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Author(s): Robin G. Marushia, Matthew L. Brooks, and Jodie S. Holt
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Phenology, Growth, and Fecundity as Determinants of Distribution in Closely Related Nonnative Taxa

Robin G. Marushia, Matthew L. Brooks, and Jodie S. Holt*

Invasive species researchers often ask: Why do some species invade certain habitats while others do not? Ecological theories predict that taxonomically related species may invade similar habitats, but some related species exhibit contrasting invasion patterns. *Brassica nigra, Brassica tournefortii*, and *Hirschfeldia incana* are dominant, closely related nonnative species that have overlapping, but dissimilar, distributions. *Brassica tournefortii* is rapidly spreading in warm deserts of the southwestern United States, whereas *B. nigra* and *H. incana* are primarily limited to semiarid and mesic regions. We compared traits of *B. tournefortii* that might confer invasiveness in deserts with those of related species that have not invaded desert ecosystems. *Brassica tournefortii, B. nigra* and *H. incana* were compared in controlled experiments conducted outdoors in a mesic site (Riverside, CA) and a desert site (Blue Diamond, NV), and in greenhouses, over 3 yr. Desert and mesic *B. tournefortii* populations were also compared to determine whether locally adapted ecotypes contribute to desert invasion. Experimental variables included common garden sites and soil water availability. Response variables included emergence, growth, phenology, and reproduction. There was no evidence for *B. tournefortii* ecotypes, but *B. tournefortii* had a more rapid phenology than *B. nigra* or *H. incana*. *Brassica tournefortii* was less affected by site and water availability than *B. nigra* and *H. incana*, but was smaller and less fecund regardless of experimental conditions. Rapid phenology allows *B. tournefortii* to reproduce consistently under variable, stressful conditions such as those found in Southwestern deserts. Although more successful in milder, mesic ecosystems, *B. nigra* and *H. incana* may be limited by their ability to reproduce under desert conditions. Rapid phenology and drought response partition invasion patterns of nonnative mustards along a gradient of aridity in the southwestern United States, and may serve as a predictive trait for other potential invaders of arid and highly variable ecosystems.

Nomenclature: Black mustard, *Brassica nigra* (L.) Koch; Sahara mustard, *Brassica tournefortii* Gouan; shortpod mustard, *Hirschfeldia incana* (L.) Lagr.-Foss.

Key words: Annual, desert, forb, invasion, mustard, exotic, drought, climate.

Mechanisms by which nonnative species invade ecosystems are often poorly understood, especially because species with high success in one ecosystem may have little to no success in others (Levine et al. 2003; Williamson and Fitter 1996). Closely related species tend to be more phenotypically similar than different, due to shared ancestry, and closely related nonnatives are likely to occupy similar broad habitats as they invade new areas (Cadotte et al. 2009). However, despite similarities in traits, closely related nonnatives are often not equivalent in their establishment success or impact, and may invade new niches that are unoccupied by their close relatives. Thus, studying the attributes of related nonnatives and their distributions might shed light on mechanisms and limitations of invasion by highlighting trait differences between relatives. Research has shown that some taxa are likely to naturalize despite climate differences across regions of introduction (Diez et al. 2009), and that distribution of related species depends on the scale of space and taxonomy considered (Proches et al. 2008). However, little research has addressed the differences in distribution within taxa across gradients in a region.

Deserts are considered resistant to invasion because plants typically require specialization to survive extremes of temperature, low precipitation, and minimal soil nutrients (Brooks 1999, 2009; Lonsdale 1999). North American warm deserts are characterized by high spatial and temporal

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* First and third authors: Doctoral Student and Professor, Department of Botany and Plant Sciences, University of California, Riverside, CA 92521 USA; second author: Research Botanist, U.S. Geological Survey, Western Ecological Research Center, Yosemite Field Station, El Portal, CA 95318. Current address of first author: Research Associate, Department of Biological Sciences, University of Toronto, Scarborough, ON M1C 1A4 Canada. Corresponding author's E-mail: rmarushia@utsc.utoronto.ca

Interpretive Summary

Sahara mustard (*Brassica tournefortii*), black mustard (*Brassica nigra*), and shortpod mustard (*Hirschfeldia incana*) are common invasive mustards throughout parts of the western United States. In particular, all three species are found in southern California, but they have different distributions. *Brassica tournefortii* is primarily an invader of warm desert ecosystems, black mustard is most common in more mesic regions, and shortpod mustard is most common in the arid Mediterranean-climate regions between the coast and warm deserts. We hypothesized that *B. tournefortii*'s adaptations to arid North Africa might predispose it to successfully invade North America's arid, warm-desert ecosystems. Our objective was to identify which traits promote *B. tournefortii's* invasiveness. Mustards were compared by growing them in common gardens under both climatic and water availability treatments. Although all three species germinate in the same number of days, *B. tournefortii* has a more rapid development to seed set than *B. nigra* or *H. incana* under all conditions. *B. tournefortii* produced fewer seeds than *H. incana* under beneficial conditions, but the three species were not different under stressful conditions. All species produced seeds under sustained drought, suggesting that invasive mustards sustain populations with low reproduction rates even during drought years. Our results suggest that mortality before seed set is the limitation to invasion by *B. nigra* and *H. incana* in the desert ecosystem.

variability in precipitation, which has particularly strong effects on vegetation (Beatley 1974; Bowers 2005; Hereford et al. 2006). Annual plants in deserts are usually described as ''ephemerals'' because they exhibit rapid phenology, responding quickly to water availability during the winter rain season, but reproduce and senesce quickly as drought conditions increase (Smith et al. 1997; Tevis 1958; Went 1949). Native desert annuals also have specific germination requirements, as opposed to many nonnative annuals, which have less stringent germination requirements, resulting in high germination rates (Brooks and Klinger 2009; Burk 1982; Went 1979). The number of plant invaders in the warm deserts of southwestern North America is relatively low, but their dominance and impact can be disproportionately high (Brooks 2009; Brooks and Berry 2006). In addition, the vast majority of invaders into these desert regions are annual rather than perennial species (Brooks 1999; Brooks and Berry 2006). Understanding the mechanisms by which species invade particular ecosystems can facilitate early detection and management of potential invaders (Brooks and Klinger 2009).

Nonnative annual plants may have specialized or preadapted mechanisms by which they dominate and displace native desert annuals under harsh and variable conditions (Levine et al. 2003; Werner et al. 2010). For instance, *Bromus tectorum* L. competes with native Great Basin plants by usurping soil water resources through early germination, and by altering nitrogen mineralization rates and fire regimes (Evans et al. 2001; Levine et al. 2003). Likewise, invaders may adapt under strong selection regimes, such as climate or drought, to become successful in novel habitats or conditions (Broennimann et al. 2007; Rice and Mack 1991). In *Brassica rapa* L., a nonnative mustard, multiyear droughts in southern California caused a heritable decrease in time to flowering, an adaptation that increased drought avoidance and fitness under drought stress (Franks et al. 2007). These processes create the potential for newly invasible niches and go against the expectations of niche conservatism, which predicts that closely related species will retain their ancestral traits and thus their environmental distributions.

Brassica tournefortii Gouan, or Sahara mustard, is an annual species native to North Africa and the Mediterranean. Now locally abundant in the southwestern deserts of North America (Minnich and Sanders 2000), *B. tournefortii* was first introduced to the Coachella Valley of California in the early 20th century (Minnich and Sanders 2000). *Brassica tournefortii* only began to invade extensively beyond disturbed sandy sites during the last two decades, and now forms dense stands in many areas of the Sonoran and Mojave deserts. *Brassica tournefortii* has prolific seed production, as high as 16,000 seeds in medium-sized (60 g [2.1 oz] dry wt) plants (Trader et al. 2006). In desert sand dunes, *B. tournefortii* impacts native annual forbs by reducing their flower and seed production by 80 to 90% (Barrows et al. 2009). This species is especially problematic in years of high rainfall, but is patchy or inconspicuous in drought years (Barrows et al. 2009). *Brassica tournefortii* is now regarded as one of the most invasive plants in deserts (Cal-IPC 2006), but it is also present in nondesert regions. Because its distribution spans both desert and more mesic sage scrub and grassland ecosystems, natural selection may have occurred within the species to produce two ecotypes: a more arid-adapted type and a more mesic-adapted type. Adaptation within the species may help explain its sudden, rapid spread after several decades of lag phase following initial invasion (e.g., Kudoh et al. 2007; Sexton et al. 2002).

In southwestern North America, *B. tournefortii* is primarily considered to be a desert invader, whereas other closely related mustard species are major invaders in nearby mesic regions. *Brassica nigra* L. and *Hirschfeldia incana* (L.) Lagr.-Foss. are locally dominant, nonnative forbs in much of southwestern North America, including urbanized areas, but neither is particularly abundant in most natural desert regions (CalFlora Database 2009). Both species are native to the Mediterranean region. *Brassica nigra*, an annual, was likely introduced to California intentionally by Franciscan missionaries more than 200 yr ago (Hendry and Kelley 1925), and is now found in nearly all lower 48 states (USDA NRCS 2009). *Brassica nigra* is one of the most prominent nonnative plants of southern California (Bell and Muller 1973), but in the deserts occurs only in locally mesic agricultural areas and along some roadsides (M.

Brooks, personal observation). *Hirschfeldia incana* (*Brassica geniculata* (Desf.) J. Ball in earlier floras) was first recorded in the San Bernardino Mountains of southern California in 1914 (Parish 1920) and is currently a nonnative species of mesic to semiarid inland regions. It can also be found periodically along desert roadsides close to the transverse ranges and southern Sierra Nevada Mountains (M. Brooks, unpublished data). *Hirschfeldia incana* is a facultative biennial, and is concentrated in California, Nevada, and Washington (USDA NRCS 2009). Both *B. nigra* and *H. incana* should have had ample opportunities for introduction and spread throughout the Southwestern deserts, and are unlikely to have been limited by dispersal in their distribution.

Brassica tournefortii, B. nigra, and *H. incana* have contrasting distributions in southwestern North America, possibly because they respond differently to variables such as temperature, moisture, and environmental stress. The goal of this research was to evaluate traits of *B. tournefortii* that might confer invasive ability in the deserts. We conducted a comparative ecological study of *B. tournefortii* from both desert and mesic nondesert habitats, and with the two related and co-occurring weedy mustards, *B. nigra* and *H. incana*, which have not substantially invaded desert areas. We hypothesized that *B. tournefortii* collected from desert sites might have greater fecundity (seed production) under desert climate or drought than *B. tournefortii* from more mesic populations. We also hypothesized that *B. nigra* and *H. incana* would prove less successful in terms of fecundity under desert climate or drought conditions than *B. tournefortii*. Finally, we measured developmental and morphological traits related to phenology and competitive ability through time to further evaluate traits that may promote invasiveness of *B. tournefortii* vs. the other two species within desert regions.

Methods

Site Effects. Common gardens were simultaneously grown in two different climate sites in 2005. Experimental sites included Blue Diamond, NV (desert site, approximately 114 mm [4.5 in] annual precipitation) in the Mojave Desert, and the University of California, Riverside (UCR; "mesic" site, approximately 265 mm annual precipitation), which has a Mediterranean climate. (See site temperatures in Results.) *Brassica tournefortii* occurs in locally high abundance in the vicinity of both locations. Because all species tested are widespread throughout western North America and we wished to test differences both between and within species, we refer to regional groups (desert vs. mesic) as populations, and locations where seeds were collected as samples of the larger regional populations. Seeds were collected from two samples for each of four mustard species/populations: (1) desert *B. tournefortii*, (2) mesic *B. tournefortii*, (3) mesic *B. nigra*, and (4) mesic *H. incana* (see Online Supplemental Material 1). Two samples were collected to ensure that they were representative and comparable for each species/population. Mesic samples were collected from various coastal sage scrub locations in cismontane California, and desert samples were collected from two sites in transmontane California, one in the Mojave Desert near the Nevada state line and one in the Sonoran Desert. (see Online Supplemental Material 1 for specific sampling locations). Seeds were collected from arbitrarily chosen, healthy individual plants at peak seed set maturity during either 2003 or 2004, and seeds were stored at room temperature throughout the project. Seeds from eight randomly chosen plants per sample were mixed for seeding both experiments in 2004 and 2005. Viability for all seed types was near 100% (Online Supplemental Material 2).

White citrus tree pots (9.6 L [2.5 gal] capacity) were filled with prewatered University of California Riverside planting mix 3 (53% plaster sand, 47% peat moss, plus micronutrients) and placed outside next to an east-facing wall at both sites to control for extreme sun exposure and allow access to water.

The four species/populations by two samples were replicated in common gardens over eight blocks in a randomized complete block design at each climate site ($n = 128$ pots total). Each pot was direct-seeded with six seeds of a given sample in late December 2004, and time to emergence was recorded (Online Supplemental Material 2). Seedlings were thinned to two individuals per pot after all plants produced their first four to six true leaves and were kept well-watered until harvest. High precipitation levels at UCR may have caused nutrient leaching, so plants at that location were watered with a dilute 21–5–20 nutrient solution (Peters® Excel at 100 ppm nitrogen, Grace-Sierra Horticultural Products Company 1001 Yosemite Drive, Milpitas, CA 95035) at the first sign of chlorosis, maintained until plants recovered, and then returned to tap water as needed. Leaching and nutrient stress were not an issue at Blue Diamond; therefore, plants were watered without added nutrients.

For all plants, height, leaf number, and life stage or stages were recorded once per week for 4.5 mo after thinning to two individuals per pot. All leaves were counted up to 20, and then > 20 was noted. Life stages included rosette (leaves only), bolting (producing flower buds), flowering (petals visible), seed set (siliques present), and senescence. With all species it was possible for a plant to be bolting, flowering, and setting seed at the same time, and all applicable stages were recorded for each plant. Air temperature at each location was recorded by HOBO Pro Series temperature recorders (Onset Computer Corp., PO Box 3450, Pocasset, MA 02559-3450) set near the pots.

Siliques were counted on all plants after vegetative senescence, at peak seed set. Seed numbers were counted in

30 siliques arbitrarily chosen from 52 plants subsampled from each population sample in the UCR plantings. Because siliques tended to vary in size at Blue Diamond, 49 siliques were sampled from the Blue Diamond plantings. Fecundity was measured by multiplying the mean number of seeds per silique per sample and site by the total number of siliques. Data were analyzed in JMP (SAS Institute, SAS Campus Drive, Building S, Cary, NC, 27513). Siliques and fecundity were tested among samples within populations and sites using a mixed model with population as the fixed effect and plant (A or B) and block as random effects. When samples were not significantly different, species/population, site, and population by site were tested as fixed effects in a mixed model with plant and sample nested within population, block, and site and block nested within site as random effects. Tukey's honestly significant difference (HSD) was used to test the differences in silique number and fecundity between population-by-site groups.

Growth (maximum height, maximum leaf number) and life stage (days from planting to emergence, and emergence to maximum leaf number, initial bolting, flowering, and seed set) data were also analyzed in JMP. All variables were calculated for each individual plant. For life stage variables, the Kaplan-Meir method of survival analysis was used to test the differences in population phenology between sites. Survival analysis is a nonparametric method that tests the proportions of subjects that have achieved an event by a given time (Hosmer and Lemeshow1999). We modeled the number of days for plants from each sample and species/population to reach various life stages from weekly observations, and used the log-rank test of significance. When few differences were found between samples, samples were pooled for survival analysis of populations. Censoring, a statistical correction for missing survival data, occurred for seeds that were planted but did not emerge, but censoring did not apply for all other stages because all individuals were accounted for. Because between-group differences are not tested by JMP's survival analyses, a mixed-model restricted maximum likelihood test was used with Tukey's HSD to separate the between-group differences for sample, population, site, and population by site interactions for all six variables. Samples were first tested as a fixed effect within site and population, then nested within population and block as a random effect for population and site tests. Block was nested within population and site as a random effect. Population, site, and population by site were the fixed effects. Differences between the maximum, minimum, and mean temperatures for the desert and mesic sites were compared using the repeated measures response via multivariate ANOVA (MANOVA) in JMP.

Drought Response. We performed two drought experiments, the first from mid-December 2005 to mid-May 2006 and the second from late January to mid-May 2007, both at UCR and both using the same 9.6-L pots. For the soil in the first experiment we used a custom mix of sand (87% plaster sand and 13% sand fines) to approximate water holding capacity and nutrient retention typical of desert soils. All-purpose slow-release fertilizer (3 g 18–6–12 Sta-Green Indoor-Outdoor Slow-Release Plant Food, Lowe's Companies, Inc. Moreno Valley, CA) was added to the top layer of soil. More fertilizer was added in 3-g increments to all pots at intervals throughout the study period at the first sign of chlorosis. Pots were placed in the same UCR outdoor location as the common garden experiment. Temperature was again monitored by the temperature recorders and soil volumetric water content (VWC, %) was monitored using eight ECH_2O EC-5 soil sensors (Decagon Devices, 2365 NE Hopkins Court Pullman, WA 99163) installed vertically 10 cm (3.9 in) deep in each species/population/treatment combination. Soil volumetric water content was read at each data collection before applying watering treatments.

In the second drought experiment, treatments were repeated from the previous experiment, with a few key adjustments to isolate the effect of water on species/populations. The sand mixture was replaced with UC Mix number 3 to improve consistency in soil water treatments. Nutrients were maintained with a dilute aqueous fertilizer solution. Seedlings were allowed to germinate outside with ample water, and time to emergence was recorded. After thinning, pots were relocated to a climate-controlled greenhouse to avoid natural precipitation. Soil water was measured using two EC-5 ECH_2O sensors per population/treatment combination.

For both drought experiments the same seeds were used as in the site effects experiment, mixing equal parts of the same samples per population. Each of the four species/populations were planted in two watering treatments (high and low) in a randomized complete block design with eight blocks. Six seeds per pot were planted and time to emergence was recorded. Seedlings were then thinned to one and watering treatments and data collection begun. For the first experiment, high-water treatments were watered to field capacity at each data collection, whereas low-water treatments received short bursts of water if they reached 5 to 8% VWC or if plants had visible wilting. Plants were rescued from drought mortality in order to record the difference in fitness (as measured by fecundity) if plants reproduced under drought conditions, rather than have no fecundity data from prematurely senesced plants. Pots were moved into a greenhouse with impending precipitation to maintain watering treatments, and moved back out again as soon as weather allowed. Due to cooler temperatures, higher humidity, and increased soil organic matter, pots in the second drought experiment did not lose water as quickly as they had in the first experiment. Low-water pots

were not watered until they reached 6 to 8% VWC and then lightly watered to maintain low soil moisture.

For both experiments, growth and phenology were recorded weekly from thinning to senescence. From the site experiments, it was known that basal leaves were determinate in number for *B. tournefortii* and *H. incana*, whereas stem resprouts were indeterminate. Therefore, leaves were counted only if they were part of the original basal rosette in *B. tournefortii* and *H. incana*. All leaves were counted for *B. nigra*, which extended the basal rosette as it bolted and had determinate leaf numbers. Life stages were recorded for all plants. Data were collected from January to May in 2006 and from March to May in 2007. Plants were allowed to senesce before harvest.

All plants were harvested and siliques counted in 2006. Since each pot contained only one plant, fecundity was measured by taking seed counts for 30 siliques arbitrarily sampled from each plant and multiplying the average number of seeds per silique per plant by the total number of siliques per plant. Silique number and total fecundity were tested across species/populations for each treatment using the mixed model REML approach with block as a random factor, and population, treatment, and population by treatment as the fixed effects. Tukey's HSD post-hoc test separated differences between means between groups. In 2007, all siliques were counted, but the mean number of seeds per silique for each population per treatment from 2006 was multiplied by the number of siliques per plant for an estimated total fecundity.

Phenology was again tested using Kaplan-Meir survival analysis and the log-rank tests, with days to each life stage tested across populations in the two watering treatments. All treatment, population, and population by treatment differences were tested as fixed effects using a mixed-model restricted maximum likelihood test with block as a random effect. Between-group differences were separated with Tukey's HSD post-hoc test. Differences between high and low soil water treatments were compared using the repeated measures response via MANOVA in JMP. Because each year was different in its location, watering treatments, or both, differences were not statistically tested across years.

Results

Site Effects. The desert site (Blue Diamond, NV) was colder than the mesic site (UCR), especially early in the experiment (Online Supplemental Materials 3 and 4). The desert had 10 d below freezing, while the mesic site had none. The average daily maximum, minimum, and mean temperatures in the desert were 32.80 C (91.04 F), 10.45 C, and 18.21 C, respectively, whereas maximum, minimum, and mean temperatures were 37.5 C, 11.97 C, and 20.57 C at the mesic site. Temperature differences between locations were significant for minimum, mean, and maximum temperatures (mean: $F_{1,434} = 0.027$, $P < 0.001$). Growth, phenology, and reproduction also differed across sites and species (Table 1), but seldom between

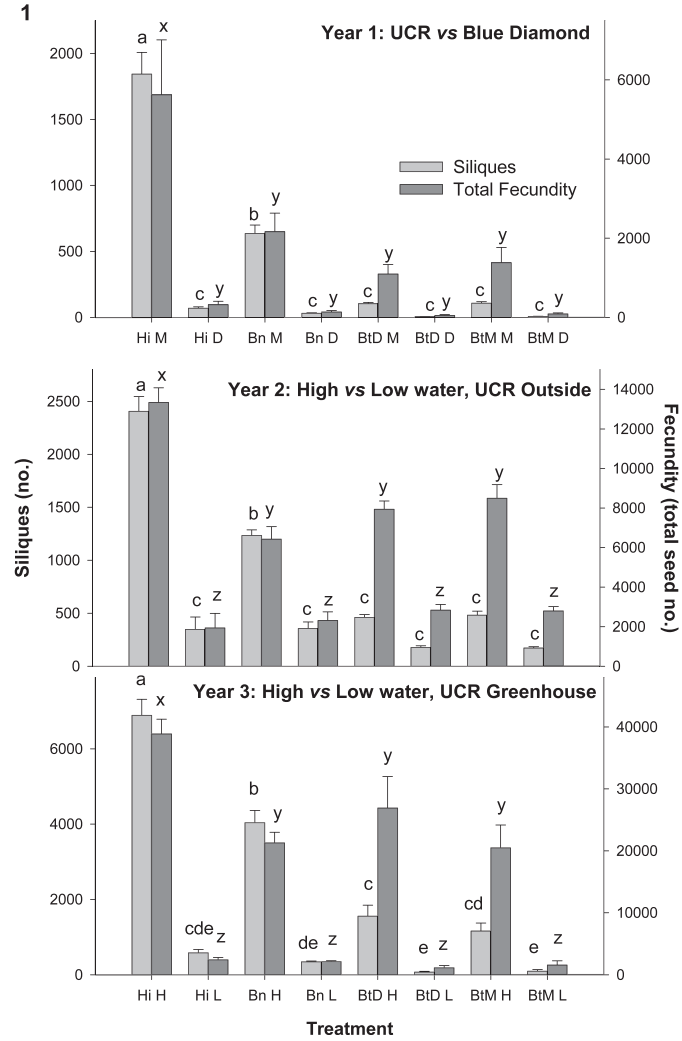

Figure 1. Mean number of siliques and mean total fecundity for *Hirschfeldia incana* (Hi), *Brassica nigra* (Bn), *Brassica tournefortii* desert (Bt D), and *Brassica tournefortii* mesic (Bt M), with standard error. (a) 2004–2005, Populations grown in the mesic site (M) (UCR) and the desert site (D) (Blue Diamond); b) (2005–2006, populations grown in two watering treatments, high (H) and low (L), outdoors at University of California, Riverside. All population, treatment and population by treatment $P \leq 0.001$. (c) 2006–2007, Populations grown in two watering treatments, high (H) and low (L), in a greenhouse at University of California, Riverside. All site, population, and site by population $P \leq 0.01$. Columns indicated by different letters are significantly different according to population by site Tukey's tests within variable (siliques or fecundity), $\alpha = 0.05$. Letters a–e indicate differences in silique number, letters x–z indicated differences in fecundity. See Online Supplemental Material 6 for parameters and tests.

Table 1. Average maximum height, maximum leaf number, and minimum days to each life stage for populations with location and watering treatments. Population abbreviations follow that of Figure 1. Mixed-model test results are shown within year, significant results are shown in **bold**. Tukey's honestly significant difference tests represent differences among treatment by population combinations for each variable each year. If treatment by population is not significant, Tukey's test is between populations only.[a]

			Maximum height (cm)			Maximum leaf no.			Days to maximum leaf no.		
Year	Treatment	Population	Average	SE	Tukey	Average	SE	Tukey	Average	SE	Tukey
Year 1, mesic and desert	Mesic site (UCR,[b] CA)	Bt D	38	2.1	ab	> 20	0.0	a	91	2.9	a
		Bt M	42	2.5	a	> 20	0.0	a	88	3.0	a
		Hi	138	3.9	c	> 20	0.0	a	110	0.9	b
		Bn	163	6.0	d	20	0.2	a	107	1.3	b
	Desert site (Blue Diamond, NV)	Bt D	23	2.5	b	10	0.8	c	69	2.8	c
		Bt M	25	3.6	b	11	1.2	bc	69	2.9	c
		Hi	44	1.8	a	19	1.1	a	141	1.6	d
		Bn	43	4.3	a	14	0.7	b	110	3.9	b
		Site		**P < 0.001**			**P < 0.001**			P = 0.383	
		Population		**P < 0.001**			**P < 0.001**			**P < 0.001**	
		Site by population		**P < 0.001**			**P < 0.001**			**P < 0.001**	
Year 2, outdoors at mesic	High water	Bt D	67	2.3	a	13	0.5	a	45	0.8	a
		Bt M	68	2.1	a	13	0.3	a	44	0.9	a
		Hi	138	5.8	c	25	1.1	b	98	4.1	b
		Bn	185	7.2	d	26	1.4	b	90	5.4	b
	Low water	Bt D	52	2.7	a	13	0.5	a	46	2.7	a
		Bt M	55	1.8	a	14	1.2	a	45	2.0	a
		Hi	96	8.5	b	28	5.5	b	89	3.4	b
		Bn	110	6.0	b	22	1.0	b	83	2.4	b
		Treatment		**P < 0.001**			P = 0.984			P = 0.089	
		Population		**P < 0.001**			**P < 0.001**			**P < 0.001**	
		Treatment by population		**P < 0.001**			P = 0.563			P = 0.159	
Year 3, greenhouse at mesic	High water	Bt D	67	5.0	abc	9	0.6	ab	73	5.0	a
		Bt M	70	4.9	ab	9	0.5	a	69	2.2	ab
		Hi	157	5.3	c	10	0.5	a	91	2.0	d
		Bn	188	1.7	bc	16	1.4	c	91	3.0	d
	Low water	Bt D	49	4.2	a	13	5.4	ab	56	1.5	c
		Bt M	46	3.3	a	9	0.3	a	59	2.4	bc
		Hi	98	5.4	c	9	0.3	a	97	2.5	d
		Bn	92	3.2	bc	15	0.5	c	90	2.7	d
		Treatment		**P < 0.001**			P = 0.239			**P = 0.004**	
		Population		**P < 0.001**			**P = 0.008**			**P < 0.001**	
		Treatment by population		**P < 0.001**			P = 0.565			**P < 0.001**	

[a] For Tukey's tests, comparisons are within variables, and treatment by population combinations not followed by the same letter are different.

[b] Abbreviations: UCR, University of California, Riverside; Bt D, *Brassica tournefortii* desert; Bt M, *Brassica tournefortii* mesic; Hi, *Hirschfeldia incana*; Bn, *Brassica nigra.*

samples of the same population (Online Supplemental Material 5). The exception was *B. nigra*, at the mesic site, which emerged in about 9 d for the Corona sample (approximately 48 km [30 mi] inland) vs. 13 d for plants from the Crystal Cove State Park (adjacent to the ocean) sample (log-rank chi-square = 14.46, DF = 1, $P < 0.001$). We therefore pooled samples within each of the desert and mesic populations for all subsequent analyses.

Table 1. Extended.

Days to bolting			Days to flowering			Days to seed set		
Average	SE	Tukey	Average	SE	Tukey	Average	SE.	Tukey
50	3.4	a	71	4.2	a	77	3.7	a
55	4.1	a	78	5.0	a	84	5.6	a
106	1.0	c	116	0.8	bc	120	0.9	bc
101	1.1	c	116	1.3	bc	122	1.0	c
61	1.9	a	73	1.7	a	78	1.2	a
59	1.3	a	71	1.3	a	76	1.1	a
112	3.6	c	125	3.3	c	127	3.3	c
84	2.0	b	105	2.9	b	108	3.4	b
	P = 0.61			P = 0.204			P = 0.07	
	P < 0.001			**P < 0.001**			**P < 0.001**	
	P < 0.001			**P < 0.001**			**P = 0.001**	
45	0.8	a	56	1.4	a	58	1.7	a
44	0.9	a	53	1.4	a	57	1.7	a
74	1.5	b	95	2.1	cd	101	2.4	c
73	1.9	b	97	3.3	d	102	2.4	c
45	1.1	a	55	1.6	a	60	1.3	a
44	1.0	a	53	1.5	a	55	1.4	a
73	2.1	b	87	2.6	bc	91	1.8	b
72	1.6	b	84	2.0	b	91	1.1	b
	P = 0.693			**P = 0.001**			**P < 0.001**	
	P < 0.001			**P < 0.001**			**P < 0.001**	
	P = 0.946			**P = 0.008**			**P = 0.001**	
46	5.5	a	53	4.3	a	54	4.1	a
42	2.2	a	49	1.1	a	51	1.0	a
52	1.2	b	65	1.8	b	67	1.6	b
49	1.7	b	64	2.6	b	68	2.8	b
38	2.2	a	45	1.5	a	49	1.7	a
40	1.5	a	47	2.2	a	51	1.4	a
53	1.4	b	65	0.1	b	70	1.7	b
50	1.2	b	60	1.1	b	66	1.0	b
	P = 0.279			P = 0.076			P = 0.446	
	P < 0.001			**P < 0.001**			**P < 0.001**	
	P = 0.196			P = 0.131			P = 0.201	

Emergence time for all species differed dramatically between sites. At the mesic site, the mean days to emergence was nine, whereas in the desert, plants took 30 d on average ($F_{1,505} = 894.3$, $P < 0.001$). Populations did not differ in emergence time in the desert (log-rank chi-square = 3.0, DF = 3, P = 0.391; Online Supplemental Material 2), but did differ at the mesic site by a day or two (log-rank chi-square = 45.4, DF = 3, $P < 0.001$; Online Supplemental Material 2). At the mesic site, *H. incana* emerged earlier than all other species (7 d), followed by *B. nigra* and *B. tournefortii* desert (9 d). *Brassica nigra* and *B. tournefortii* mesic (10 d) were also different, although the two *B. tournefortii* populations were not different (Tukey's test not shown). Overall, few differences existed in

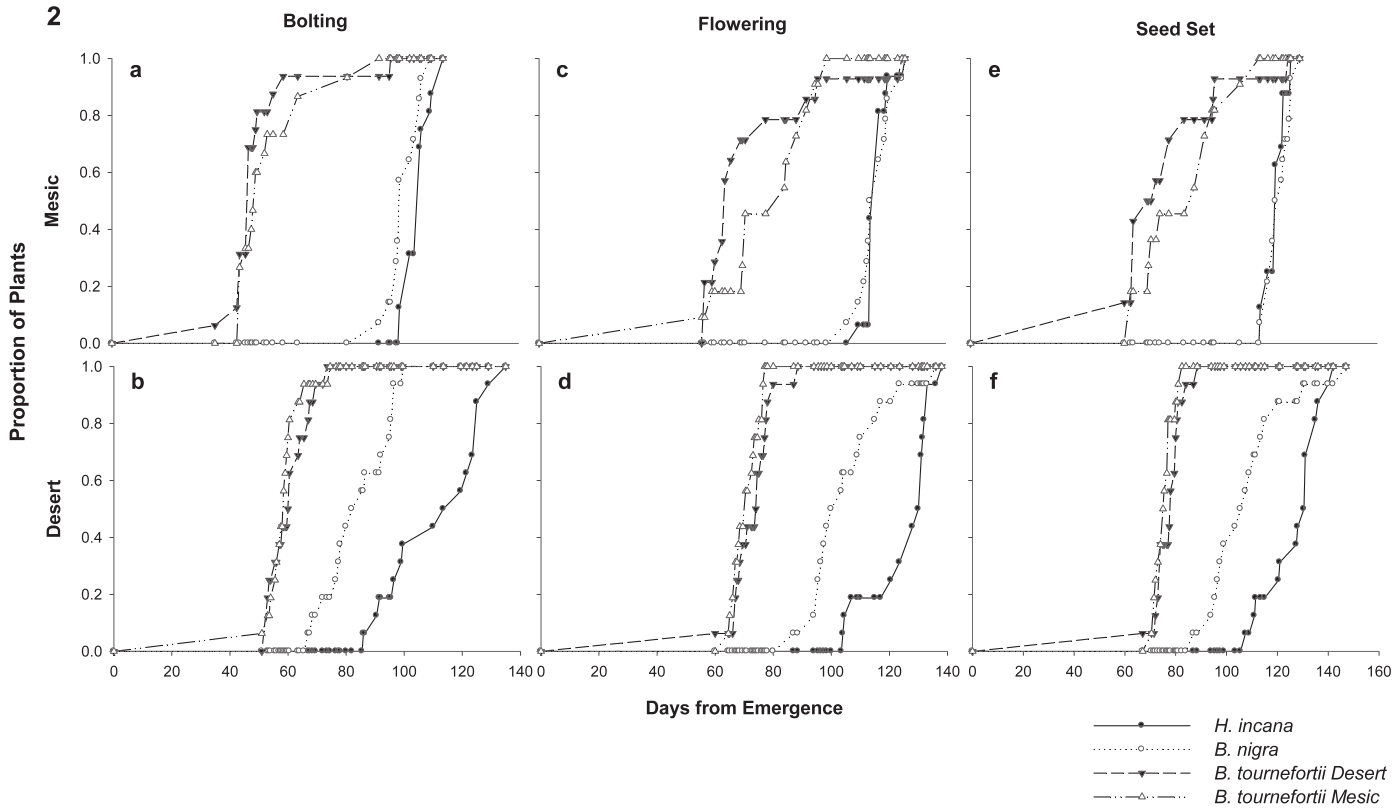

Figure 2. Phenology of four populations grown outdoors at the mesic (UCR) and desert (Blue Diamond) sites. For survival analyses within location and life stage, all $P < 0.001$. (a) Bolting at the mesic site; (b) bolting at the desert site; (c) flowering at the mesic site; (d) flowering at the desert site; (e) seed set at the mesic site; (f) seed set at the desert site.

emergence time between species in all experiments; therefore, subsequent comparisons of phenology are presented as time from emergence to life stage.

Growth, phenology, and reproduction did not differ between mesic and desert populations of *B. tournefortii*. However, *B. tournefortii* differed from both *B. nigra* and *H. incana. Brassica tournefortii* produced fewer siliques and had lower fecundity than its relatives at the mesic site (Figure 1a; Online Supplemental Material 6). Fecundity in all three species was reduced from that in the mesic site by 93% (*B. tournefortii*) to 97% (*H. incana*) in Blue Diamond (Figure 1a; Online Supplemental Material 6). Maximum height for *B. tournefortii* was reduced by 40%, whereas *H. incana* and *B. nigra* were reduced by 68 and 73%, respectively (Table 1). Overall, *B. tournefortii* was smaller in stature but grew more rapidly than either of the other species, and bolted, flowered, and set seed as much as 50 d earlier than either of the other species at both sites (Table 1; Figure 2). Although fertilizer additions may have increased size and reproduction at the mesic site, site did not change relative differences in size or phenology between *B. tournefortii* and the congeneric mustards studied.

Hirschfeldia incana took longer to bolt, flower and set seed in the desert than at the mesic site, whereas *B. nigra* exhibited similar phenology across sites (Figure 2). Although *B. nigra* set seed earlier in the desert, it was less than half the size reached at the mesic site and had fewer leaves (Table 1). The most successful species in the desert in terms of leaf number was *H. incana*, which also attained the same height as *B. nigra* in the desert garden. However, in the desert, *H. incana* required the longest time to reach its maximum leaf number (Table 1). All populations had 20 or more leaves at their maximum at the mesic site, but both *H. incana* and *B. nigra* required more days to reach their maximum number of leaves than either population of *B. tournefortii. Brassica nigra* towered over the other species at the mesic site at 1.6 m, on average (Table 1). However, *H. incana* had by far the greatest fecundity, with nearly 2,000 siliques produced per plant (Figure 1a). All populations had a similar level of reproduction in the desert (Figure 1a).

Drought Response. For the first drought experiment, temperatures at UCR were similar to the previous year (Online Supplemental Material 3). Soil VWC was an average of 7.01% in drought treatments, whereas fully watered pots had an average VWC of 11.71% ($F_{1,3} = 9.92$, $P = 0.051$; Online Supplemental Material 7). Fully

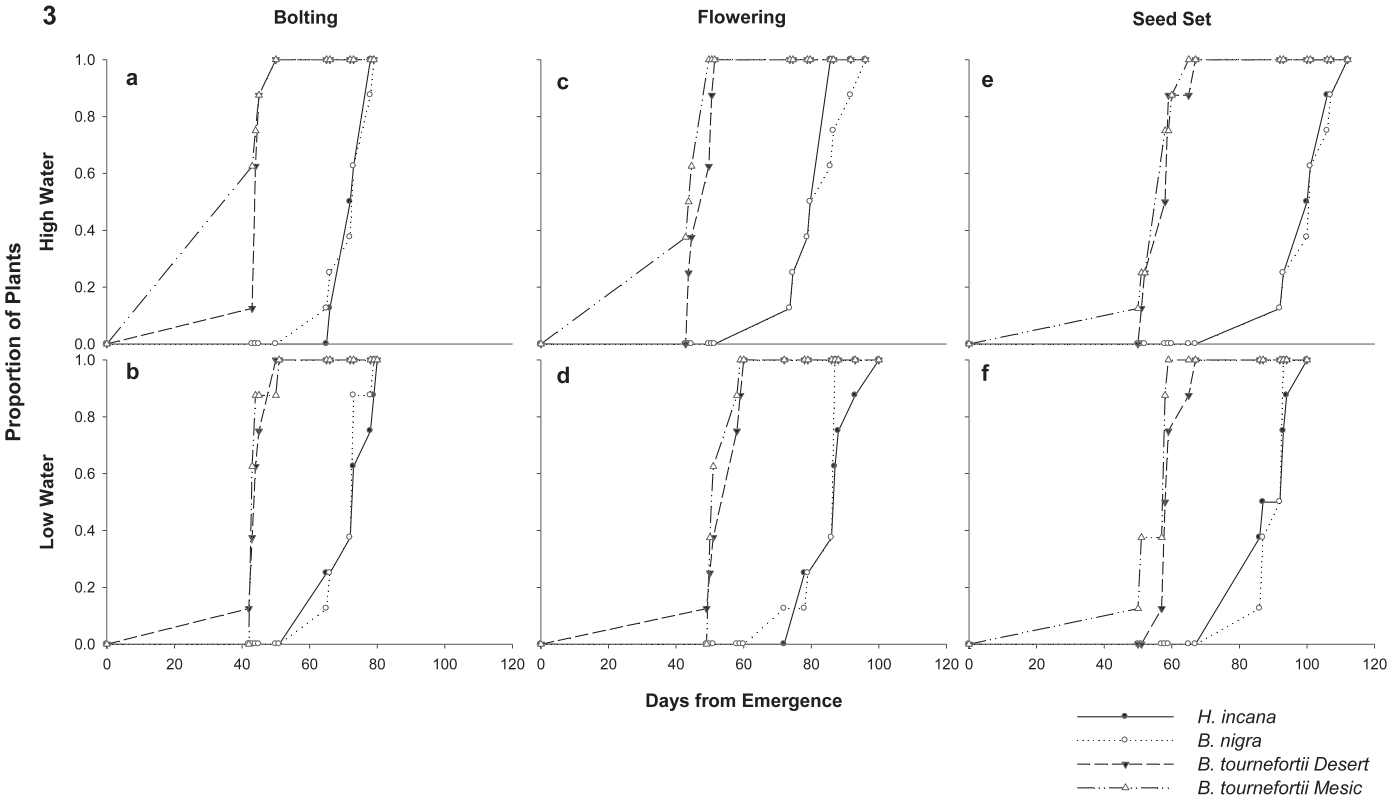

Figure 3. Phenology of four populations grown outdoors at University of California, Riverside (year 2) under high- and low-watering treatments. For survival analyses within treatment and life stage, all log-rank chi-square $P < 0.001$. (a) Bolting in high-water treatments; (b) bolting in low-water treatments; (c) flowering in high-water treatments; (d) flowering in low-water treatments; (e) seed set in high-water treatments; (f) seed set in low-water treatments.

watered pots had VWC values as high as 16% before watering, whereas drought treatments had a maximum of 10% VWC (Online Supplemental Material 7). Soil water VWC was low overall due to the sandy growth medium, however. For the second experiment, the climate-controlled greenhouse had steady, warm temperatures throughout the experiment (Online Supplemental Material 3). Soil water was initially between 17 and 20% VWC due to the greater water holding capacity of the growth medium. However, low-water treatments had an average VWC of 9.79%, significantly lower than the average high-water treatment VWC of 13.74% ($F_{1,111} = 176.6$, $P < 0.001$; Online Supplemental Material 7).

In the first experiment, drought treatments reduced both silique number and fecundity in *H. incana* by 85% and in *B. nigra* by about 70%, whereas *B. tournefortii* was reduced by only 64% (Figure 1b; Online Supplemental Material 6). Although *B. tournefortii* was less impacted by drought than *H. incana* or *B. nigra*, all species ended up with the same low silique number and fecundity under drought treatments (Figure 1b). Whether in high or low water, *B. tournefortii* bolted, flowered, and produced seeds in the same amount of time (40 to 60 d from emergence), which was often approximately 30 to 40 d ahead of either *B. nigra* or *H. incana* (Table 1; Figure 3). Phenology did not differ between *B. nigra* and *H. incana* or between watering treatments for these species (Table 1; Figure 3). Within species, bolting, flowering, and seed set occurred almost simultaneously for nearly all plants and within a few days (Figure 3). *Hirschfeldia incana* was as tall as *B. nigra* under low water conditions, but *B. nigra* was, on average, almost 2 m tall under high water and 0.5 m taller than *H. incana* (Table 1). Both populations of *B. tournefortii* were just as large under drought conditions as when fully watered (Table 1). Maximum leaf number differed across species overall in a manner similar to height, but there were no other differences (Table 1).

For the second drought experiment, mean days to bolting, flowering, and seed set differed across species but not treatments (Table 1). In both cases *B. tournefortii* was more rapid in bolting, flowering, and setting seed than *B. nigra* or *H. incana* (Figure 4). Patterns of reproduction between populations and treatments were similar to the first drought experiment, except that silique counts, and therefore, estimated fecundity, were dramatically higher among all populations in high-water treatments (Figure 1c;

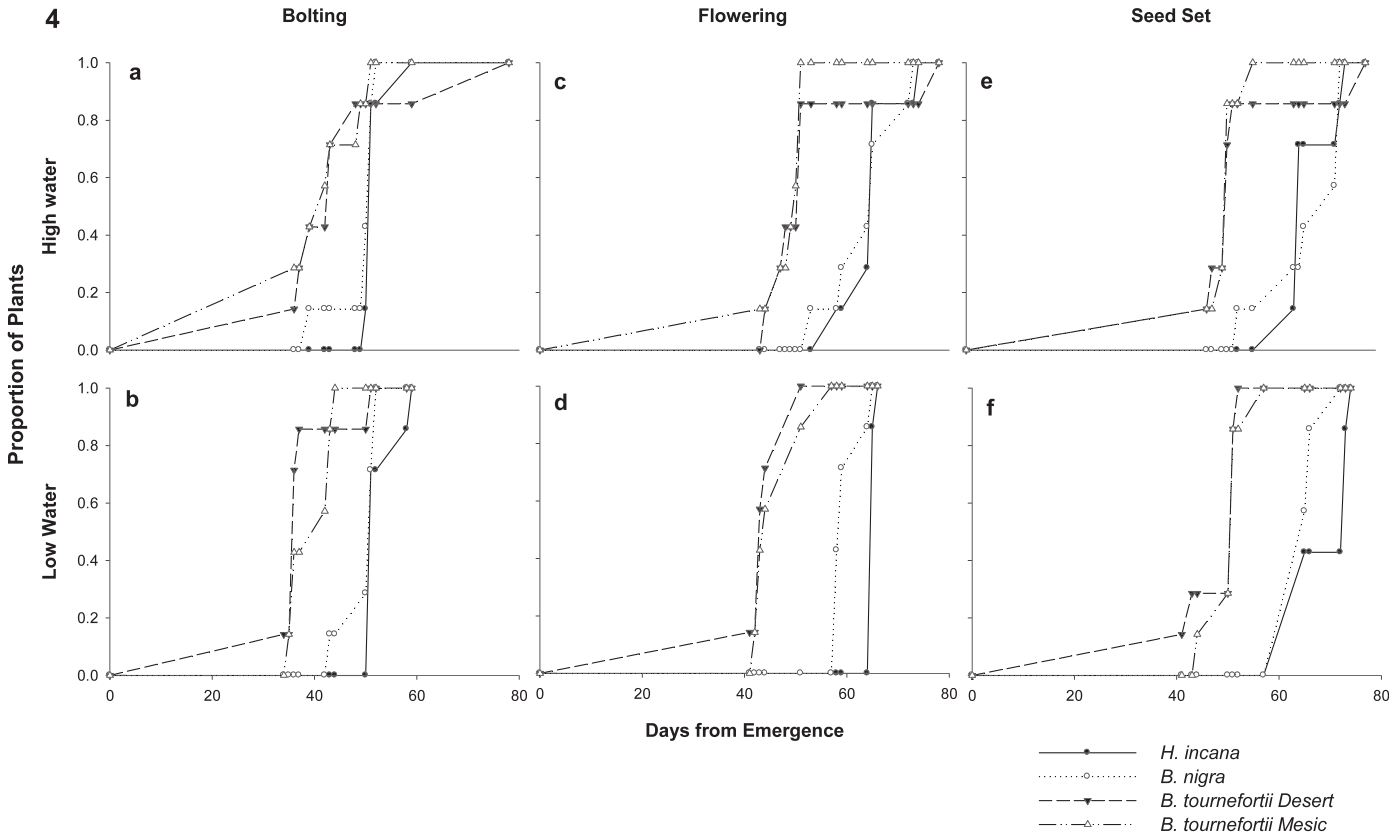

Figure 4. Phenology of four populations in a greenhouse (year 3) at University of California, Riverside, under high- and low-watering treatments. Survival analyses log-rank chi-square: bolting, high-water $P = 0.036$, low-water $P < 0.001$; flowering, high-water $P = 0.003$, low-water $P < 0.001$; seed set, high-water $P = 0.004$, low-water $P < 0.001$. (a) Bolting in high-water treatments; (b) bolting in low–water treatments; (c) flowering in high-water treatments; (d) flowering in low-water treatments; (e) seed set in high-water treatments; (f) seed set in low-water treatments.

Online Supplemental Material 6). This produced a 91 to 95% reduction in fecundity among all species in the drought treatment, such that all populations were equivalent (Figure 1c).

Across years, all combinations of population and treatment were important for differences in mean height (Table 1). *Brassica tournefortii* mesic grown under high-watering conditions was taller than all other *B. tournefortii*, but both *B. nigra* and *H. incana* were taller than *B. tournefortii* under both high- and low-water conditions (Table 1). Although maximum leaf number differed across species and treatments, there was no effect or interaction of treatment. *Brassica tournefortii* desert required a lower mean number of days to reach maximum leaves under drought than both populations of *B. tournefortii* with ample water (Table 1). Days to maximum leaf number was affected by species and treatment in both drought experiments, and population by treatment interactions occurred in the greenhouse. Overall, *B. tournefortii* had a faster mean time to maximum leaf number than either *B. nigra* or *H. incana* (Table 1). Time to bolting was significant only between species. Treatment and species were both important for days to flowering and setting seed, but there was no interaction effect (Table 1). Time to seedling emergence after planting was the same for all species in both experiments.

Discussion

Because arid and low-resource ecosystems frequently create stressful conditions, plants that are preadapted to handle such conditions might be expected to have greater invasion success and dominance (Maron 2006; Pearson and Dawson 2003). Alternatively, species may adapt to these conditions after invading (Broennimann et al. 2007). In our research, three nonnative and closely related species in the family Brassicaceae were capable of germinating, growing, and reproducing in a desert climate. Although *B. nigra* and *H. incana* showed greater potential height, *B. tournefortii*'s height was less affected by desert temperatures and low water. Plants grown in common gardens under different temperature and drought conditions showed no

evidence for selection of ecotypes in *B. tournefortii*. Instead, data show strong support for drought avoidance and an ephemeral life history through rapid phenology as an explanation for the success of *B. tournefortii* as a desert invader.

All three species tested had high fecundity under well-watered conditions, but they were severely diminished under desert or drought conditions. Therefore, our hypothesis that *B. tournefortii* would have greater relative fecundity under drought conditions than its relatives was rejected. The major difference among species was that *B. nigra* and *H. incana* required at least two more weeks to produce seed. Colder temperatures in the desert may have slowed germination among all three species, resulting in a shorter growing season, but *B. tournefortii*'s rapid phenology enabled it to produce seed by the time summer temperatures reached their peak.

Brassica tournefortii had consistently lower fecundity overall, but was less affected by drought conditions outdoors. Our results suggest that *B. tournefortii* has a rapid phenology that enables it to produce seed in a short period of time and under a wide range of temperature and drought conditions, a potential benefit for desert habitats where climate varies greatly and soil moisture levels can become rapidly depleted as winter turns quickly to spring conditions. Rapid phenology is a stress avoidance strategy that maximizes use of highly variable precipitation during the few months of availability (Smith et al. 1997). Therefore, *B. tournefortii* exhibits a tradeoff between rapid phenology, size, and fecundity relative to *B. nigra* and *H. incana*.

MacDougall et al. (2009) recently proposed that successful invasions are the result of a balance between niche differentiation and greater fecundity in comparison to native species, with fecundity as the key to species displacement. Our research suggests that differences in phenology may also have important consequences for fecundity, and therefore dominance and distribution among nonnatives. Mortality prior to reproduction is a more likely limitation for *H. incana* and *B. nigra* distribution in desert ecosystems than germination or growth. In this research, plants were "rescued" by a pulse of water as soon as they reached a wilting point in order to record fecundity. Otherwise the drought treatments would have yielded very few results, as *B. nigra* and *H. incana* wilted rapidly and would certainly have senesced before seed set. In the desert, precipitation is highly variable (Chesson et al. 2004), and our results suggest that *B. nigra* and *H. incana* plants would be likely to succumb to drought in longer periods between precipitation events. *Brassica tournefortii* may occupy arid habitats because it can survive and reproduce under small, infrequent rainfall events, while larger, more competitive mustards cannot. *Brassica tournefortii* is currently found throughout southern California (CalFlora Database 2009) and as far east as Texas; it is a problem in southern Nevada (USDA NRCS 2009). With rapid phenology and a consistent ability to reproduce, *B. tournefortii* may be adapted to invade beyond the Southwestern deserts, perhaps into the Great Basin and Colorado Plateau.

Other research has found that novel life history traits can enable invaders to dominate in low-resource, high-stress environments. For example, *Acacia longifolia* (Andr.) Willd., a drought-sensitive invader of low-resource dunes in Portugal, has higher nutrient utilization than drought-tolerant native species, giving it a competitive edge within the same community (Werner et al. 2010). Although smaller than related mustards, *B. tournefortii* is larger than native annuals in deserts and has impacts on growth and fecundity (Barrows et al. 2009). *Brassica tournefortii* is also more likely to survive and reproduce than native annuals under both wet and dry conditions (Barrows et al. 2009; Marushia 2009; Trader et al. 2006), and germinates rapidly at high percentages under a wide range of conditions (Bangle et al. 2008). In contrast, native annuals have more specific germination requirements (Brandle et al. 2003; Burk 1982; Went 1979), which are considered bet-hedging strategies against long-term variability (Went 1979). Nonspecific germination requirements can pose problems for local populations of *B. tournefortii*. For example, late winter rainfall events followed by early onset of spring conditions of high winds, warming temperatures, and rapidly declining soil moisture levels can lead to high prereproduction mortality rates (M. Brooks, personal observation). This leads to a new question: Are invasives with broad germination requirements susceptible to population crashes? As our data show, some *B. tournefortii* seed set is likely within a short time period, even under highly stressful conditions. Consistency in seed set may preclude some requirements for seed dormancy in arid or other low-resource environments, at least within shorter invasion time scales such as decades or centuries.

Broad germination requirements are a common trait among the mustards studied here, but differences in phenology between otherwise similar species may allow them to occupy contrasting distributions across a gradient of aridity. Some taxa are overrepresented among invasive plants (Daehler 1998) or have higher success rates upon introduction (Diez et al. 2009), suggesting that invasiveness might be predicted by traits among taxa (van Kleunen et al. 2010). Differences in phenology are coupled with morphological differences between species. Although *B. tournefortii* is well-suited to survive and compete in arid desert environments, it may be outcompeted by larger, more fecund nonnative mustard species under less stressful conditions, such as in more mesic communities. *Brassica nigra*, the tallest mustard, also has the largest leaves and few trichomes, traits consistent with high water use and low

reflectivity and suited to a moderate climate (Lambers et al. 1998). *Hirschfeldia incana* has thick silver trichomes, perhaps reducing evapotranspiration and contributing to its success in the hotter climate of California's nondesert interiors (Gibson 1996; Smith et al. 1997). However, *H. incana* also required the most time to reach its maximum leaf number, which may inhibit its success in desert ecosystems. *Hirschfeldia incana* and *B. tournefortii* both have short-lived basal rosettes that senesce after bolting, reducing evaporative surface area and leaving stems behind to disperse seeds.

It is surprising that *B. tournefortii*'s fecundity was as negatively impacted by the desert (Blue Diamond) climate in this experiment as that of *H. incana* and *B. nigra. Brassica tournefortii* is an invader in the vicinity of the experimental site, although not as dominant at Blue Diamond's higher altitude as it is in many lower habitats throughout the desert. *Brassica tournefortii* may depend on key microsites that are fertile, sheltered in the desert landscape, or both, such as the fertile islands beneath shrubs (Marushia et al. 2010). Shrubs may enable *B. tournefortii* to invade locations that are more stressful, such as higher altitudes. Therefore, we might have measured success more realistically by planting these species in the ground, rather than pots, and in sheltered vs. unsheltered locations. Likewise, rather than rescuing plants at the wilting stage, future research should attempt to cease watering at increasing time points among species and observe the interaction of phenology, fecundity, and mortality.

In predicting future desert invaders, rapid phenology and consistent reproduction of certain species under stress may enable ecologists to predict those that have the potential to be invaders of low-resource, high-stress environments. Studies comparing related nonnative species with contrasting distributions are another tool in the prediction of invasions, especially in situations where distribution is unlikely to be limited by introduction. Such comparisons control for phylogenetic relatedness and act as natural, selective experiments to bring important traits into sharper focus.

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