $n = 146$):				
Competition	1, 136	20.07		<.0001
Biotype	1, 6	9.84		.0201
Competition \times biotype	1, 136	.40		.5259
Population(biotype)	1		.04	.4204
No. flowers per flowering plant (lognormal, identity; $n = 84$):				
Competition	1, 74	15.63		.0002
Biotype	1, 6	.24		.6386
Competition \times biotype	1, 74	.52		.4747
Population(biotype)	1		.08	.3859
Proportion of flowers maturing to fruit + 1 (lognormal, identity; $n = 84$):				
Competition	1, 80	14.38		.0003
Biotype	1, 80	.45		.5045
Competition \times biotype	1, 80	.74		.3919
No. seeds per fruit (normal, identity; $n = 56$):				
Competition	1, 52	.00		.9873
Biotype	1, 52	2.10		.1530
Competition \times biotype	1, 52	.41		.5272
Population fecundity + 1 (lognormal, identity; $n = 156$):				
Competition	1, 152	47.83		<.0001
Biotype	1, 152	6.28		.0132
Competition \times biotype	1, 152	.64		.4266

Appendix from S. M. Hovick et al., Hybrid Colonization in a Novel Region

Table A1 (Continued)

Response and parameter	df	F	χ^2	P
Phenological responses:				
Time to emergence (gamma, log; $n = 146$):				
Competition	1, 136	.49		.4863
Biotype	1, 6	23.15		.0030
Competition \times biotype	1, 136	.03		.8682
Population(biotype)	1		.36	.2743
Time to flowering (gamma, log; $n = 84$):				
Competition	1, 80	8.30		.0051
Biotype	1, 80	.04		.8440
Competition \times biotype	1, 80	1.52		.2208
Flowering duration (gamma, log; $n = 84$):				
Competition	1, 74	19.45		<.0001
Biotype	1, 6	.37		.5633
Competition \times biotype	1, 74	4.93		.0295
Population(biotype)	1		1.12	.1452
Plant size at flowering:				
Stem diameter + .5 (lognormal, identity; $n = 84$):				
Competition	1, 80	12.88		.0006
Biotype	1, 80	.30		.5852
Competition \times biotype	1, 80	.01		.9311
Length of longest leaf (lognormal, identity; $n = 84$):				
Competition	1, 74	16.07		.0001
Biotype	1, 6	.57		.4798
Competition \times biotype	1, 74	.05		.8287
Population(biotype)	1		.45	.2523

Note: For each response, the underlying distribution, link function, and sample size are given. Significance of the random population effect was assessed by testing the change in log likelihood (or pseudo-log likelihood) with elimination of the population effect from the model (against a χ^2 distribution). Where the population effect could not be estimated, it was eliminated from the statistical model. Significant effects are noted in bold.