

**SELECTION ON SEEDLING EMERGENCE TIMING AND SIZE
IN AN ANNUAL PLANT, *HELIANTHUS ANNUUS* (COMMON
SUNFLOWER, ASTERACEAE)¹**

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- **Premise:** Variation in seedling emergence timing is considered adaptive over the long term in wild populations, but early emergence can result in a fitness advantage. To explore the adaptive significance of seedling emergence timing, it should be studied under realistic conditions and in the context of other traits that influence fitness.
- **Methods:** In a common garden, we monitored maternal families from seed to flowering (including over winter) with intra- and interspecific competition. We assessed the effects of emergence timing and plant size on survival to anthesis in different genetic backgrounds and under varying competition.
- **Key Results:** We found genetic variation for emergence (probability and timing), size, and survival to anthesis. We also found negative selection, both phenotypic and genetic, on emergence time, such that early emergers (day 8) had almost twice as great a predicted probability of surviving as later emergers (day 28). Size had strong positive effects on survival and, furthermore, the beneficial effects of early emergence may be mediated through size. Maternal family and competitive environment can also affect selection on emergence timing.
- **Conclusions:** Our results indicate that early emergence is related to greater survival in wild sunflower, although there may be little direct selection on this trait; rather, its importance may be mediated by its effects on highly adaptive traits associated with size. Also, the effects of early emergence may vary across genetic backgrounds and competitive conditions, facilitating the maintenance of variation for this trait across a diverse landscape.

Key words: adaptive; common sunflower; evolution; fitness; genetic variation; life history; seedling emergence; selection.

Seedling emergence, when the dormant seed germinates and begins life as a seedling, is the most fragile of stages in the life cycle of annual plants. The timing or phenology of seedling emergence can strongly influence plant fitness, as well as the composition of a plant's neighborhood, the environment which it experiences, its potential mates, and the maternal effects it imparts to its progeny. Many environmental factors that vary across a species' range, over time, and among microsites can influence emergence time (Cruden, 1974; Kalisz, 1986). In some environments, seedling emergence is finely tuned to particular cues, such as the arrival of a limiting resource. For instance, spring monsoon rains can induce rapid emergence of desert annuals, while light flashes and nutrient pulses indicative of tillage stimulate seeds of agricultural weeds (Venable, 1989; Dyer, 1995; Baskin and Baskin, 2001). These examples indi-

cate some level of genetic control over emergence time, germination, and dormancy, all of which have been shown to be genetically variable traits (Platenkamp and Shaw, 1993; Baskin and Baskin, 2001; Finch-Savage and Leubner-Metzger, 2006; Mercer et al., 2006; Leger et al., 2009). Biotic or abiotic conditions present during seed ripening may affect variation in seed germination, such that seeds from different maternal plants (Roach and Wulff, 1987) or from samples within plants (e.g., Simons and Johnston, 2000) may differentially emerge. Effects of paternal variation have also been demonstrated, as in a study of percent emergence among seeds produced by crosses between plants of more and less distant provenances (Waser et al., 2000). Thus, it is important to understand both the genetic and environmental factors that could affect variation in emergence timing and selection on this crucial trait.

Emergence timing can have varying effects on plant survival, growth, and fecundity (Verdú and Traveset, 2005), as well as on patterns of genetic variation found in the standing population (Cabin et al., 1997). Therefore, variation in emergence, whether genetically determined or not, may play an important role in directing the early life history and the ultimate fitness of plants (Roach and Wulff, 1987; Stratton, 1992; Geber and Griffen, 2003). Early, intermediate, and late emergence timings can all be beneficial for particular species or conditions (Baskin and Baskin, 2001, p. 573), and a meta-analysis by Verdú and Traveset (2005) found that early emergence benefited growth and fecundity more strongly than survival. Early-emerging seedlings may have an advantage because of (1) greater availability of resources, (2) protection from disease or predators, or (3) an indirect relationship between emergence time and seed

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size (Weekley et al., 2007; Abe et al., 2008). In some cases, later emergence can reduce the exposure of the plant to random mortality events, such as severe frost. In addition, seed-size variation under competitive conditions has been shown to generate competitive hierarchies such that larger seeds tend to produce seedlings that dominate stands (Stanton, 1984, 1985). Similar results could be found if emergence time affects seedling size and, thus, competitive hierarchies (Stratton, 1992). Later-emerging seedlings may encounter larger neighbors than earlier-emerging seedlings, which could suppress growth. Such competitive conditions are known to affect plant size. This suggests that we might find variation in selection on emergence time and plant size in different competitive or biotic environments (Stratton, 1992; Weinig, 2000).

Although much is known about the causes and consequences of variation in emergence time, it is still rare to find studies that provide a complete understanding of selection on emergence timing under natural conditions. Most field studies of variation in emergence time have been done with little knowledge of the genetic relationships of the seeds or seedlings, with the net result that differences in timing could capture environmental variation, or a combination of environmental and genetic variation (Castro, 2006; Weekley et al., 2007; Abe et al., 2008). Conversely, researchers have explicitly studied genetic differences in percent germination and timing of germination, but, to keep track of the identities of different seed lots, many studies of seed characteristics have been conducted under laboratory conditions or utilizing seed germination bags in the field (e.g., Cruden, 1974; Jain, 1982; Meyer et al., 1990; Adler et al., 1993; Simons and Johnston, 2006; Mercer et al., 2006; Kudoh et al., 2007). There is a much smaller, but intriguing, literature on genetic differences in percent emergence or emergence timing under field conditions (Jones et al., 1997; Waser et al., 2000; Leger et al., 2009).

Our goal is to understand the fitness consequences of variable emergence time, so a rigorous examination of selection on this trait is required. In particular, while studies that explore the average fitness consequences of being from a particular emergence cohort are important, regression techniques can be used to evaluate the relationship between fitness and timing of emergence with greater precision. Estimating directional selection on timing of emergence (e.g., Stratton, 1992; Weinig, 2000) can aid in predicting evolutionary change (Lande and Arnold, 1983). However, given that selection on a given trait is often not independent of other traits because of genetic linkage disequilibrium or pleiotropy, estimating selection in the context of other traits that affect fitness is also important (Lande and Arnold, 1983). Therefore, estimating both selection differentials (which relate each trait to fitness) and selection gradients (which relate multiple traits to each other and fitness) is essential. Estimates of phenotypic selection, which are calculated from individual plant data, can differ from those of genotypic selection, which can be calculated using family means as data (e.g., Rausher, 1992) or directly from calculated genetic covariances (e.g., Etterson and Shaw, 2001; Hadfield et al., 2010). Environmental correlations between fitness and the traits of interest can affect estimates of phenotypic selection. If phenotypic and genotypic selection analyses differ, environmental correlations may have influenced phenotypic selection, indicating that indirect selection could be operating on a trait.

Given the strengths of both phenotypic and genetic analyses, we took an ecological genetic approach to studies of emergence; such an approach can be powerful for two reasons. First, data on natural emergence percentage and timing provide a realistic

understanding of how well particular genotypes or family groups produce viable seedlings under field conditions (e.g., Jones et al., 1997; Leger et al., 2009). Second, such studies track the same individuals through their life cycles to better relate these early traits to ultimate fitness (e.g., Stratton, 1992; Weinig, 2000). Although different plant species and environmental systems require different temporal scales for study of emergence, variation in seedling emergence often operates on a time-scale of days, not weeks. As a consequence, an ecological genetic approach to emergence timing can be logistically challenging. For many weedy annuals, for example, one needs to (1) follow plants from seed to seed in the field, including the overwintering period; (2) census seedling emergence frequently to examine emergence patterns at a time-scale relevant for the species; (3) examine not just emergence of known seeds, but also the subsequent fate of seedlings under intraspecific and interspecific interactions; and (4) keep track of genotypes of interest throughout. Our work was designed with these challenges in mind.

Here, we quantify the fitness of *Helianthus annuus* L. (common sunflower) plants emerging from overwintering seed and developing into dense stands in the field. Common sunflowers are excellent subjects for studies of seed and seedling traits because seeds are relatively large (approximately 6–16 mg; K. Mercer et al., personal observation), dormancy is common, and plants typically establish in disturbed habitats where competition with other weedy species is likely (Mercer et al., 2006; Alexander et al., 2009). Emergence can occur over a period of several weeks, which suggests that plant fates may differ between early and late emergers. We aimed to answer four questions: (1) To what degree is there genetic variation in the timing of seedling emergence in wild sunflower? (2) Is there a relationship between emergence timing, traits important for competitive ability (i.e., plant size), and fitness, and should we expect selection for earlier or later emergence in wild populations? (3) Do phenotypic selection and genotypic selection coincide? And (4) does selection vary across genetic backgrounds or competitive environments?

MATERIALS AND METHODS

Study system—The native common sunflower colonizes prairies, roadsides, rights-of-way, construction zones, and agricultural fields throughout the Great Plains and into Mexico. Factors that affect its emergence and abundance include size and timing of disturbance, size of the existing seed bank, habitat type, metapopulation dynamics, and genetic variation (Alexander and Schrag, 2003; Mercer et al., 2006; Moody-Weis and Alexander, 2007; Alexander et al., 2009). Wild sunflower seeds remain dormant over winter, but show variation among populations for levels of dormancy in the spring (Linder, 2000; Mercer et al., 2006). In northeastern Kansas, where we conducted the study, sunflowers emerge from late March through early May and bloom between July and September.

Design and establishment of the field experiment—Our analysis of wild seedling emergence was performed in the context of a field experiment designed to study the ecology of sunflower populations containing both wild and crop-wild hybrid plants. Because of questions about the genetic identity of the “hybrid” seed, we did not analyze the hybrid plants in this study and focus entirely on the biology of the wild plants, though hybrids are among the neighbors of focal wild plants. The presence of crop-wild hybrid seedlings in our experimental populations is not relevant to the focus of this paper, and tests evaluating effects of hybrids were not statistically significant (data not shown). For brevity, we will limit our description to only the most relevant aspects of the experimental setup (for further information, see Appendix S1; see Supplemental Data with the online version of this article).

To establish the study, we produced sunflower seeds (technically achenes) in 2007 in field plots in Columbus, Ohio. Crosses were performed using hand-pollinations in which 20 wild plants were used as maternal parents to maintain diversity. These plants were derived from a bulk collection of seeds gathered in fall 2006 at 10 sites near Lawrence, Kansas (sites ranged from 5 to 30 km from the main field experiment; see below). Each head on a wild plant received pollen from a randomly chosen, synchronously flowering individual plant from within the group of 20. On each plant, all seeds from the multiple pollinated heads (i.e., 5–7 full-sib families from randomly chosen pollen parents) constituted a given maternal family. Focal seeds in this study are from these maternal families.

During the last week of October 2007, we established six experimental wild sunflower populations by planting seed in 6.1×6.1 m plots (i.e., blocks) in a 5.4-ha brome field at the University of Kansas Field Station (Jefferson County, Kansas), a research unit of the Kansas Biological Survey and the University of Kansas. Each plot had been roto-tilled in the spring, left fallow to allow evaluation of the resident sunflower population through the spring and summer—during which time no sunflower seedlings emerged—and then tilled again to prepare for planting. Within each plot, we marked two 1×4 m strips into which we planted 650 seeds/m² to mimic establishment of small populations; such small populations are commonly found along roadsides and edges of crop fields (Alexander et al., 2009). This density was chosen based on seedling and adult plant densities recorded in the literature and by estimating 10% and 50% emergence of wild and hybrid seed, respectively (Alexander and Schrag, 2003; Mercer et al., 2006; Moody-Weis and Alexander, 2007).

Seeds were added to each strip as either “focal seeds” (seeds of known family and cross-type that we monitored) or “matrix seeds” (the bulked seeds from the same families surrounding the focal seeds). Individual focal seeds were glued to plastic swizzle sticks (i.e., cocktail stirrers 14.8 cm long and 0.4 cm wide) about 10 cm from the tip using a dot of Gorilla Glue (Gorilla Glue Company, Cincinnati, Ohio) (for further discussion of this method, see Appendix S1). Swizzle sticks were labeled with family number and planted on a 10-cm grid at least 20 cm from the edge of the strips. All focal seeds were planted just below the soil surface (i.e., with 10 cm of the swizzle stick below ground to reduce the likelihood of movement of the stick in winter freeze–thaw cycles). Sticks were planted with the seed on the south-facing side to make it easier to identify an emerging focal seedling. Focal seed locations were then covered with cups of 5 cm diameter while a “matrix” of hybrid and wild seed was broadcast in the strips; these cups reduced the likelihood of matrix seed germinating immediately next to a focal seed. About 1 cm of sieved field soil was then sprinkled over the strips and the cups were removed. There were a total of 415 wild focal seeds in the two strips in each of the six plots.

Seedling emergence and seedling traits—Of the 2490 wild focal seeds planted, we lost 11% to frost heaving, which left 2216 seeds to monitor. Starting in mid-March, the plots were observed for seedling emergence at intervals of 2–3 d until 6 May, and less frequently thereafter. The first seedling emerged on 24 March, >99% emerged by 6 May, and we monitored emergence through 5 June. In our analyses, we considered emergence date as days since 23 March (i.e., 24 March = day 1). Seedlings emerging too far from the stick (more than ~1.5 cm) were not considered focal seedlings. If multiple seedlings emerged at the location of a focal seedling, we removed that location from the data set (2% were removed for this reason); this likely resulted from overwinter movement of matrix seed by frost heaving, water dispersal, or predator activity. Focal seeds that did not emerge either remained dormant or died. Past studies indicated that we could expect ~10% overwinter mortality (Mercer et al., 2006). Nearly all plants in the plots were either sunflowers or common ragweed (*Ambrosia artemisiifolia*); thus, we quantified competition by counting the number of ragweed and sunflower seedlings within a 5-cm radius of each focal seedling on 29 April.

In May, we chose 524 of the 1369 emerged wild focal seedlings to follow through the season (“marked plants”). First we randomly chose 416 from a list of those that had emerged in each plot. Then, to improve our ability to assess the effects of emergence timing on fitness, we chose 53 additional early- and 55 additional late-emerging wild seedlings to ensure coverage of the range of emergence timing.

Plant survival, size, and fitness—Our goal was to relate emergence timing to plant survival, size, and reproduction. All marked plants were followed until reproduction (or death). To quantify size, we used plant height (to apical meristem) and length of longest leaf, which, taken together, represented the overall space that a given plant took up; for these analyses, we focus on data from 7 July, when plants were fully established but not reproductive.

To assess fitness, we recorded whether the plants survived to anthesis (reproduction) and kept track of seed production in all inflorescences (hereafter “heads”) produced. Once all florets within a given head had opened and were pollinated (i.e., stigmas had all shriveled), the head was covered with a bag of fine netting to collect maturing and dispersing seeds. Heads were collected at seed maturity. Because of an unexpected die-back after plants had flowered, but prior to maturation of seeds, our seed production data were unusually low and not typical of our past work with sunflowers at this field site (Moody-Weis and Alexander, 2007) or at other nearby sites on the University of Kansas Field Station (Snow et al., 1998; Cummings et al., 2002; Cummings and Alexander, 2002). Specifically, a minority of plants flowered and only 10% of them ($n = 22$) produced >10 seeds per head—extremely low seed numbers for this species. Therefore, we used survival to anthesis as our fitness measure, which allowed us to relate emergence time to a late-season fitness component that was independent of the die-back. According to our 10 yr of experience with natural and experimental sunflower populations in northeast Kansas, survival to anthesis is likely a more relevant measure of fitness than the unusual seed production that occurred in 2008.

Statistical analyses—All analysis was performed with SAS version 9.1 (SAS Institute, Cary, North Carolina, USA).

Variation among maternal families—We examined the effects of the maternal family on life history, size, phenology, and fitness. Analysis of probability of emergence included all 2216 focal seeds from intact swizzle sticks. Analysis of emergence timing, height in July, length of the longest leaf in July, and survival to anthesis included all individuals that remained of the 416 randomly marked wild plants that we followed throughout the season. Proc Glimmix was used for all analyses of variance on binary and continuous response variables. The models included the fixed effect of family, as well as block and edge as random factors. The variable “edge” indicates whether a focal plant was located on the outer two rows or columns in the gridwork of planted focal seeds; such “edge” plants tended to be slightly larger than plants more internal in the gridwork.

We also employed a failure-time analysis using Proc Lifetest to assess the timing of seedling emergence and how family affects it. Through failure time analysis, Proc Lifetest takes into account right-censoring of data (e.g., seeds that have not yet emerged, be they dead or dormant; Fox, 2001) and allows us to examine impacts of genetics (i.e., family) on emergence patterns.

Phenotypic selection analysis with logistic regression—We used logistic regression (Proc Logistic) for phenotypic selection analysis because survival to anthesis is a binomial response variable (Janzen and Stern, 1998). We elucidated the effects of three traits of interest—emergence timing, height in July, and length of longest leaf in July—on survival to anthesis in the context of experimental factors, such as block and edge (Lande and Arnold, 1983; Donohue et al., 2005b). Three types of analysis of phenotypic selection were performed. First, we did a simple test of overall phenotypic selection by having only a single trait of interest in the model. Second, we assessed how selection might proceed differently in different genetic backgrounds (i.e., maternal families) by introducing interactions between our traits of interest and family. Third, we explored how selection might differ under different competitive environments by introducing interactions between each trait and number of competitors.

For each of the three types of analysis, we ran logistic regression models in which each phenotypic trait was used to predict survival singly and in which the three traits (and any interactions with those traits and family or number of competitors) were analyzed jointly to take into account the covariances between pairs of traits. Any difference between these two analyses clarifies the degree to which apparent selection on a trait can be mediated by selection on another (e.g., Mitchell et al., 1998; Etterson and Shaw, 2001). Partial regression coefficients representing selection differentials (s) and selection gradients (β) are presented to adhere to common usage in evolutionary studies (e.g., Kalisz, 1986). Standardized partial regression coefficients are presented and would need to be transformed to be interpretable for evolutionary equations (Lande and Arnold, 1983) since they do not result from linear regressions (Janzen and Stern, 1998). We used data from the random, early, and late groups of marked focal plants because preliminary analyses indicated that the inclusion of extreme emergence times improved the precision and accuracy of effects of emergence time (data not shown).

Genotypic selection analysis with linear regression—We performed genotypic selection analysis, using means from maternal families as estimates of genotypic effects, to reduce confounding environmentally induced associations

between fitness and traits (Rausher, 1992). We produced least-squares means for each family in each block and assessed the relationship between probability of survival to anthesis and our traits of interest (singly and jointly), while taking block into account. Because family means of survival to anthesis were no longer binary, we performed linear regressions to produce the partial regression coefficients (again, s and β). The means of family block combinations were produced from variable numbers of individuals (1 to 10), so their associated error varies, which could possibly lead to an underestimation of additive genetic variance (σ_a^2) (Hadfield et al., 2010).

RESULTS

Trait variation among families—For all traits investigated, we found significant variation among maternal families (Figs. 1 and 2). Of the 2216 wild focal seeds monitored in spring 2008, 61% emerged as seedlings between 24 March and 6 May (i.e., day 1 and day 43) and only two seedlings emerged later. In addition to finding variation among families in their emergence curves (Fig. 1: log rank, $\chi^2 = 141.6$, $df = 19$, $P < 0.0001$), we determined that families varied in probability of emergence (range: 0.31–0.77; $F = 6.86$, $df = 19$ and 2177, $P < 0.0001$), day of emergence (12.7–21.8; $F = 2.77$, $df = 19$ and 389, $P < 0.0001$), height in July (16.2–28.1 cm; $F = 3.49$, $df = 19$ and 360, $P < 0.0001$), length of longest leaf in July (2.6–4.4 cm; $F = 5.13$, $df = 19$ and 360, $P < 0.0001$), and for the probability of survival to anthesis (0.13–0.67; $F = 1.83$, $df = 19$ and 389, $P = 0.0183$; Fig. 2); all chi-square and F statistics refer to tests of the effect of family. Emergence date, height in July, leaf length in July, and survival to anthesis were all significantly correlated with one another, and early emergence was correlated with greater height, leaf length, and survival to anthesis (Table 1).

Selection analyses—When assessing phenotypic selection on traits individually, the selection differentials and the odds ratios indicate that fitness increases with earlier emergence, greater height, and greater leaf length (Table 2A and Fig. 3).

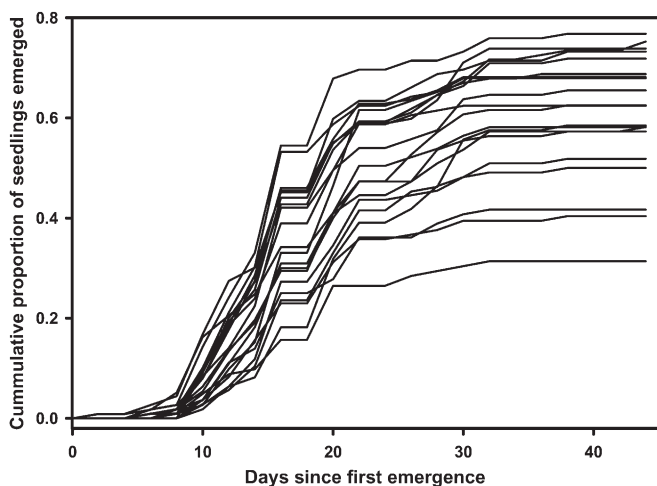


Fig. 1. Emergence curves by family for wild sunflower seedlings emerging, based on all focal seeds that were not disturbed by frost heaves ($n = 2216$). Proportion emerged for each family can be read as the end points for each curve. Two late emergence events, one on day 52 and one on day 73 have been removed for clarity, as were the standard error bars, which can be as high as 0.048. First emergence was noted 24 March (= day 1). Failure-time analysis, family effect: $P < 0.0001$.

The odds of surviving decrease slightly for every increase in emergence day, whereas the odds of surviving increase by a multiplier of 1.26 for each additional 1-cm increase in height and by a multiplier of 5.75 for each 1-cm increase in leaf length (see Odds Ratios, Table 2A). Despite this clear importance of early emergence for survival to anthesis, when the three traits are analyzed jointly, selection for early emergence is no longer significant, which indicates that apparent selection on this trait was actually mediated by selection on another (Table 2D). In other words, selection on emergence timing may have been indirect through selection on size or another trait that we did not measure. Selection gradient analyses that include both emergence time and height (data not shown) also show no significant effect of emergence, so it is likely that early emergence is beneficial, in part, via its effect on height and/or leaf length. Selection gradient analysis predicts smaller effects on the odds of surviving than selection differentials (Table 3D), again suggesting a role for indirect selection.

Analysis of genotypic selection, which removes the joint effect of environment on different traits (Rausher, 1992), shows very similar results to phenotypic selection, with emergence timing being significantly related to survival when analyzed singly (Table 3A) but not when analyzed jointly with other traits (Table 3B). Because genotypic selection analyses were linear regressions, these coefficients can be directly interpreted as the increase in probability of surviving to anthesis for every increase in one unit of the trait (Table 3).

Phenotypic selection appears to vary by genetic background (i.e., by maternal family) for emergence time, whether traits are analyzed separately or jointly (Table 2B, E). Selection is for earlier emergence in most families, although there are families in which selection differentials and gradients were positive or close to zero (family \times emergence-day partial regression coefficients in Appendix S2). Thus, for example, the percent survival to anthesis typically varies for early versus late emergers, with some families showing very strong declines in fitness with late emergence and others showing the opposite response (Fig. 4; note that for illustration purposes, emergence was divided into two categories). In fact, the negative effects of late emergence appear to be greater for families whose average emergence is later (Appendix S2). The interaction between emergence-day and family endures in the selection gradient analysis, indicating that variation among families for fitness cannot be accounted for solely by size traits or the interactions of size traits with family. Therefore, genetic background affects phenotypic selection.

Although sunflower survival and size generally increased as the number of neighbors declined (Fig. 5A–C), the relationship between survival to anthesis and each trait depended on the number of neighbors; that is, phenotypic selection varied by number of competitors. This was true when traits were analyzed singly (Table 2C) but not when they were analyzed jointly (Table 2F). The relationship between early versus late emergence time and survival was similar when 0–2 and 3–4 competitors were present, but with more competitors, the effect of emergence time was less pronounced (Fig. 5A). By contrast, for height, shorter plants with few competitors were at less of a disadvantage compared with their tall counterparts than were those with more competitors (>3 ; Fig. 5B). For leaf length, plants with relatively high competition (5–6 competitors) appeared to experience less of an effect of leaf length on survival (Fig. 5C). It may be that leaf length predicts survival more closely at low and high competition, but less well at intermediate competition. However, these results must be interpreted

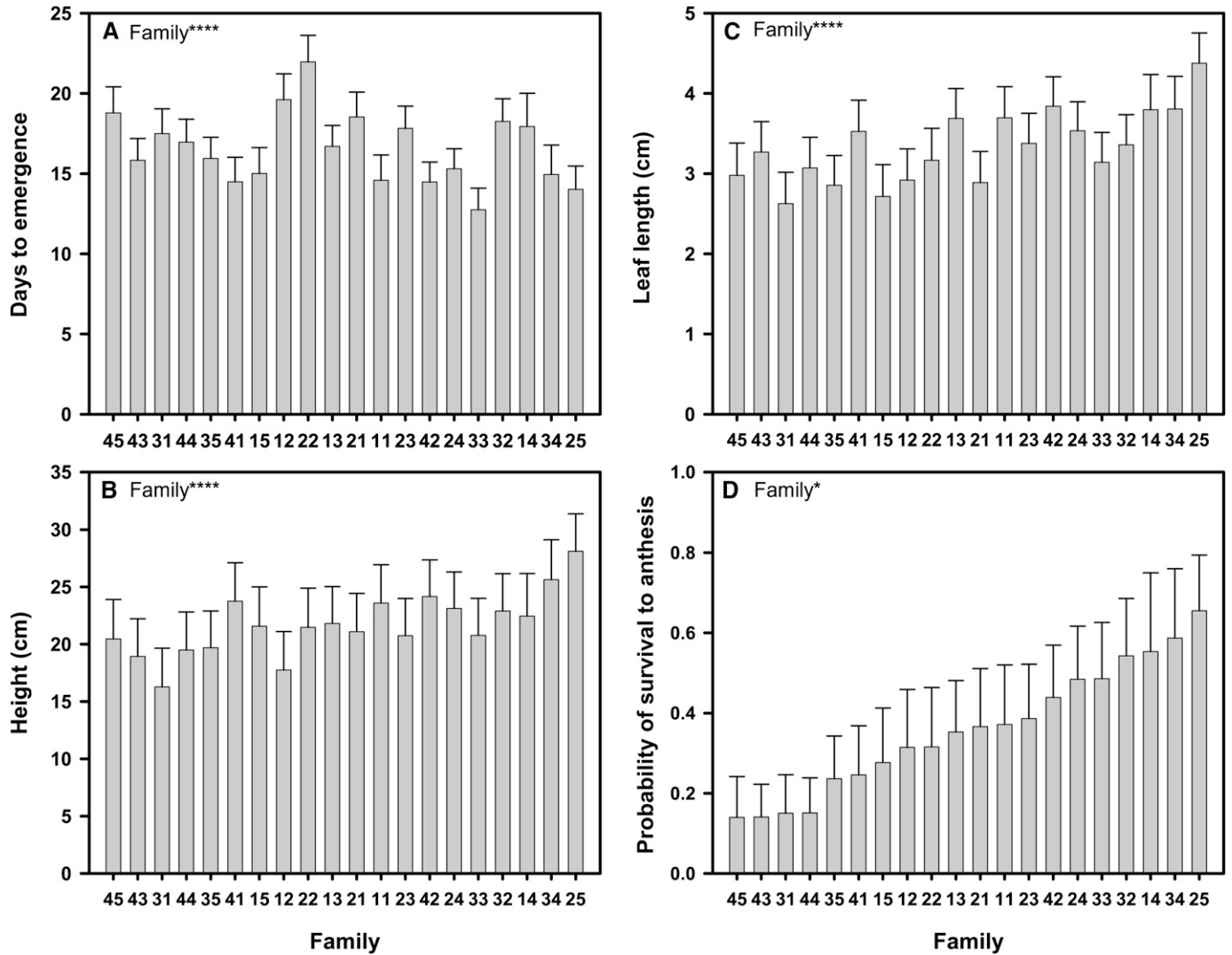


Fig. 2. Least-square means of (A) days to emergence, (B) height in July, (C) length of longest leaf in July, and (D) survival to anthesis for each of 20 maternal sunflower families. Only data from randomly marked focal plants were used ($n = 416$). Families are ordered by probability of survival to anthesis. The significance of the family effect in the analysis of variance for each trait is indicated (* $P < 0.05$, **** $P < 0.0001$).

with caution because they were not created through the joint analysis. Instead, for all of Figure 5, the predictor variables (emergence time, height, or leaf length) were divided into two categories, so they do not directly reflect selection gradients.

DISCUSSION

Evolutionary ecology of emergence timing—To our knowledge, the present study is the first to quantify phenotypic, as

well as genotypic, selection on emergence time under natural conditions. Our methods allowed us to follow seeds from known crosses throughout their life cycle, including overwintering and while competing with the plant community (for merits and drawbacks of this method, see Appendix S3). We identified genetic variation for seedling emergence, plant size, and survival to anthesis. Earlier emergence and greater size increased survival to anthesis, as seen from both phenotypic and genotypic selection analyses. However, selection on emergence time appeared to wane when all traits were analyzed jointly, which

TABLE 1. Simple covariances (below the diagonal) and correlations (above the diagonal), as well as variances (on the diagonal) for fitness and three traits of interest. Tests for significance for correlations employed 487–522 degrees of freedom, depending on the traits (** $P < 0.001$, **** $P < 0.0001$).

	Survival to anthesis	Emergence day	Height in July	Leaf length in July
Survival to anthesis	0.229	-0.154***	0.485****	0.527****
Emergence day	-0.574	60.668	-0.274****	-0.275****
Height in July	2.058	-18.535	76.316	0.802****
Leaf length in July	0.278	-2.318	7.609	1.179

TABLE 2. Selection differentials and selection gradients (partial regression coefficients) calculated for phenotypic selection using logistic regression. Selection differentials were calculated from several analyses, each with a single trait (A) or a single trait and its interaction (B, C). Selection gradients were calculated from a single analysis with multiple traits (D) or multiple traits and their interactions (E, F). For selection differentials, separate models focusing on different traits are designated by roman numerals (i, ii, and iii). Standardized values (std) are presented for comparison. Abbreviations: ED = emergence day, Ht = height in July, and LLLF = length of longest leaf in July. Significance indicated by * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$, ns (not significant) $P > 0.05$.

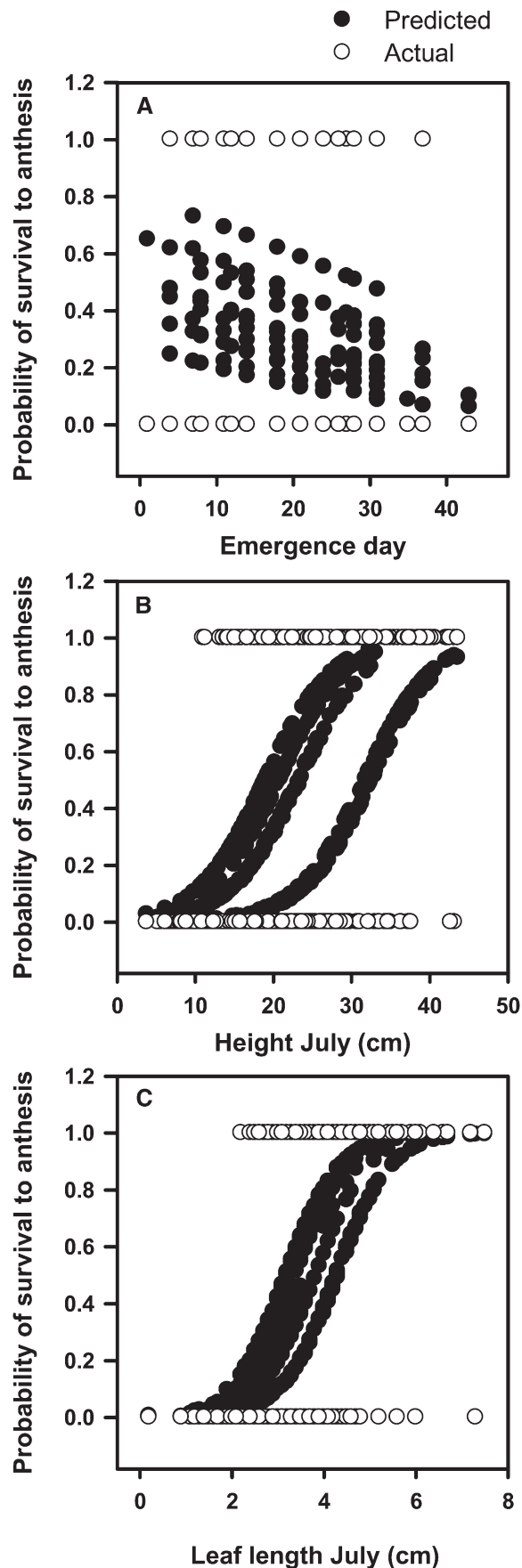
Selection differentials									
	<i>s</i>	SE	Odds ratio	95% CI	<i>s</i> (std)	SE	Wald χ^2		
A. Selection—simple									
(i)	ED	-0.046	0.013	0.96	0.93–0.98	-0.36	0.1	11.7	***
(ii)	Ht	0.23	0.024	1.26	1.21–1.32	2.05	0.21	99.41	****
(iii)	LLL F	1.75	0.18	5.75	4.02–8.22	1.9	0.2	92.06	****
B. Selection varying by genetic background									
(i)	ED	-0.049	0.015	0.95	–	-0.38	0.12	10.25	**
	ED*Family	-0.082 to 0.064	Varies	–	–	-0.64 to 0.5	Varies	33.92	*
(ii)	Ht	0.26	0.028	1.3	–	2.29	0.24	89.54	****
	Ht*Family	-0.042 to 0.061	Varies	–	–	-0.37 to 0.53	Varies	23.23	ns
(iii)	LLL F	2.087	0.22	8.062	–	2.26	0.24	87.91	****
	LLL F*Family	-0.27 to 0.46	Varies	–	–	-0.29 to 0.50	Varies	28.56	ns
C. Selection varying by competitive environment ^a									
(i)	ED	-0.021	0.016	0.98	–	-0.16	0.13	1.7	ns
	ED*No. of competitors	-0.0064	0.0023	0.99	–	-0.05	0.018	7.86	**
(ii)	Ht	0.29	0.029	1.34	–	2.53	0.25	98.11	****
	Ht*No. of competitors	-0.0076	0.0018	0.99	–	-0.066	0.015	18.38	****
(iii)	LLL F	1.91	0.2	6.77	–	2.077	0.22	90.3	****
	LLL F*No. of competitors	-0.035	0.012	0.97	–	-0.038	0.013	7.89	**
Selection gradients									
	β	SE	Odds ratio	95% CI	β (std)	SE	Wald χ^2		
D. Selection—simple									
	ED	-0.038	0.017	1	0.96–1.03	-0.03	0.14	0.048	ns
	Ht	0.14	0.029	1.16	1.091–1.22	1.26	0.25	25.021	****
	LLL F	1.048	0.22	2.85	1.86–4.39	1.14	0.24	22.83	****
E. Selection varying by genetic background									
	ED	-0.066	0.04	0.94	–	-0.52	0.31	2.69	ns
	ED*Family	-0.59 to 0.21	Varies	–	–	-4.57 to 1.62	varies	31.32	*
	Ht	0.18	0.05	1.2	–	1.56	0.44	12.65	***
	Ht*Family	-0.72 to 0.65	Varies	–	–	-6.26 to 3.47	varies	23.12	ns
	LLL F	2.024	0.46	7.57	–	2.2	0.5	19.45	****
	LLL F*Family	-3.66 to 7.50	Varies	–	–	-3.97 to 8.14	varies	25.27	ns
F. Selection varying by competitive environment ^a									
	ED	-0.003	0.029	1	–	-0.024	0.23	0.011	ns
	ED*No. of competitors	-0.00046	0.0053	–	–	-0.0036	0.041	0.0077	ns
	Ht	0.19	0.052	1.21	–	1.64	0.45	13.1	***
	Ht*No. of competitors	-0.0043	0.0086	–	–	-0.037	0.076	0.24	ns
	LLL F	1.022	0.37	2.78	–	1.11	0.4	7.8	**
	LLL F*No. of competitors	-0.017	0.059	–	–	-0.019	0.064	0.087	ns

^aCompetitors counted before some later emergence, so fewer individuals ($n = 480$).

likely suggests that emergence time is effective, in part, through its influence on plant size. Families varied in how emergence time affected survival: the majority showed advantages of early emergence, but 3 of 20 families experienced greater fitness among their later emergers. We also found that selection varied by competitive environment, such that selection on early emergence time was reduced under more competitive conditions whereas selection on height increased with competition. Thus, genetic correlations, genetic background, and biotic interactions all affect selection dynamics in stands of common sunflower.

Variation—Variation in seedling emergence time is well documented in wild and experimental populations. In addition

to microsite effects, variation in percent emergence and emergence time in our study was partly due to genetic differences among maternal families. Variation in emergence infers that seed dormancy also varied across families, which could carry its own fitness consequences (Venable and Brown, 1988). However, variation in dormancy could not be quantified in the present study, given the challenge of recovering dormant seeds in the spring (seeds remained glued to their stick only for days or weeks). The variation in emergence and emergence time, though not unexpected, is nevertheless unique, given the considerable sources of variation in biotic and abiotic conditions that usually obscure genetic differentiation for these traits in the field. Variation among families for germination has typically



been visible under controlled laboratory conditions, but not in the field environment. For example, although Leger et al. (2009) found variation among maternal lines of cheatgrass for germination timing under controlled conditions, they could not differentiate them in the field, partly because of the difficulties of closely monitoring emergence. Similarly, Jones et al. (1997) did not find a family effect on emergence time in maple in the field while working with only four families. We do not expect that much of the variation we found among maternal families is attributable to differences among environments experienced by the original maternal plants because, in our study, seeds from each family were produced on a relatively uniform, fertile field. Thus, most variation among maternal families should be genetic—from either maternal or paternal sources.

In addition to distinguishing variation among families, we found that variation within families and among blocks for emergence time was also high, which points to possible genetic variation within families. The genetic variation within these maternal families, each a mixture of full-sib families, could be due to maternal, paternal, or combined genetic contributions. Environmental and microsite variation were other important determinants of emergence time. Although most emergence occurred between days 10 and 25 (Fig. 1), emergence was recorded in our study until day 73 (6 June), and even later in a neighboring study (S. Bodbyl-Roels, personal communication). This wide range in emergence time would result in seedlings emerging into vastly different biotic and abiotic environments, which likely was instrumental in establishing important variation in fitness (Abe et al., 2008). Finally, plants with the greatest number of competitors were more likely to have emerged early than late (data not shown), a possible indication of microsite effects or an effect of seed density on seed emergence.

Earlier emergence favored—We saw a significant negative relationship between survival and days to emergence when traits were analyzed singly, but to what degree was early emergence favored? With an odds ratio of surviving to anthesis of 0.96, each day later that a plant emerges results in a 0.96 change (i.e., a reduction) in the odds of surviving to reproduce. The resulting predicted values of the probability of surviving to anthesis for an early emerger (8 d) and a late emerger (28 d) indicate that, for the late emerger, the probability of surviving to anthesis has halved (day 8: 0.42 probability of survival, day 28: 0.23 probability of survival). Of the 10 latest emergers, only one survived to anthesis. Given that we see an interaction between genetic background (family) and emergence time, there is variability in these numbers across families. For instance, predicted probabilities of survival to anthesis for plants that emerge on day 8 vary from 0.27 to 0.54 across families, whereas those for plants that emerge on day 28 range from 0.03 to 0.62 across families.

Fig. 3. The relationship between each of three traits, (A) emergence day, (B) height in July, and (C) leaf length in July, and actual as well as predicted survival to anthesis. These transformed predicted values resulted from the logistic regressions that produced the selection differentials (Table 3A). Variation in predicted values (i.e., different curves within panel) is due, in part, to differential predictions across the other predictor variables in the model, such as block and edge. For emergence time, $n = 523$; for other traits, $n = 488$.

TABLE 3. Selection differentials and selection gradients (partial regression coefficients) calculated for genotypic selection. Selection differentials (A) were calculated using separate models focusing on each trait, which are designated by roman numerals (i, ii, and iii). Selection gradients were calculated from a single analysis with multiple traits (B). Standardized and relativized regression (std/rel) coefficients are presented for comparison. Significance indicated by * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$, ns (not significant) $P > 0.05$.

		s	SE	s (std/rel)	SE	t	
A. Selection differential							
(i)	Emergence day	-0.014	0.0051	-0.18	0.066	-2.76	**
(ii)	Height in July	0.027	0.003	0.53	0.059	9.1	****
(iii)	Length of longest leaf in July	0.22	0.024	0.5	0.055	9.1	****
		β	SE	β (std/rel)	SE	t	
B. Selection gradient							
	Emergence day	-0.0026	0.0041	-0.033	0.054	-0.62	ns
	Height in July	0.015	0.0053	0.29	0.1	2.85	**
	Length of longest leaf in July	0.11	0.043	0.26	0.099	2.65	**

Many studies have found a positive effect of early emergence on percent survival (Stanton, 1985; Kalisz, 1986; Stratton, 1992; Jones et al., 1997; Leger et al., 2009), possibly due to reduced disease, competition, and seed predation (Abe et al., 2008), although this is not always the case (Baskin and Baskin, 2001; Weekley et al., 2007). The degree or presence of a benefit of early emergence on fitness has varied more across studies on annuals than on perennials, and is especially strong for large-seeded species (Verdú and Traveset, 2005). Some variation in the effect of early emergence could also be due to habitat-specific effects (Donohue et al., 2005b; Castro, 2006) or microsite variation (Kalisz, 1986; Stratton, 1992). Our study is unique in closely assessing genetic variation for seed traits in the field and establishing a genetic relationship between this variation and a fitness characteristic.

Benefits of early emergence for survival are thought to be stronger for early census dates than for later ones, presumably because other traits and biotic or abiotic factors dominate as more of the life cycle is completed (Kalisz, 1986; Verdú and Traveset, 2005; but see Stratton, 1992). In contrast to Harper (1977), who observed that the seedling portion of the life cycle has the greatest mortality, we found that many plants that had stopped growing did not die early but persisted in a stunted state. Although the effects of emergence time on growth and development were evident at census dates even earlier than July (K. Mercer et al., unpublished data), stunted plants persisted in surviving and most simply never flowered. Thus, selection on emergence time was greatest at survival to anthesis as opposed to survival to earlier dates (data not shown).

Competition as affected by emergence time—Many studies have shown that the density of neighbors around a given plant has important implications for its reproduction (Stanton, 1984; Miller et al., 1994). The fact that selection on emergence time appears to have been mediated by height in our study indicates that emergence time is important because of its effect on competitive hierarchies. Given that early emergers can experience reduced competition (Abe et al., 2008) and that more competitors reduced survival (Fig. 5), it might follow that the importance of early emergence for survival would be amplified for the plants with a denser neighborhood (7–16 competitors; Fig. 5A). Instead, we saw the opposite, possibly because, past a certain point, the negative effects of too many competitors dominate any positive effect that early emergence might bring. However, height became more important in more competitive

environments, as we expected (Fig. 5B). Weinig (2000) found that emergence time was key in mediating what would be adaptive periods of growth in different environmental conditions; early emergers did better with early elongation in one ecosystem and with late elongation in another, which calls for a nuanced study of the responses of plants to competition.

Evolutionary dynamics and maintenance of genetic variation—There has been considerable interest in the formal assessment of selection on seedling traits under field conditions because of their importance in life-history evolution (Kalisz, 1986; Stratton, 1992; Weinig, 2000; Donohue et al., 2005a); however, most work has been focused on phenotypic selection. A landmark study by Kalisz (1986) demonstrated that the strength and direction of multivariate phenotypic selection gradients on emergence timing varied across space and time, but, overall, selection on emergence timing tended to be for earlier emergence. The effects of emergence time on survival were comparable to ours (somewhat larger), and the relative size of selection gradients was greater when using reproduction as the

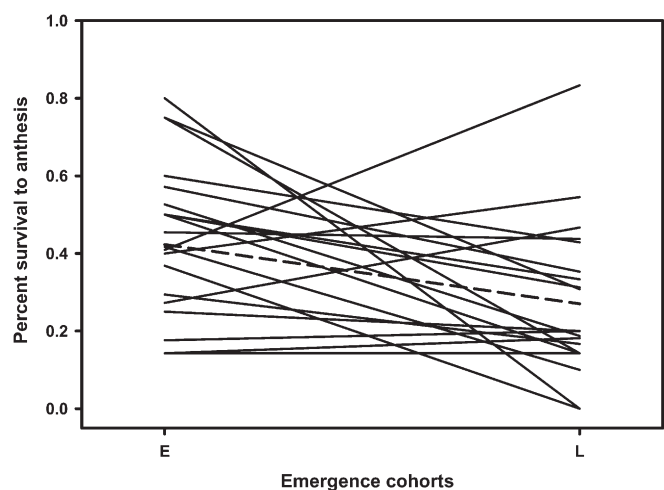


Fig. 4. Percent survival to anthesis by family for early (E) and late (L) emergence cohorts. To illustrate patterns, emergence was divided into two categories: early (emerged ≤ 14 d [$n = 286$]) and late (emerged ≥ 18 d [$n = 237$]). No emergence data were taken between days 14 and 18. The average response is plotted with a dashed line. Sample sizes for individual families and emergence cohorts ranged from 5 to 26 plants.

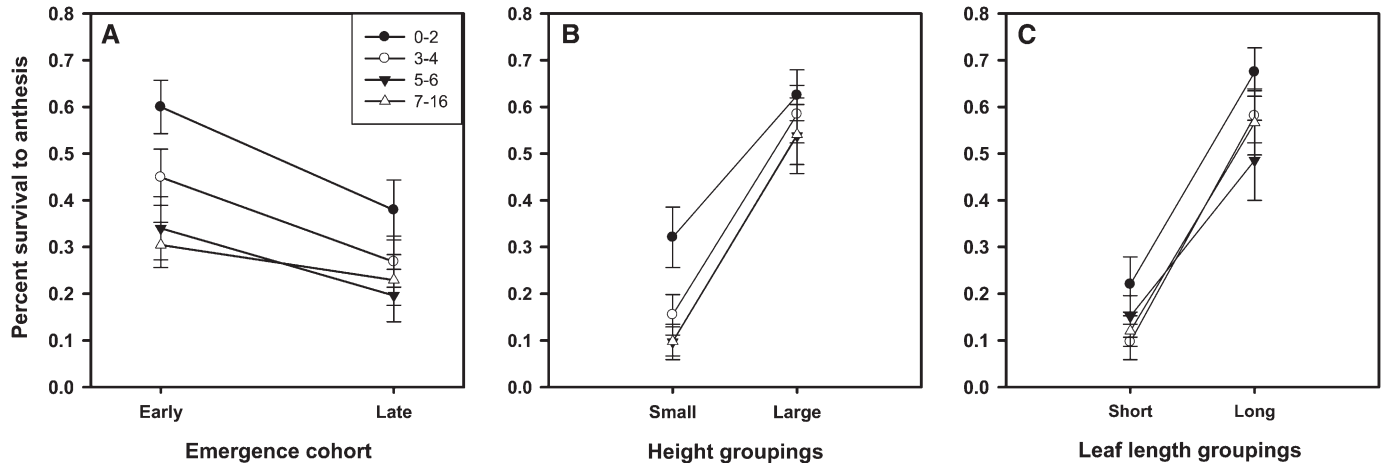


Fig. 5. The probability of surviving to anthesis for combinations of low and high levels of each sunflower trait and various numbers of competitors. Panels illustrate (A) emergence day, (B) height in July, and (C) leaf length in July. To illustrate patterns, each panel shows means for eight groups of plants (i.e., combinations above and below the median for each sunflower trait and four approximate quartiles for number of competitors: 0–2, 3–4, 5–6, or 7–16). Categories for emergence day were “early” (≤ 14 d, $n = 286$) and “late” (≥ 18 d, $n = 237$); categories for height were “small” (< 20.7 cm, $n = 243$) and “large” (≥ 20.7 cm, $n = 245$); and categories for leaf length were “short” (< 3.3 cm, $n = 243$) and long (≥ 3.3 cm, $n = 245$). No emergence data were taken between days 14 and 18. Sample sizes for any given combination of trait values with number of competitors varies from 35 to 100. In panel B, lines representing 5–6 and 7–16 competitors completely overlap.

fitness measure rather than survival. Stratton (1992) also found that phenotypic selection varied, but overall selection promoted early emergence. The only study other than ours (of which we are aware) that has assessed genotypic selection on emergence time is that by Donohue et al. (2005b). Their study differed from ours in that they manipulated emergence time of recombinant inbred lines of *Arabidopsis* derived from a New World and an Old World population by planting them at different times of year. This work did not aim to represent realistic conditions of natural emergence, but rather was intended to elucidate the factors affecting evolution of large life-history differences. These studies, along with ours, indicate that early emergence is generally favored, but why does substantial variation in emergence persist within populations?

Heritable variation for emergence timing may be maintained for several reasons. First, such variation could result from conflicting selection pressures over time and space. Variation in emergence time has been seen as adaptive for the population over time, especially given that it encourages survival of some seedlings despite errant mortality events during seedling emergence (Baskin and Baskin, 2001). Thus, biotic and abiotic variation across locations or years could reduce or enhance the importance of emergence timing for fitness, thereby affecting the patterns or strength of selection (Kalisz, 1986; Stratton, 1992; Castro, 2006). Venable’s concept of “predictive” germination is useful here, because the predictability of an environment as suitable for germination can influence genetic variation. Patch-to-patch variation in factors such as topography can result in variability in germination cues, as well as variation over time and space in the fitness consequences of responding to these cues (Venable and Lawlor, 1980). Although we did not, some studies have explicitly tested for stabilizing or disruptive selection. Although Weinig (2000) did not find evidence of stabilizing selection on emergence timing in her study, Stratton (1992) did and postulated that a tradeoff between size and survival kept emergence from occurring too early. Thus, selection in many years for early emergence might be counteracted infrequently, but significantly, by selection for populations with in-

intermediate or later emergence time. If environmental conditions and selection are not constant, variability in emergence genotypes may remain in the population. However, the theoretical conditions that would maintain rather than purge such variation are restrictive (Felsenstein, 1976). For instance, in the year of our study, no devastating stochastic seedling-mortality event occurred, so there was no obvious benefit to emerging late.

To illustrate a second idea of how selection for emergence timing could vary over time, we consider a stochastic abiotic stress such as a late frost. Such “late” frosts (here, defined as after the median day of emergence in 2008 = 10 April), have occurred in Lawrence, Kansas, in 5 of the past 18 yr (Appendix S4). Sunflower seedlings are surprisingly resilient in the face of freezing temperatures (K. Mercer et al., unpublished data), but long periods of freezing, such as six straight days in the spring of 2007 (4–9 April; Appendix S5), can kill emerged seedlings (H. Alexander, personal observation). We did not see cold-induced death in 2008, although the soil temperature went below zero on days 10 and 14, a phenomenon not seen after 24 March in any of the other previous 18 yr (Appendix S5). These cold days may have affected fitness, however. In our study, the earliest emergers (days 1 to 7, which had small sample sizes), do not seem to benefit as much as the next group of early emergers (Appendix S6). It may be that these very early emergers were exposed to biotic or abiotic stresses (e.g., root pathogens) during the first week of the season, which remained wet, with cold soil temperatures. If so, the balance of benefits and dangers of early emergence may have finally shifted toward benefits by day 8. Thus, the lack of benefit to the earliest emergers suggests that some stabilizing selection may have operated.

Two other mechanisms exist that could retain genetic variation in emergence timing. Our selection analyses show that phenotypic and genetic correlations between emergence time and size result in considerable indirect selection on emergence time, as seen by comparing the size of the selection differentials (direct and indirect selection) with the size of the gradients (direct only). Such correlations among traits can retard responses to selection, unless the genetic covariances support the direction

of selection (Etterson and Shaw, 2001). In essence, if much of the selection on emergence time operates through its effects on height, some of the variation in emergence time would likely be retained in many populations. For instance, yearly variation in competitive dynamics and, thus, the effects of height on fitness, could influence the selection on emergence timing, even without genetic association between the traits. Similarly, any variation in the heritability of emergence time over time or space could also retard or hasten evolution toward earlier emergence. Finally, it is also possible that the variation itself, rather than the mean, of emergence timing is directly favored (Simons and Johnston, 2006).

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