Title
Brassica tournefortii: Phenology, Interactions and Management of an Invasive Mustard

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Brassica tournefortii: Phenology, Interactions and Management of an Invasive Mustard

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

Doctor of Philosophy

in

Plant Biology

by

Robin Gene Marushia

June 2009

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"The earth never tires… The earth is rude, silent, incomprehensible at first – …Nature is rude and incomprehensible at first; …Be not discouraged – keep on – …There are divine things; …well envelop'd; …I swear to you there are divine things more beautiful than words can tell." From Walt Whitman, 'Song of the Open Road'

My dissertation has been a long road of discovery, and although I was often discouraged, I end it with a deep appreciation of having found beautiful, "divine things." I truly believe that science is the worthiest of pursuits, both professionally and personally. I could not have become a PhD without immeasurable support and inspiration from a great many people, and I would like to thank and acknowledge a few.

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ABSTRACT OF THE DISSERTATION

Brassica tournefortii:
Phenology, Interactions and Management of an Invasive Mustard

by

Robin Gene Marushia

Doctor of Philosophy, Graduate Program in Plant Biology
University of California, Riverside, June 2009
Dr. Jodie S. Holt, Chairperson

Brassica tournefortii (Gouan), or Sahara mustard, is a nonnative, invasive annual forb currently invading the deserts of North America. Despite its increasing distribution and dominance in desert plant communities, little is known about the biology or impacts of *B. tournefortii*, and few options exist for management. This dissertation sought to answer three basic questions. First, this dissertation questioned "Why is *B. tournefortii* able to invade desert ecosystems, whereas closely-related invasive mustards are not?" Four biotypes of invasive *Brassicaceae,* including desert and more mesic populations of *B. tournefortii*, *Brassica nigra,* and *Hirschfeldia incana* were grown with climate and watering treatments over three years. Results show that all biotypes are capable of equal fitness under desert and drought conditions. Although no differences were found between mesic and desert populations of *B. tournefortii*, the species had a more rapid phenology than its congeners, suggesting that *B. tournefortii* succeeds because it can reproduce quickly. Second, this dissertation asks, "What are the interactions of *B. tournefortii* with native annual forbs?” Because native annuals fill a similar ecological niche, I hypothesized that *B. tournefortii* would have negative impacts on natives with increasing density and cover. Success of the plant community and individual native species was correlated to *B. tournefortii* dominance. Results show that *B. tournefortii* has mostly negative interactions with natives with high precipitation, but positive relationships with low precipitation, suggesting that interactions of *B. tournefortii* with natives change from negative to positive based on resource availability. Finally, this dissertation asks, “Can *B tournefortii* be selectively managed in desert ecosystems?” This research compared hand-weeding, a common control technique, to an emergence-stage application and rosette-stage application of glyphosate, *vs.* no treatment. Emergence-stage application was hypothesized to selectively control *B. tournefortii* and other invasives by taking advantage of their non-specific germination requirements and rapid emergence. This hypothesis was supported by results showing that native cover can be maintained by applying herbicide at emergence while reducing exotic cover. Hand-weeding selectively removed *B. tournefortii*, but promoted annual cover and richness only underneath shrubs at a site with few other invasives present. Late herbicide produced high mortality in all species. Results suggest that herbicide can be used as a selective technique to remove most desert invasives, not just *B. tournefortii.* In conclusion, *B. tournefortii* is a unique case study for biological invasions in extreme ecosystems, and presents challenges for ecologists and land managers alike.

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INTRODUCTION

Vast landscapes in western North America are characterized as desert ecosystems. Deserts are defined as areas that lose more water by evapotranspiration than they receive through precipitation, or 25 – 50 cm of precipitation per year (Meigs 1953). Deserts are generally harsh, arid, and have highly variable climates both within and between years (Went 1949; Beatley 1974; Chesson, Gebauer et al. 2004; Bowers 2005; Hereford, Webb et al. 2006). Such extreme and unpredictable conditions require special mechanisms for plants to survive, and thrive, in a desert environment (Gibson 1996; Smith, Monson et al. 1997; Chesson, Gebauer et al. 2004). In particular, desert plants tend to fall into one of the two following categories representing two opposite life history strategies: stress tolerators, long-lived, slow-growing perennials that retain water and nutrients through succulence or drought tolerance, and stress avoiders, short-lived, fast-growing annuals that are ephemeral, rapidly using water and nutrients before they reproduce and senesce (Gibson 1996; Smith, Monson et al. 1997). With adequate winter precipitation, these ephemerals transform the seemingly barren landscape into a lush, diverse flora that is critical to the survival and reproduction of higher trophic levels (Davidson, Samson et al. 1985; Guo and Brown 1996; Chesson, Gebauer et al. 2004). The spring wildflower displays are also a valuable cultural asset of desert parks and communities that attract tourism and are a source of civic pride (Schiermeier 2005; Minnich 2008).

In the last century, however, desert ecosystems in the United States have become increasingly threatened by human activities. As settlers moved west in the 1800's, they introduced cattle grazing, roads, railways and agriculture (Tellman 2002; Minnich 2008). As human populations have grown, recreation and urbanization have also impacted desert ecosystems (Gelbard and Belnap 2003; Hansen and Clevenger 2005). All of these land uses have increased disturbance in a relatively undisturbed ecosystem and introduced non-native species that have had unanticipated effects on the native flora and fauna of desert communities (Tellman 2002; Minnich 2008). Some non-native plants, such as *Erodium cicutarium* and *Brassica nigra*, were introduced with the Spanish missionaries and have long since invaded much of the western United States (Mensing and Byrne 1998; Mensing 1998; Minnich 2008). Others, such as *Bromus rubens*, were introduced more recently as seed contaminants (Salo 2005). In the warm deserts of the United States, such as the Mojave, Sonoran, and Colorado Deserts, the annual grasses *Bromus rubens, Schismus arabicus,* and *Schismus barbatus* are often common and even dominant in plant communities (Beatley 1966; Brooks 1999; Brooks and Matchett 2003; Salo 2004; Schiermeier 2005; Brooks and Berry 2006; Brooks and Matchett 2006; Steers 2008). Exotic annual grasses increase the fine fuels biomass production of the landscape, altering ecosystem processes such as nutrient cycling (Evans, Rimer et al. 2001; Levine, Vila et al. 2003), hydrology (Levine, Vila et al. 2003; Dukes and Mooney 2004), and fire regimes (D'Antonio and Vitousek 1992; Brooks 2002; Brooks, D'Antonio et al. 2004; Brooks and Matchett 2006). Desert plants, particularly perennials, are poorly adapted to fire (Brooks and Matchett 2003; Steers 2008), but as annual grass invasion has increased across desert landscapes, fires have also increased (Brooks 1999; Brooks and Matchett 2003; Schiermeier 2005; Brooks and Matchett 2006; Steers 2008). Wildfire is now a major cause of vegetation conversion in the United States' desert southwest ecosystems, and a mounting source of concern for land managers and residents alike.

While exotic annual grasses have captured the attention of ecologists and land managers, non-native forbs did not receive the same consideration until only recently. *E. cicutarium* has always been a member of desert plant communities, but was not recognized as an invasive species with impacts on native plants until the last few decades (Brooks 2000; Tellman 2002; Brooks 2003; Brooks and Berry 2006). However, the invasion of *Brassica tournefortii*, or Sahara mustard, has brought the issue of non-native annual forbs to the forefront of desert ecology.

B. tournefortii was likely introduced to the Coachella Valley in the early 1900's as a contaminant of date palm plantations (Minnich and Sanders 2000). It was noted as a ruderal weed of roadsides, gravel pits and other highly disturbed areas by midcentury (Brooks, personal communication), but it was not until the 1980's that population booms of *B. tournefortii* were observed in undisturbed landscapes during years of high precipitation (Barrows, Allen et al. 2009). *B. tournefortii* is now a major invader of threatened dune ecosystems, creosote bush scrub, Joshua Tree woodlands, and other desert communities across the western United States (Trader, Brooks et al. 2006; Bangle, Walker et al. 2008; Abella, Spencer et al. 2009; Barrows, Allen et al. 2009). In a single century it has invaded California, Arizona, New Mexico, and Texas (Minnich and Sanders 2000; USDA NRCS 2009), and its range is expanding.

B. tournefortii is problematic for ecologists and land managers alike. Little is known about its status as an invasive species. Recently, ecological research on this species has documented the distribution of *B. tournefortii* in sandy washes, disturbed places, and roadsides (Malusa, Halvorson et al. 2003; Trader, Brooks et al. 2006), shown that *B. tournefortii* has increasing seed production with increasing plant size (Trader, Brooks et al. 2006), and shown that *B. tournefortii* has broad germination requirements (Bangle, Walker et al. 2008, Holt and Tayyar unpublished data), with seeds that can survive submergence for days at a time (Bangle, Walker et al. 2008). Furthermore, Barrows et al. (2009) found that *B. tournefortii* reduces native annual reproduction in dunes, and Steers (2008, Chapter 2) found that *B. tournefortii* may proliferate after wildfire. These results suggest that *B. tournefortii* is well-suited as a desert invader, but they do not explain the mechanisms of invasion in the deserts' largest community, creosote bush scrub, or the impacts of *B. tournefortii* on native annuals outside of dune communities.

As the widespread impacts of invasive, non-native annuals in deserts have become recognized, interest in managing these species has also increased. Currently, few methods are available. Steers (2008) compared the relative impacts of grasses *vs.* grasses and forbs together, and investigated methods of removing grasses and forbs with grass-specific herbicide, hand-weeding, and raking. Although the results with grass-specific herbicide were promising for the removal of invasive grasses and *E. cicutarium*, the methods tested were not as successful for *B. tournefortii.* Steers (2008) and Barrows et al. (2009) have suggested that rapid emergence in invasive annuals may provide a brief window after germination to manage not only *B. tournefortii*, but invasive annuals as a group. Steers (2008) tested the hypothesis by raking seedlings immediately after emergence, but was unsuccessful, and suggested that a broad-spectrum herbicide might be a better option.

This dissertation pursues three questions related to *B. tournefortii* invasion and management. First, why has *B. tournefortii* invaded the desert, whereas congeneric invasive mustards have not? Comparing *B. tournefortii* to closely related species may help highlight important traits that allow it to invade arid desert regions. Second, how is *B. tournefortii* interacting with native annual species that fill a similar ecological niche in creosote bush scrub? Investigating these relationships may show the relative impact of *B. tournefortii* at different life stages for different species under changing conditions. Third, this dissertation asks the following question: can *B. tournefortii* be effectively and efficiently managed in desert landscapes? Testing and comparing different methods of removal may inform land managers and assist in the large-scale removal of *B. tournefortii* populations, slowing its spread and reducing future impacts on arid ecosystems.

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CHAPTER 1

Growth, Fecundity, and Phenology as Determinants of Distribution for Three Exotic Mustards in Southern California.

Invasive species researchers often ask: why do some species invade certain habitats while others do not? Where closely-related non-native plants occur in contrasting distributions, traits can be compared to determine the limitations to invasion. *Brassica nigra, Hirschfeldia incana,* and *Brassica tournefortii* are dominant, closely related exotic species in southern California that have overlapping, but dissimilar, distributions. *B. nigra* and *H. incana* are primarily limited to coastal and semi-arid inland sites west of the San Bernardino Mountains, while *B. tournefortii* is a rapidly spreading in deserts east of the mountains. The goal of this research was to investigate traits of *B. tournefortii* that might confer invasiveness in the deserts where it is expanding in range, and compare these to traits in related species that have not invaded desert ecosystems. In addition, we compared desert and inland shrubland populations of *B. tournefortii* to investigate the possibility of local adaption as a driver for desert invasion. Both *B. tournefortii* populations were compared with *B. nigra* and *H. incana* in controlled pot experiments over three years. Environmental variables included climate (desert *vs.* coastal inland and outdoors *vs.* greenhouse) and soil water availability (high water *vs.* low water). Response variables included emergence, growth, phenology, and reproduction. Results show no evidence for ecotypes within *B. tournefortii*, but that *B. tournefortii* has a more rapid phenology than *B. nigra* or *H. incana* under all circumstances. *B. tournefortii* was less

affected by climate and water availability than *B. nigra* and *H. incana*, but was smaller and less fecund regardless of treatment. We conclude that rapid phenology allows *B. tournefortii* to reproduce consistently under highly variable conditions, such as those found in southwest deserts. Although more successful under mild, mesic conditions, *B. nigra* and *H. incana* may be limited by an inability to reach seed set in desert ecosystems.

Introduction

Exotic plant invasions are of increasing concern worldwide because of their ecological and economic impacts (Pimentel, Lach et al. 2000; Pimentel, Zuniga et al. 2005; Ricciardi 2007). The mechanisms by which non-native species impact ecosystems are often poorly understood, however, especially because species with high impacts in one ecosystem may have little to no impact in others (Williamson and Fitter 1996; Levine, Vila et al. 2003). In some regions, related non-native species occur in different niches or habitats with varying degrees of overlap. Studying the attributes of these species and their distributions might shed light on mechanisms and limitations of invasion.

Desert ecosystems are among the least disturbed by human activity and exotic species invasions. Deserts have traditionally been considered resistant to invasion because species require specialization to survive in extremes of temperature, low precipitation, and minimal resources, such as soil nutrients (Brooks 1999; Lonsdale 1999). North American deserts such as the Mojave, Sonoran, and Colorado Deserts are characterized by high spatial and temporal variability in precipitation, which has strong effects on vegetation (Beatley 1974; Bowers 2005; Hereford, Webb et al. 2006). Exotic annual plants may have specialized mechanisms by which they dominate and displace native annuals under harsh and variable conditions (Levine, Vila et al. 2003). For instance, *Bromus tectorum* has transformed Great Basin sagebrush ecosystems into annual grasslands by usurping soil water resources through early germination, and by altering nitrogen mineralization rates (Melgoza, Nowak et al. 1990; Evans, Rimer et al.

2001; Levine, Vila et al. 2003). The number of plant invaders in the southwestern U.S. deserts is relatively low, but their dominance and impact can be disproportionately high (Brooks and Berry 2006). These invaders are exotic, ephemeral annual grasses and forbs, including *Bromus* spp., *Schismus* spp., *Erodium cicutarium,* and *Brassica tournefortii*. Furthermore, a high diversity of exotic and invasive species is found in southern California, one of the world's plant biodiversity hotspots (Myers, Mittermeier et al. 2000). Despite a high rate of invasion in the region as a whole, few of the same invasive species have succeeded in expanding their range into nearby desert environments. Understanding the mechanisms by which particular species invade desert ecosystems may assist in predicting potential invaders and provide keys to their management.

B. tournefortii, or Sahara mustard, is a weedy annual species native to the Mediterranean region that is locally abundant in the U.S. desert southwest (Minnich and Sanders 2000). First introduced in the Coachella Valley in the early 20th century (Minnich and Sanders 2000; Brooks 2005), *B. tournefortii* has only begun to invade extensively beyond disturbed areas in the last two decades (M. Brooks, personal observation). In desert sand dunes, *B. tournefortii* impacts native annual forbs by reducing flower and seed production by 80-90% (Barrows, Allen et al. 2009). Similar to some other mustard species, it is adapted to fire and in dense stands can increase fuel loads and fire hazard, which can lead to conversion of desert scrub to grassland (Minnich and Sanders 2000). In addition, many mustard species contain glucosinolates, which can be toxic to livestock and wildlife (Horn and Vaughan 1983) and may increase invasiveness by altering biotic interactions (Mueller 2009). *B. tournefortii* is now regarded as one of the most invasive desert wildland pest plants in California (Cal-IPC 2006). This species is especially problematic in years of high rainfall, but is patchy or inconspicuous in drought years (Barrows, Allen et al. 2009). *B. tournefortii* is one of the top priorities for land managers in the Mojave Weed Management Area (MWMA) and the Low Desert Weed Management Area (LDWMA) in California, but it is also present in coastal and arid inland regions. Because there are invasive populations in both desert and coastal sage scrub ecosystems, selection may have occurred within the species to produce two ecotypes, a more desert-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 (e.g. Sexton, McKay et al. 2002; Kudoh, Nakayama et al. 2007).

Although *B. tournefortii* is considered primarily a desert invader, other closely-related mustard species are major invaders in nearby Mediterranean-climate coastal sage scrub ecosystems. *Brassica nigra* and *Hirschfeldia incana* are locally dominant, invasive annual species throughout most of southern California including urbanized areas, but neither occurs in most natural desert landscapes (CalFlora Database 2009). *B. nigra* was likely introduced intentionally by Franciscan missionaries more than 200 years ago (Hendry and Kelley 1925), and is now found in nearly all lower 48 states (USDA NRCS 2009). *B. nigra* is one of the most prominent exotic invasives of southern California coastal areas (Bell and Muller 1973). *H. incana* was probably introduced at the turn of the previous century, and was recorded in the San Bernardino Mountains as early as 1914 (Parish 1920). *H. incana* is currently an invasive mustard of arid inland areas between the coasts and mountains of southern California, where it alternates with *B. tournefortii* as the dominant exotic forb in annual grasslands. *H. 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 habitat distribution.

One of the central questions of invasion ecology is why some species establish and spread while others do not. *B. tournefortii, B. nigra* and *H. incana* have contrasting distributions in a single region, southern California, and thus may respond differently to climatic variables such as temperature and moisture. The goal of this research was to investigate traits of *B. tournefortii* that might confer invasive ability in the desert areas where it is expanding in range. We conducted a comparative ecological study of *B. tournefortii* from both desert and more mesic habitats, and the two related and co-occurring weedy mustards, *B. nigra* and *H. incana*, which have not invaded desert areas. We hypothesized that desert-collected *B. tournefortii* might have greater drought tolerance, greater survivorship, and/or greater fecundity than *B. tournefortii* from more mesic populations in the inland coastal regions. We also hypothesized that *B. nigra* and *H. incana* would prove more successful in terms of survivorship and fecundity under mesic conditions than *B. tournefortii* found in deserts.

Materials and Method*s*

2004-2005: Two identical common gardens were simultaneously grown in different climates in 2005. Experimental sites included a Mojave Desert location in Blue Diamond, NV, and an “inland coastal" location with a Mediterranean climate, hereafter called the inland location, at the University of California, Riverside. Citrus tree pots (9.6 L capacity; 16.5 cm bottom diameter, 19.5 cm top diameter, 38 cm height) painted white to minimize solar heating of the soil were used for all plants. Pots were filled with UC mix #3 (53% plaster sand, 47% peat moss, plus micronutrients) and pre-watered to field capacity before direct seeding. Pots at both locations were placed outside next to an east-facing wall of a greenhouse.

Three species were used in experiments, *Brassica tournefortii* (desert and inland populations), *Brassica nigra*, and *Hirschfeldia incana*. The latter species is names *Brassica geniculata* in earlier floras, indicating its morphological similarity to other *Brassica* species. The four groups are hereafter referred to as “biotypes.” Two populations were collected for each biotype in different regions of southern California. For *B. tournefortii* Desert, populations were collected in the Coachella Valley (33°41'19.77"N, 116° 6'46.45"W) and from dunes at the Mojave National Preserve (35° 9'28.59"N, 115°33'17.63"W). *B. tournefortii* Inland populations were collected at the University of California, Riverside and on nearby Box Springs Mountain. *H. incana* populations were collected on Box Springs Mountain (33°58'52.06"N, 117°17'22.87"W) and in Fallbrook, CA (33°22'35.56"N, 117°14'17.43"W). *B. nigra* populations were collected at Crystal Cove State Park (33°34'25.13"N, 117°48'59.16"W) and near Corona, CA (33°46'15.27"N, 117°29'8.13"W). Seeds were collected from each location in either 2003 or 2004 and stored at room temperature throughout the research. Viability for all seed types was near 100% (data not shown). Seeds from 8 plants per population were mixed for seeding both gardens in 2004-2005.

The 4 biotypes x 2 populations were replicated in common gardens over 8 blocks in a randomized complete block design at each location for a total of 64 pots per location. Each pot was direct-seeded with 6 seeds of a given population. Pots were seeded on December 22, 2004 in Blue Diamond and December 23, 2004 at UCR. Time to emergence was recorded for all 6 seeds. Seedlings were then thinned to 2 on February 4, 2005, once all seedlings produced their first 4-6 true leaves, leaving 2 seedlings since some early mortality occurred. All seedlings were kept well-watered until plants were harvested at the end of the experiment. High precipitation levels at UCR may have caused nutrient leaching, so plants at that location were watered with a dilute N-P-K nutrient solution at the first sign of stress, maintained until plants recovered, and then returned to water without nutrients. Leaching was not an issue at Blue Diamond and plants did not experience nutrient stress; therefore, they were watered without added nutrients. A solution of insecticidal soap plus release of ladybugs were used for aphid control as needed.

Data were recorded once per week after thinning. Growth data was collected by recording height, width at the longest axis, and width 90° from the longest axis. Phenology was recorded by noting the life stage of each plant, including rosette (leaves only), bolting (producing flower buds), flowering (petals visible), or seed set (siliques present). With all biotypes it was possible for a plant to be bolting, flowering, and setting seed at the same time. Temperature at each location was recorded by HOBO Pro Series temperature recorders set near the pots (Onset Computer Corp. PO Box 3450, Pocasset, MA 02559-3450). Data were collected from February 4, 2005 – June 23, 2005 at both locations.

Plants at Blue Diamond were harvested as soon as they reached seed maturity to prevent seed dispersal and introduction of new genotypes to nearby conservation areas. Plants at UCR were allowed to fully senesce, then harvested. Siliques were counted on all plants from both locations at harvest. Silique numbers were averaged per pot (unless one of the two plants experienced early mortality, in which case the count of the remaining plant was taken) and then averaged per population. When populations were not significantly different, biotypes were grouped and averaged within location. ANOVA was used to test differences between all biotypes across locations.

Seed numbers were counted in 30 siliques subsampled from 52 plants from the UCR plantings and 49 from the Blue Diamond plantings. Plants were arbitrarily chosen to distribute them as equally as possible across all biotypes, populations, and blocks without choosing two plants from the same pot. The number of plants subsampled per biotype population at each location ranged from a minimum of 4 to a maximum of 10. The mean number of seeds/silique was taken for each plant subsampled, then multiplied by the total number of siliques per plant sampled to measure fecundity. Average fecundity per population within biotype was tested within location using one-way ANOVA. When populations within biotypes were not significantly different, populations were grouped and biotypes were tested within a location, also using one-way ANOVA. Tukey’s HSD was used to test the differences between means within silique number and fecundity across locations.

Data were analyzed by grouping data as growth variables or life stage variables. For growth, height was chosen over width or volume because it was the most consistent measure of size both within and across biotypes. Maximum height, maximum leaf number, and days to maximum leaf number were calculated for each individual plant at both locations and averaged across the 2 plants within a pot (where applicable). For life stages, days to initial bolting, flowering, and seed set were calculated for each individual plant, then averaged across the 2 plants within a pot. For all 6 variables, ANOVA was used to test the differences between populations within biotypes, biotypes within climate treatments (locations) and biotype/location interactions. Tukey's HSD test was used to separate differences in means between biotypes/locations.

Survival analysis was used to test the differences in biotype phenology between locations. For each plant, the number of days to each life stage was calculated from the date of emergence. Differences between biotypes were compared for each life stage within each location using survival analysis. Also called failure-time analysis, survival analysis is a nonparametric method that tests the proportions of subjects that have achieved an event by a given time. In this research, time was days from emergence, and the event was the life stage in question. Climate data for the two locations were compared using repeated measures ANOVA. Differences between the maximum, minimum, and mean temperatures were tested.

2005-2006: In the second year, the climate treatment was replaced by a drought treatment, and the common garden experiment was conducted at UC Riverside only. Populations were replaced by high water and low water treatments applied to all four biotypes. Experiments were conducted in the same pots and same location at UCR as in 2004-2005, but the soil was replaced with a custom mix of sand (87% plaster sand and 13% sand fines) to approximate water holding capacity and nutrient retention conditions that might be found in the desert. 3 g of all-purpose slow-release fertilizer was added to the top layer of soil in each pot. More fertilizer was added in 3 g increments to all pots at intervals throughout the study period with the first sign of nutrient stress. Temperature was monitored by HOBO Pro Series temperature recorders set near the pots (Onset Computer Corp. PO Box 3450, Pocasset, MA 02559-3450). Soil volumetric water content (% VWC) was monitored using 8 ECH_20 EC-5 soil sensors (Decagon Devices, 2365 NE Hopkins Court Pullman, WA, USA 99163) installed 10 cm deep in pots in each biotype/treatment combination. Soil volumetric water content was read at each data collection before watering treatments were applied.

The same seeds for all biotypes were used, mixing equal parts of the same populations per biotype tested in 2004-2005. Each of the 4 biotypes was planted in 2 watering treatments (high and low) in a randomized complete block design with 8 blocks. Six seeds per pot were planted on December 21, 2005 and time to emergence was recorded. Seedlings were then thinned to 1 on January 23, 2006 when all seedlings had at least 4-6 true leaves. Watering treatments and data collection began at thinning. High water treatments were watered to field capacity at each data collection, while low water treatments received short bursts of water if they reached 5% - 8% VWC, or if plants had visible wilting. Pots were moved into a greenhouse with impending precipitation in order to maintain watering treatments, and moved back out again as soon as weather allowed.

As in 2004-2005, growth and phenology were recorded weekly by taking two widths, height, and leaf number of each plant from thinning to senescence. Leaves were counted only if they were part of the original basal rosette in *B. tournefortii* and *H. incana*; leaves on bolting shoots were not counted because they tended to occur unpredictably as resprouts with continued watering, whereas basal rosette declined predictably after bolting for both species. All leaves were counted for *B. nigra*, which extended the basal rosette as it bolted and exhibited no resprouting with continued watering. Bolting, flowering, seed set and senescence date were recorded for all plants. Data was collected from January 23 to May 10 2006, when watering ceased and plants were allowed to senesce before harvest.

Phenology was again tested using survival analysis, with days to each life stage tested across biotypes in the two watering treatments. Maximum height and leaf number were averaged across biotypes within treatment. Days from emergence to maximum leaf number, days to bolting, days to flowering, and days to seed set were also averaged across biotypes within treatments. All means were tested using ANOVA and Tukey's HSD post-hoc test.

All plants were harvested and siliques counted from May 20 – May 26, 2006. Since pots contained only 1 plant, thirty siliques were arbitrarily sampled from all plants and seeds per silique counted for an average number of seeds/silique/plant. Fecundity was measured by multiplying average number of seeds per silique by the total number of siliques per plant. Silique number and total fecundity were tested across biotypes for each treatment using one-way ANOVA and Tukey's HSD post-hoc test.

2006-2007: In the third year, the same common garden was repeated from year 2, with a few key adjustments to isolate the effect of water on biotypes. Because it was difficult to maintain steady high and low water levels in sand, and because nutrient stress in sand affected plants differently based on size, watering treatment, and species, the sand mixture was replaced with UC Mix #3, the same mix used in year 1. Nutrients were maintained with a dilute aqueous fertilizer solution. Pots were placed in a climate-controlled greenhouse to maintain watering treatments without complications from natural precipitation. Soil water was measured using two EC-5 ECH$_2$O sensors per biotype/treatment combination rather than one.

The same seeds with the same population mixtures for each biotype were again planted 6 to a pot on December 12, 2006. However, germination was poor because the seeds were planted into pots in the greenhouse. The initial experiment was terminated, and the experiment reseeded outside January 23, 2007. Pots were allowed to grow outside with full water, and time to emergence was recorded until thinning to 1 seedling at 4-6 true leaves. Thinning date varied from February 26 to March 1, 2007. Pots were relocated inside the greenhouse on March 1 and data collection began on March 6. Due to cooler temperatures and higher humidity inside the greenhouse, pots did not lose water as quickly as they had in the previous two years. Although pots in the high water treatment were lightly watered to maintain field capacity, low water pots were not watered until they reached 6% - 8% VWC in mid-April, when they were lightly watered to maintain low soil moisture.

The same data were recorded as in 2005-2006 for all pots from March 6 to May 17, 2007. Watering ceased when plants appeared to have completed their seed set and any continued growth was due to resprouting (in *B. tournefortii* and *H. incana* only). Plants were left until dry and harvested. All siliques were counted. However, seeds per silique were not counted. Instead, the mean number of seeds/silique for each biotype per treatment from year 2 was multiplied by the number of siliques per plant for an estimated total fecundity. Data were analyzed identically to data from 2005-2006.

Differences in the means of maximum height, maximum leaf number, and days to maximum leaf number, bolting, flowering and setting seed were tested across years with nested ANOVA. Year was tested independently, but biotype, treatment (including locations in year 1), and treatment x biotype interactions were nested within year.

Results

2004-2005: Blue Diamond had lower temperatures than UC Riverside (Figures 1.1a and 1.1b). Maximum, minimum, and mean temperatures at Blue Diamond were 61.29 C, 10.45 C, and 18.21 C, respectively, while maximum, minimum, and mean temperatures were 62.01 C, 11.97 C, and 20.57 C at UC Riverside. Temperature differences between locations were significant during the experimental period (max. = $P=0.042$, min. $P = 0.043$, mean $P = 0.039$). Growth, phenology, and reproduction of the four biotypes also differed across locations and species, but not between populations of the same biotype. Therefore, populations were pooled for all further analyses.

Emergence time for all biotypes differed dramatically between locations. At UC Riverside, the mean days to emergence was 8.79, while at Blue Diamond, plants took an average of 30.58 days to emerge (ANOVA $P < 0.001$). Biotypes also differed at Blue Diamond (nested ANOVA $P = 0.002$); *H. incana* emerged latest (36.24 days), while *B. tournefortii* Desert and *B. nigra* emerged earliest (26.63 and 29.04 days, respectively). *B. tournefortii* Inland was later to emerge (30.42 days) but was not different from *B. tournefortii* Desert at the Blue Diamond location. There were no differences in time to emergence among biotypes at UC Riverside.

Growth, phenology, and reproduction did not differ between Inland and Desert populations of *B. tournefortii*. However, *B. tournefortii* differed from both *B. nigra* and *H. incana*. *B. tournefortii* produced fewer siliques and had lower overall fecundity than its congeners at UCR (Figure 1.2a). Both *B. nigra* and *H. incana* had dramatically lower reproduction in Blue Diamond, the desert location, than at UC Riverside, while reproduction by *B. tournefortii* was relatively lower at both sites (Figure 1.2a). Overall, *B. tournefortii* was smaller in stature but grew more rapidly than either of the other species (Table 1.1.1). It also bolted, flowered, and set seed as much as 50 days earlier than either of the other species at both sites (Table 1.1.1, Figure 1.3). Location of the common garden did not change relative differences in size or phenology between *B. tournefortii* and the congeneric mustards studied.

H. incana was more gradual in bolting, flowering, and seed set at Blue Diamond than at UC Riverside, while *B. nigra* exhibited very similar phenology across locations (Figure 1.3). Although *B. nigra* phenology did not change with location, this species was less successful in terms of growth in the desert compared to UC Riverside. *B. nigra* was less than half the size at Blue Diamond reached at UC Riverside, and had fewer leaves

(Table 1.1.1). The most successful species at Blue Diamond in terms of leaf number was *H. incana*, which also attained the same height as *B. nigra* in the desert garden. *H. incana* required the most days of all biotypes in the desert to reach its maximum leaf number, however (Table 1.1.1). All biotypes had over 20 leaves at their maximum at UC Riverside, but both *H. incana* and *B. nigra* required more days to reach their maximum leaves than either biotype of *B. tournefortii*. *B. nigra* towered over the other species at UC Riverside at 1.6 m, on average (Table 1.1). However, *H. incana* had by far the greatest fecundity, with nearly 2,000 siliques produced per plant at UC Riverside (Figure 1.2a). All biotypes had the same level of reproduction at Blue Diamond (Figure 1.2a).

2005-2006: In year 2, temperatures at UC Riverside were similar to year 1 (Figure 1.1c). Soil volumetric water content (VWC) was lower in low water (drought) treatments than in high water treatments; drought treatments had an average VWC of 7.01%, whereas fully watered pots had an average VWC of 11.71% ($P<0.001$, Figure 1.4a). Fully watered pots had VWC values as high as 16% before watering, while drought treatments had a maximum of 10% VWC (Figure 1.4a). Soil water VWC was low overall, however, due to the sandy growth medium.

The drought treatment produced similar patterns between species and biotype as the desert climate treatment produced in year 1. Drought treatments reduced both silique number and fecundity in *H. incana* and *B. nigra*, but did not affect silique number in *B. tournefortii* (Figure 1.2b). Drought did, however, reduce overall fecundity of *B. tournefortii* by reducing the seed number per silique (Figure 1.2b). All biotypes had the same fecundity and silique number under drought treatments (Figure 1.2b). Whether in high or low water, *B. tournefortii* bolted, flowered, and produced seeds in the same amount of time (40-60 days from emergence), which was often ~30 - 40 days ahead of either *B. nigra* or *H. incana* (Table 1.1, Figure 1.5). Although mean days to bolting were not different across treatments, *B. tournefortii* had fewer mean days to flowering and seed set (Table1.1). Phenology did not differ between *B. nigra* and *H. incana* or between watering treatments (Table 1.1, Figure 1.5). For all species, bolting, flowering, and seed set occurred almost simultaneously for nearly all plants and within a few days (Figure 1.5).

Bolting, flowering, and seed set persisted from meristem resprouts for *H. incana* and *B. tournefortii* with continued watering, whereas *B. nigra* was determinant in the course of its life stages regardless of water availability (personal observation). Both *H. incana* and *B. nigra* grew taller in high water than low water. *H. 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 1.1). Both biotypes of *B. tournefortii* was just as large under drought conditions as when fully watered (Table 1.1). Maximum leaf number differed across biotypes overall but there was no difference between treatments and no interaction between watering treatment and biotype leaf number (Table 1.1).

2006-2007: The climate-controlled greenhouse had steady, warm temperatures throughout the experiment (Figure 1.1d). Soil water was initially between 17 and 20% VWC due to the greater water holding capacity of peat moss included in the growth medium and required about half the study period to dry down to VWC levels similar to year 2. However, low water treatments had an average VWC of 9.79 %, significantly lower than the average high water VWC of 13.74% ($P<0.001$, Figure 1.4b).

Mean days to bolting, flowering, and seed set differed across biotypes but not treatments in year 3. Phenology, as measured by survival analysis, was different across biotypes within high water (log rank = 0.036) and low water (log rank <0.001) treatments. In both cases *B. tournefortii* was more rapid in bolting, flowering, and setting seed than *B. nigra* or *H. incana* (Figure 1.6).

Patterns of reproduction between biotypes and treatments were similar to year 2, except that silique count, and therefore estimated fecundity, were both dramatically higher among all biotypes in high water treatments (Figure 1.2c). Low water again decreased silique production to the point where all biotypes were equivalent (Figure 1.2c).

B. tournefortii Inland 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 1.1). *H. incana* and *B. nigra* were again the same size under low water. Although the maximum number of leaves did not differ between biotypes under different treatments, *B. tournefortii* Desert took a lower mean number of days to reach maximum leaves under drought conditions than *B. tournefortii* in high water conditions (Table 1.1). *B. tournefortii* Inland was also faster in reaching maximum leaf number, but differed only from *B. tournefortii* Desert at high water. Overall, *B. tournefortii* had a faster mean time to maximum leaf number than either *B. nigra* or *H. incana* (Table 1.1).

Across years, all combinations of year, biotype, and treatment were important for differences in mean height (Table 1.1). Although maximum leaf number differed across year, biotypes, and treatments, there was no interaction effect of treatment with biotypes. Days to maximum leaf number was affected by year, biotype, treatment, and biotypes x treatments. For bolting time, treatments within years alone were not different, but days to bolting within year, biotype, and biotype x treatment were significant. All factors were important for days to flowering time and setting seed (Table 1.1).

Discussion

Common gardens under different climate and drought conditions showed no evidence for selection of desert *vs.* inland coastal ecotypes of *B. tournefortii*. Instead, data show strong support for drought avoidance and an ephemeral life history as an explanation for the increasing success of *B. tournefortii* as a desert invader. Germination does not appear to be a limiting factor for either *B. nigra* or *H. incana*, as both have as broad or broader temperature and moisture tolerances as *B. tournefortii* (Holt and Tayyar, unpublished data). Mortality prior to reproduction is a more likely influence on the distribution of these species in desert ecosystems. In our research, growing *B. nigra* and *H. incana* in the Mojave Desert produced patterns similar to those produced by drought, even though plants were well watered, indicating that climate also plays an important role for the success of these species.

One of the most prominent findings of this research is that *B. tournefortii* phenology is consistently more rapid than that of *B. nigra* and *H. incana*. Rapid phenology is a common characteristic among both invasive and native annual plants of southern California, especially in arid inland and desert ecosystems (Went 1949; Tevis 1958; Smith, Monson et al. 1997). Rapid phenology is a drought avoidance strategy that makes maximum use of highly variable precipitation during the few months of availability (Smith, Monson et al. 1997). Aronson et al. (1992) found that similar Mediterranean annuals reproduced earlier and at smaller sizes under drought stress than well-watered plants. In our research, the desert climate and drought reduced plant size and occasionally reduced time to reproductive phases, but only for *H. incana* and *B. nigra*. *B. tournefortii* phenology was unaffected by drought or climate. In contrast, *B. tournefortii* silique production was affected by drought only when the limitations of climate and herbivory were removed by growing plants in a greenhouse.

All three species were capable of germinating, growing, and reproducing in a desert environment, although all species required far more time to emerge than in the Mediterranean-type climate. *B. tournefortii* was less affected by desert environments and low water than its congeners, and more successful in terms of height and productivity. *B. tournefortii* was also the only species that decreased its time to maximum leaf number in the desert, exhibiting plasticity in response to colder temperatures despite late emergence. Plasticity is often cited as an important mechanism in plant invasions, and may be especially important for exotics in low-resource habitats (Funk 2008), or where conditions are likely to be in flux (Daehler 2003), which are important factors in desert ecosystems (Titus, Nowak et al. 2002; Hereford, Webb et al. 2006).

B. nigra was by far the largest species tested, and had greater seed production than *B. tournefortii* when grown in a mild climate with ample water. However, *B. nigra* could not maintain its large biomass in the desert and was severely diminished in size and fecundity. *H. incana* was the greatest seed producer under well-watered conditions, but was similarly diminished under desert or drought conditions. Both results show that tradeoffs may exist for *B. tournefortii*; although rapid phenology imparts the ability to reach maturity quickly, *B. tournefortii* cannot reach as large a size or produce as many seeds as related invasives. However, *B. tournefortii* had the same time to bolting, flowering, and seed set under desert or drought conditions, suggesting that *B. tournefortii* can produce seed under a wide range of conditions. *B. tournefortii* produces the most seeds and biomass during years with warm winters and abundant rainfall (Trader, Brooks et al. 2006; Barrows, Allen et al. 2009), however it has also been observed to produce seeds from small plants during years of low rainfall (M. Brooks, personal observation).

B. tournefortii's rapid phenology and ability to speed up in response to desert conditions may allow it to reach maturity and produce seed even in cold, dry years with extremely short periods of soil water availability, whereas other exotic mustards may be more likely to die before they reproduce. These results imply that *B. tournefortii* is well suited to survive and compete in arid desert environments, but may be outcompeted by larger, more fecund exotic mustard species under less stressful conditions. Differing patterns of phenology, size, and reproductive output may help explain why *B. nigra, H. incana,* and *B. tournefortii* have historically occurred in different environments in California. As the largest species, *B. nigra* may require the more mesic coastal environment to reach its full competitive potential. As a shorter, highly prolific species, *H. incana* often thrives in the arid inland coastal sage scrub habitats, where native shrubs and annuals are also more compact.

Although smaller than related mustards, *B. tournefortii* is not small compared to native annuals in deserts and generally forms an overstory in annual forb communities (Barrows, Allen et al. 2009). *B. tournefortii* appeared less competitive than its congeners with a mild climate and plentiful water, but in comparison to desert annuals, *B. tournefortii* is larger, hardier, and more likely to reproduce than common native species under both wet and dry conditions (Ch. 2). *B. tournefortii* germinates rapidly in high percentages under a wide range of conditions (Bangle, Walker et al. 2008; Holt and Tayyar unpublished data), which in a natural environment may translate to a greater emergence rate and higher densities early in the season than native plant species. Early, rapid, plentiful germination may allow *B. tournefortii* to usurp resources and gain an early competitive edge over native annuals, which have more precise germination requirements or slower germination (Went 1979; Burk 1982).

B. tournefortii is found throughout southern California, including coastal regions, and is not limited to inland areas (CalFlora Database 2009). Moreover, it is currently spreading as far east as Texas and is a problem in southern Nevada (USDA NRCS 2009). With rapid phenology, germination possible at relatively cold temperatures, and consistent reproduction among years of contrasting rainfall, *B. tournefortii* may be adapted to invade beyond the southwestern deserts , perhaps into the northern Great Basin deserts and the Colorado Plateau. Management strategies and options for control will be critical tools to protect uninvaded regions from potential impacts.

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Figure Legends

Figure 1.1: Daily maximum, minimum, and mean temperatures in °C. a) 2004-2005, outdoors at UC Riverside (UCR), CA; b) 2004-2005, outdoors at Blue Diamond (BD), NV; c) 2005-2006, outdoors at UC Riverside, CA; d) 2006-2007, greenhouse at UC Riverside, CA.

Figure 1.2: Mean number of siliques and mean total fecundity for *Hirschfeldia incana* (H.i), *Brassica nigra* (B.n), *Brassica tournefortii* Desert (B.t D) and *Brassica tournefortii* Inland (B.t I). a) 2004-2005, biotypes grown in two common garden locations, UC Riverside, CA (UCR) And Blue Diamond, NV (BD); b) 2005-2006, biotypes grown in two watering treatments, High and Low, outdoors at UC Riverside, CA; c) 2006-2007, biotypes grown in two watering treatments, High and Low, in a greenhouse at UC Riverside, CA.

Figure 1.3: Phenology of 4 biotypes grown outdoors at UC Riverside, CA and Blue Diamond, NV. For survival analyses within location and life stage, log-rank chi-square < 0.001. a) Bolting at UCR; b) bolting at Blue Diamond; c) flowering at UCR; d) flowering at Blue Diamond; e) seed set at UCR; f) seed set at Blue Diamond.

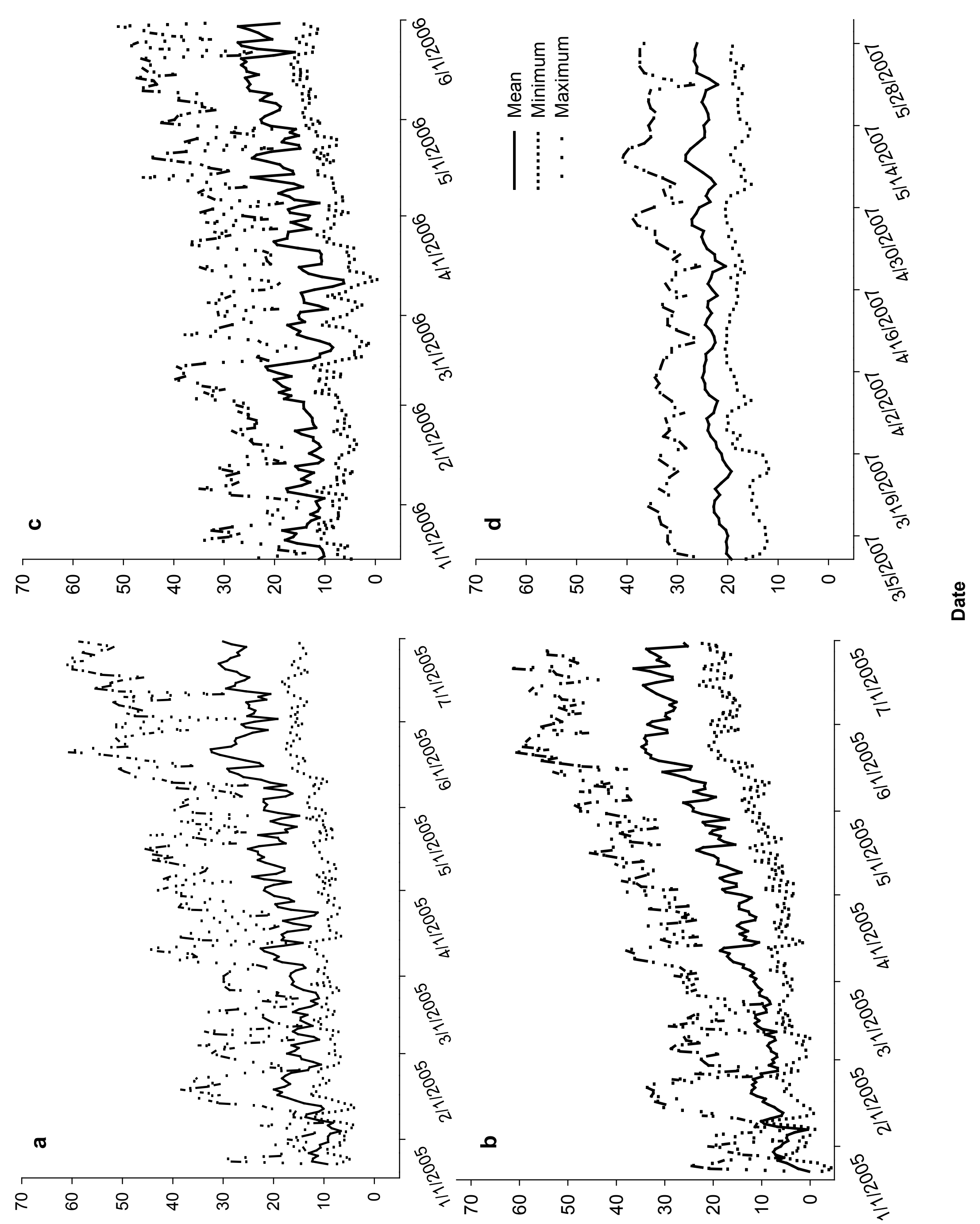
Figure 1.4: Percent (%) volumetric water content (VWC) of soil water treatments. a) 2005-2006, sandy growth medium, pots placed outdoors; b) 2006-2007, peat and sand growth medium, pots placed in greenhouse.

Figure 1.5: Phenology of 4 biotypes grown outdoors at UC Riverside, CA under high and low watering treatments. For survival analyses within treatment and life stage, log-

rank chi-square < 0.001. a) bolting in high water; b) bolting in low water; c) flowering in high water; d) flowering in low water; e) seed set in high water; f) seed set in low water.

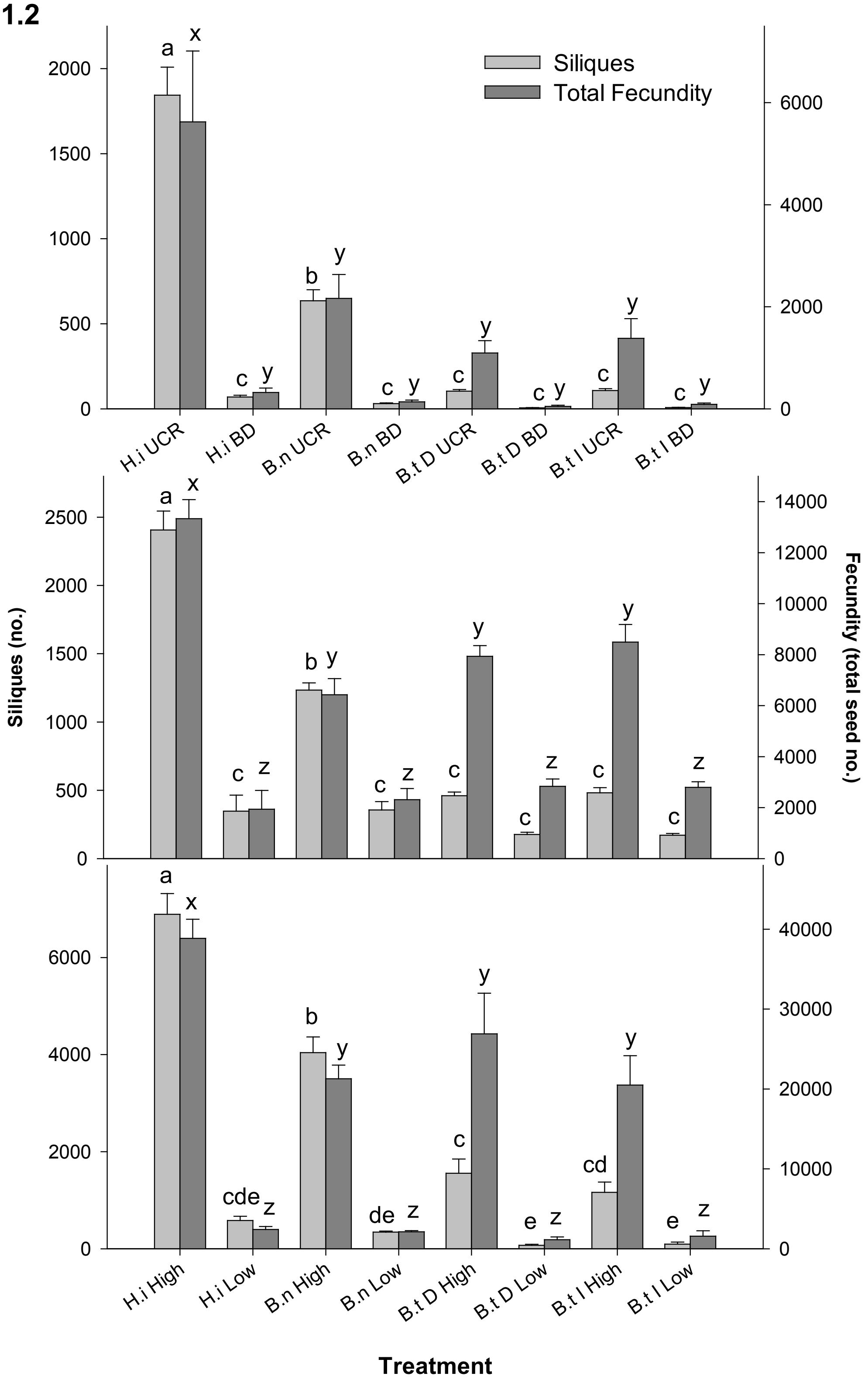
Figure 1.6: Phenology of 4 biotypes in a greenhouse at UC Riverside, CA under high and low watering treatments. Survival analyses log-rank chi-square: bolting, high = 0.036, low < 0.001; flowering high = 0.003, low < 0.001; seed set high = 0.004, low < 0.001. a) bolting in high water; b) bolting in low water; c) flowering in high water; d) flowering in low water; e) seed set in high water; 3f) seed set in low water.

1.1

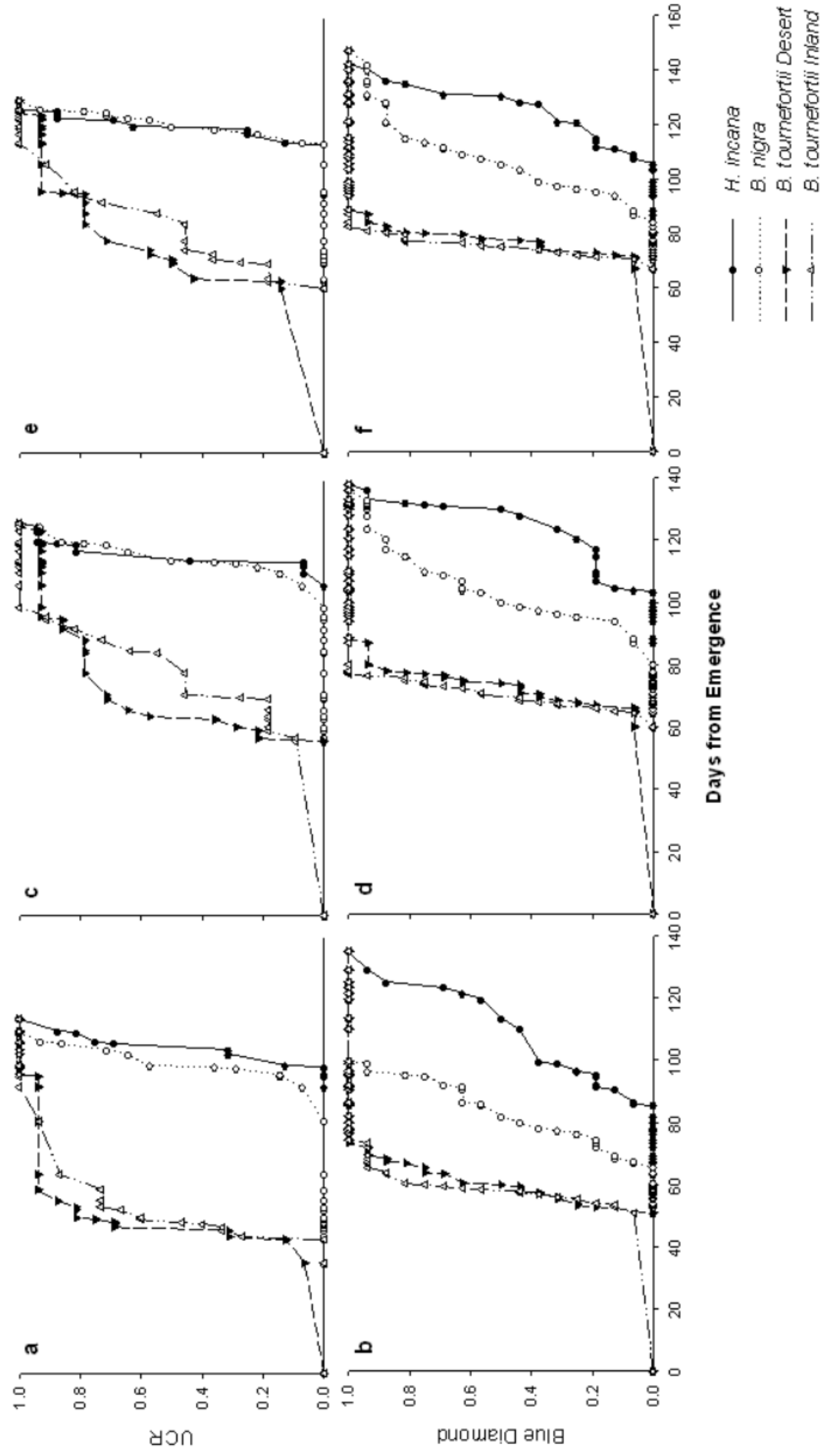


a
b
c
d
Temperature (C)
0
10
20
30
40
50
60
70
1/1/2005
2/1/2005
3/1/2005
4/1/2005
5/1/2005
6/1/2005
7/1/2005
1/1/2006
2/1/2006
3/1/2006
4/1/2006
5/1/2006
6/1/2006
3/5/2007
3/19/2007
4/2/2007
4/16/2007
4/30/2007
5/14/2007
5/28/2007
Mean
Minimum
Maximum
Date

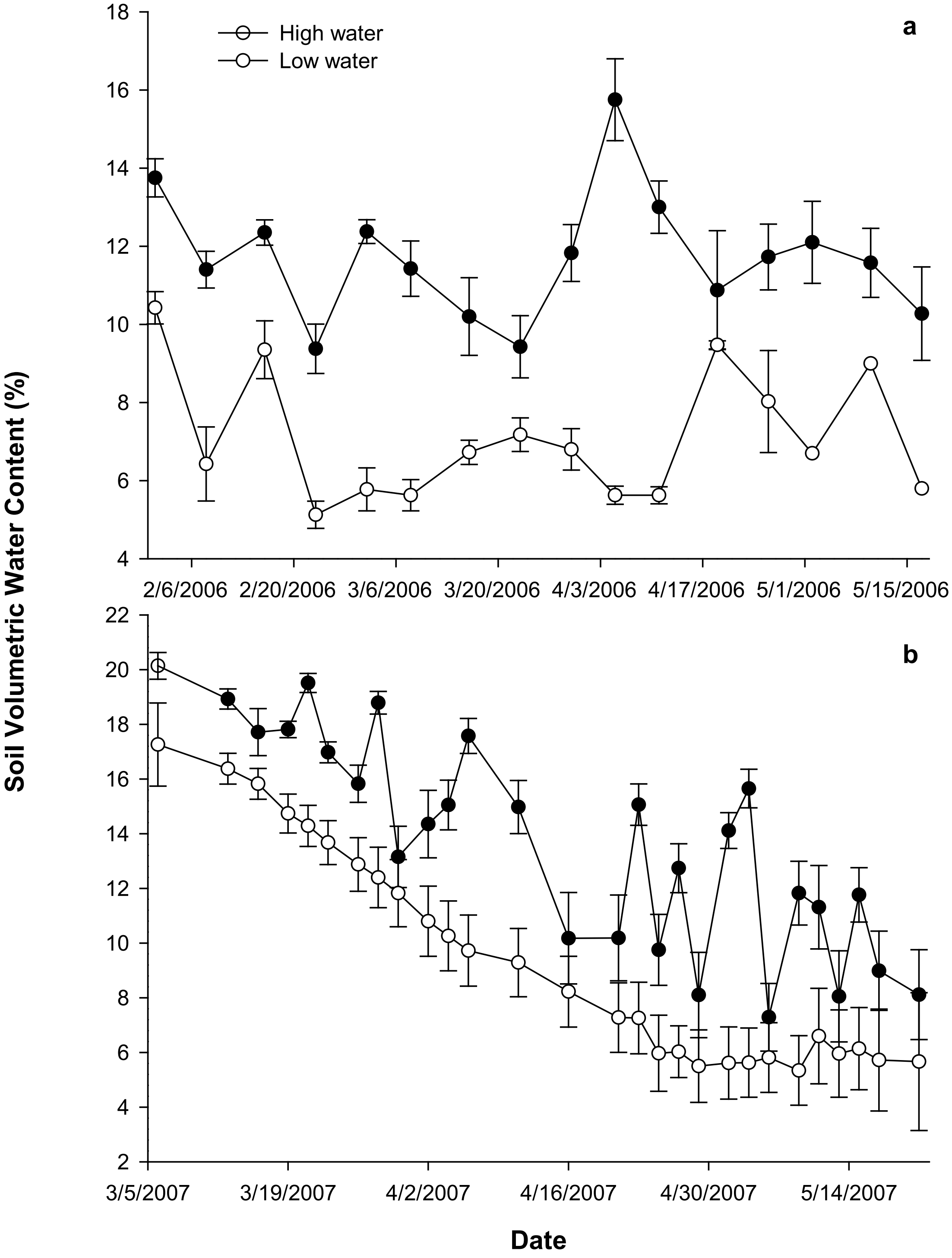
1.2


Siliques
Total Fecundity
2000
1500
1000
500
0
6000
4000
2000
0
a x
c y
b y
c y
c y
c y
c y
c y
H.i UCR
H.i BD
B.n UCR
B.n BD
B.t D UCR
B.t D BD
B.t I UCR
B.t I BD
2500
2000
1500
1000
500
0
14000
12000
10000
8000
6000
4000
2000
0
a x
c z
b y
c z
c y
c z
c y
c z
Siliques (no.)
Fecundity (total seed no.)
6000
4000
2000
0
40000
30000
20000
10000
0
a x
cde z
b y
de z
c y
e z
cd y
e z
H.i High
H.i Low
B.n High
B.n Low
B.t D High
B.t D Low
B.t I High
B.t I Low
Treatment

1.3

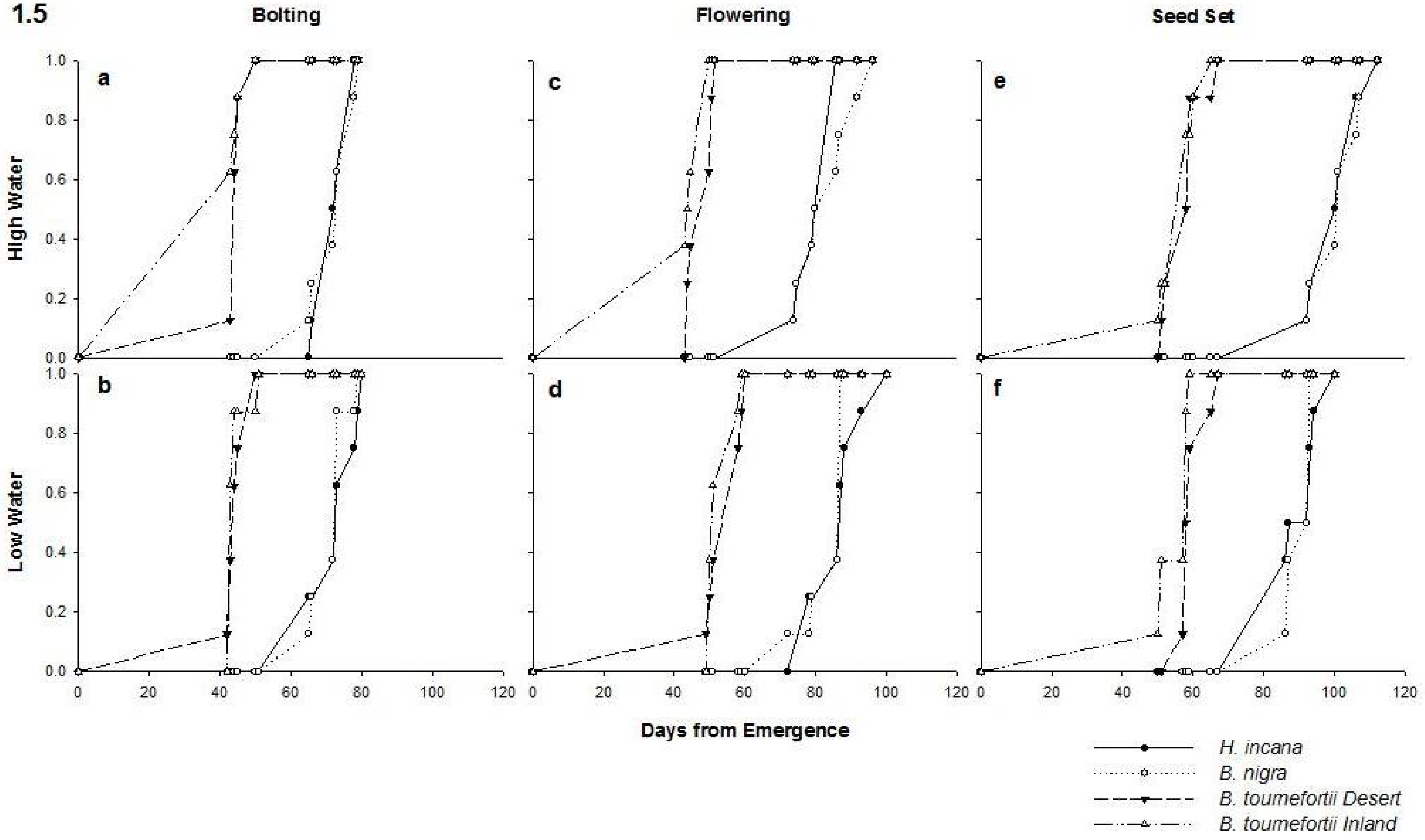

Bolting
Flowering
Seed Set
a
b
c
d
e
f
UCR
Blue Diamond
Days from Emergence
1.0
0.8
0.6
0.4
0.2
0.0
0
20
40
60
80
100
120
140
160
H. incana
B. nigra
B. tournefortii Desert
B. tournefortii Inland

1.4



Soil Volumetric Water Content (%)
High water
Low water
a
18
16
14
12
10
8
6
4
2/6/2006
2/20/2006
3/6/2006
3/20/2006
4/3/2006
4/17/2006
5/1/2006
5/15/2006
b
22
20
18
16
14
12
10
8
6
4
2
3/5/2007
3/19/2007
4/2/2007
4/16/2007
4/30/2007
5/14/2007
Date

1.5


Bolting
Flowering
Seed Set
High Water
Low Water
a
b
c
d
e
f
1.0
0.8
0.6
0.4
0.2
0.0
0
20
40
60
80
100
120
Days from Emergence
H. incana
B. nigra
B. toumefortii Desert
B. toumefortii Inland

1.6

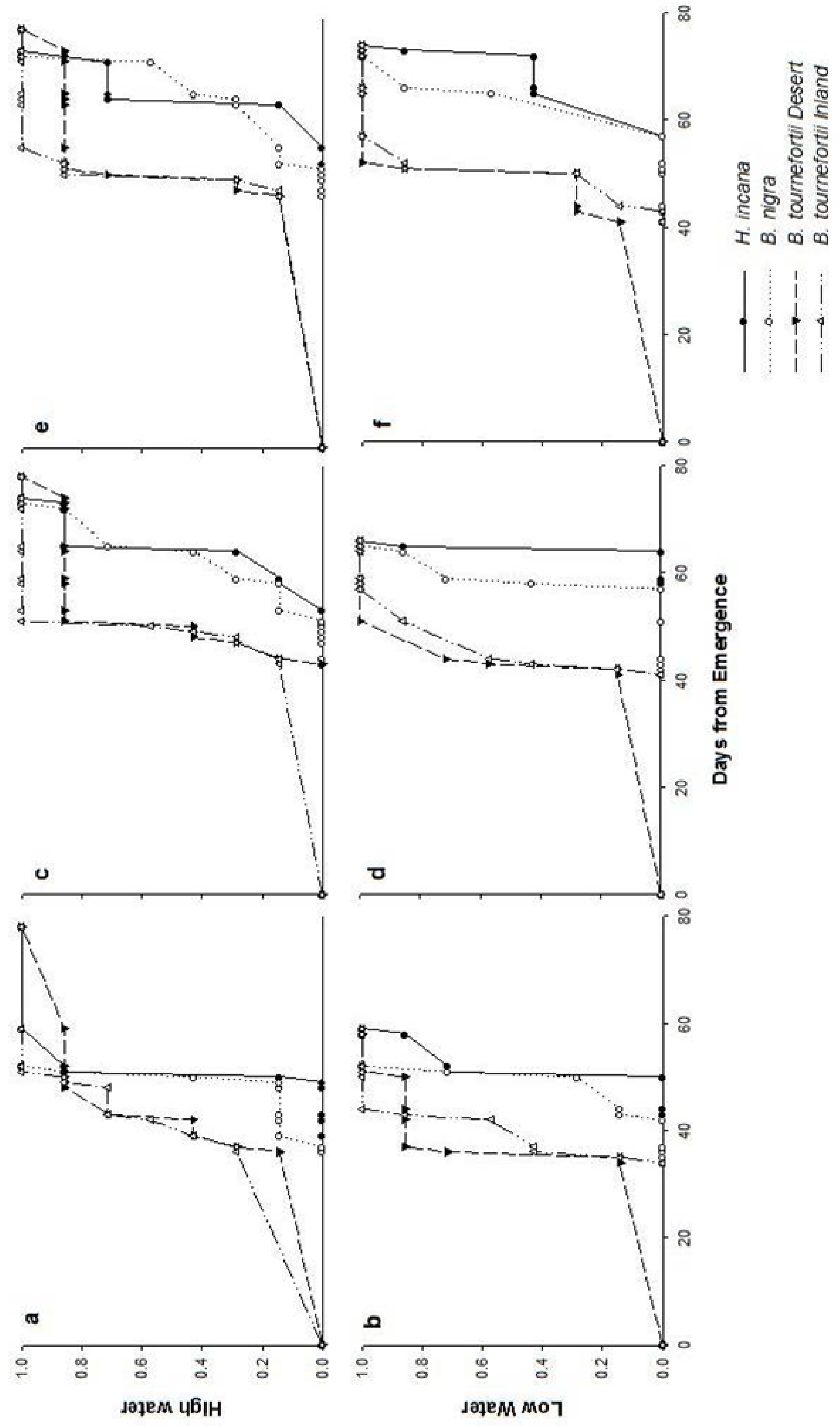

Bolting
Flowering
Seed Set
a
b
c
d
e
f
High water
Low Water
Days from Emergence
1.0
0.8
0.6
0.4
0.2
0.0
0
20
40
60
80
H. incana
B. nigra
B. tournefortii Desert
B. tournefortii Inland

Table 1.1.1: Average ± 1 standard error (s.e.) maximum height, maximum leaf number and minimum days to each life stage for biotypes at two locations and in two watering treatments. Biotype abbreviations follow that of Figure 2. ANOVA tests are within variable and year across locations, treatments and biotypes. Tukey's HSD tests represent differences for location*biotype and treatment*biotype for each variable each year. For Tukey's tests, location*biotype and treatment*biotype combinations not followed by the same letter are different at P not significant. P values with * are significant at α = 0.01.

			Max height (cm)			Max leaf #			Days to max leaf #			Days to bolting			Days to flowering			Days to seed set		
Year	t	Biotype	e	s.e.	y	e	s.e.	Tukey	Average	s.e.	Tukey	e	s.e.	Tukey	e	s.e.	Tukey	Average	s.e.	Tukey
Year 1	UCR	Bt D	37.9	2.1	ab	> 20	0.0	a	90.9	2.9	a	50.2	3.4	a	71.3	4.2	a	76.5	3.7	a
		Bt I	41.8	2.5	a	> 20	0.0	a	88.3	3.0	a	54.6	4.1	a	78.4	5.0	a	83.7	5.6	a
		Hi	138.3	3.9	c	> 20	0.0	a	109.9	0.9	b	106.0	1.0	c	116.3	0.8	bc	120.3	0.9	bc
		Bn	163.4	6.0	d	19.8	0.2	a	107.3	1.3	b	100.7	1.1	c	115.9	1.3	bc	121.6	1.0	c
	Blue Diamond	Bt D	22.5	2.5	b	10.3	0.8	c	68.8	2.8	c	60.6	1.9	a	73.2	1.7	a	77.6	1.2	a
		Bt I	24.9	3.6	b	10.9	1.2	bc	69.0	2.9	c	59.0	1.3	a	70.7	1.3	a	75.6	1.1	a
		Hi	44.2	1.8	a	18.6	1.1	a	141.4	1.6	d	111.9	3.6	c	125.4	3.3	c	127.4	3.3	c
		Bn	43.3	4.3	a	13.5	0.7	b	109.8	3.9	b	84.3	2.0	b	105.2	2.9	b	108.3	3.4	b
		site	P < 0.001			P < 0.001			P = 0.309			P = 0.553			P = 0.354			P = 0.11		
		biotype(site)	P < 0.001			P < 0.001			P < 0.001			P < 0.001			P < 0.001			P < 0.001		
Year 2: outdoors at UCR	High water	Bt D	66.7	2.3	a	13.1	0.5	a	44.9	0.8	a	44.9	0.8	a	56.0	1.4	a	57.9	1.7	a
		Bt I	68.3	2.1	a	12.6	0.3	ab	44.3	0.9	a	44.3	0.9	a	53.4	1.4	a	57.3	1.7	a
		Hi	138.1	5.8	c	25.4	1.1	c	98.0	4.1	c	73.6	1.5	b	94.8	2.1	cd	101.3	2.4	c
		Bn	185.4	7.2	d	25.6	1.4	c	89.8	5.4	bc	73.0	1.9	b	97.3	3.3	d	101.5	2.4	c
	Low water	Bt D	51.8	2.7	a	12.9	0.5	ab	46.1	2.7	a	45.1	1.1	a	55.4	1.6	a	60.1	1.3	a
		Bt I	54.9	1.8	a	13.6	1.2	ab	45.3	2.0	a	44.3	1.0	a	53.4	1.5	a	55.4	1.4	a
		Hi	96.1	8.5	b	27.9	5.5	c	88.6	3.4	bc	73.1	2.1	b	87.1	2.6	bc	90.6	1.8	b
		Bn	110.4	6.0	b	22.3	1.0	bc	82.8	2.4	b	71.8	1.6	b	84.0	2.0	b	90.5	1.1	b
		treatment	P < 0.001			P = 0.984			P = 0.111			P = 0.709			P = 0.001			P < 0.001		
		biotype(tmt)	P < 0.001			P < 0.001			P < 0.001			P < 0.001			P < 0.001			P < 0.001		
Year 3 greenhouse at UCR	High water	Bt D	66.5	5.0	ab	8.9	0.6	NS	73.4	5.0	a	46.3	5.5	abc	52.9	4.3	ab	54.0	4.1	a
		Bt I	69.6	4.9	a	8.9	0.5	NS	69.4	2.2	ab	42.3	2.2	abc	48.9	1.1	a	51.0	1.0	a
		Hi	156.5	5.3	d	9.6	0.5	NS	91.0	2.0	d	52.0	1.2	a	65.1	1.8	c	67.3	1.6	b
		Bn	188.4	1.7	e	15.9	1.4	NS	91.1	3.0	d	49.1	1.7	abc	64.4	2.6	c	67.7	2.8	b
	Low water	Bt D	49.4	4.2	b	12.6	5.4	NS	55.9	1.5	c	38.0	2.2	c	45.1	1.5	a	48.6	1.7	a
		Bt I	45.9	3.3	b	8.5	0.3	NS	58.9	2.4	bc	39.9	1.5	bc	47.3	2.2	a	50.7	1.4	a
		Hi	97.6	5.4	c	8.6	0.3	NS	97.4	2.5	d	53.1	1.4	a	65.1	0.1	c	69.7	1.7	b
		Bn	91.7	3.2	c	15.0	0.5	NS	90.4	2.7	d	50.0	1.2	ab	60.1	1.1	bc	66.3	1.0	b
		treatment	P < 0.001			P = 0.242			P = 0.008			P = 0.224			P = 0.033			P = 0.441		
		biotype(tmt)	P < 0.001			P = 0.032			P < 0.001			P < 0.001			P < 0.001			P < 0.001		
	† nested within year	year	P < 0.001			P < 0.001			P < 0.001			P < 0.001			P < 0.001			P < 0.001		
		treatment†	P < 0.001			P < 0.001			P = 0.013			P = 0.504			P = 0.002			P = 0.002		
		biotype(tmt)	P < 0.001			P < 0.001			P < 0.001			P < 0.001			P < 0.001			P < 0.001		

CHAPTER 2

Is Native Annual Success Reduced by *Brassica tournefortii*? Relationships of Density and Cover in the Mojave Desert.

Brassica tournefortii (Gouan) is one of a few non-native annual forbs currently invading southwestern desert ecosystems in the U.S., yet little is known about its impacts to native annual forb communities. A series of plots with a range of *B. tournefortii* densities was established in a central Mojave Desert native annual community and monitored during the winters of 2004-2005, a year of record high precipitation, and 2005-2006, a year of below-average precipitation. Community richness, density, and cover were recorded monthly, and individuals of *B. tournefortii, Chaenactis stevioides,* and *Cryptantha angustifolia* were measured for growth and phenology bimonthly. Density and cover of native annuals as a group were negatively correlated to *B. tournefortii* density and cover in 2005, but were positively correlated in 2006. Density, cover, and height of *C. stevioides* were always positively correlated with *B. tournefortii*, but mortality also increased with *B. tournefortii* density late in the season in 2005. In contrast, *C. angustifolia* density was negatively correlated with *B. tournefortii* density in 2005, but cover and height were greater and mortality reduced with greater *B. tournefortii* density and cover. *C. angustifolia* was positively correlated with *B. tournefortii* density and cover in the dry year, 2006. *B. tournefortii* was always more successful at higher conspecific density and cover regardless of precipitation. Results suggest that *B. tournefortii* may impact native annual success more during wet years than dry years, but that individual

species may be affected by *B. tournefortii* differently both within and across growing seasons depending on precipitation. Interactions between native and non-native annuals are complex, and both competition and facilitation may play a role in success of desert forbs.

Introduction

The Mojave Desert has a low proportion of non-native species in its flora, which is typical of deserts worldwide (Abella, Spencer et al. 2009; Brooks 2009). Human disturbances such as livestock grazing, urbanization, pollution, and vehicular routes have facilitated the introduction, spread, and establishment of non-native plants (Brooks and Pyke 2001; Tellman 2002; Brooks 2003; Gelbard and Belnap 2003; Trader, Brooks et al. 2006; Zwaenepoel, Roovers et al. 2006; Steers 2008; Brooks 2009; Steers and Allen 2009). Some species, such as *Erodium cicutarium*, were introduced centuries ago (Mensing and Byrne 1998) and have become ubiquitous throughout the southwestern United States. Others, such as *Brassica tournefortii*, were introduced less than 100 years ago and have spread with unexpected rapidity (Minnich and Sanders 2000). The diversity and distributions of non-native species invading North American deserts are increasing and are a major ecological issue (Brooks and Pyke 2001; Schiermeier 2005; Bowers, Bean et al. 2006; Brooks 2009).

Despite containing relatively low numbers of non-native species, deserts landscapes can be dominated by their biomass and cover (Brooks and Berry 2006; Brooks 2009). As the frequency and dominance of non-native annual grasses and forbs has increased, ecologists and land managers alike have become increasingly concerned about the impacts of these species on the structure and function of desert ecosystems (Brooks and Pyke 2001; Schiermeier 2005). Exotic annuals are now known to impact fauna (Barrows, Allen et al. 2009), change soil nutrient cycling and ecology (Evans, Rimer et al. 2001; Duda, Freeman et al. 2003), change seedbank composition

(McLaughlin and Bowers 2007), and increase fire frequency, intensity, and size (Brooks 1999; Schiermeier 2005; Brooks and Berry 2006; Brooks and Matchett 2006; Brooks and Minnich 2006; Steers 2008), among other impacts.

One of the most important concerns about disturbance in deserts is whether invasive annuals compete with native annual and perennial species (Brooks 2000; DeFalco, Bryla et al. 2003; Salo, McPherson et al. 2005; Brooks and Berry 2006; DeFalco, Fernandez et al. 2007). Research findings have not been consistent. Both negative and positive relationships have been found between non-native annuals and native plants (Beatley 1966; Holmgren, Scheffer et al. 1997; Briones, Montana et al. 1998; Brooks 2000; Maestre, Valladares et al. 2006; DeFalco, Fernandez et al. 2007; Valiente-Banuet and Verdu 2008). The relative importance of competition and facilitation can be explained by the level of stress experienced by plants in a desert environment, which include a harsh environment, low resource availability, or both. As stress increases and resources decrease, facilitation becomes more common than competition (Bertness and Callaway 1994; Callaway 2007; Maestre, Callaway et al. 2009).

Although North American deserts are considered high in stress and low in resources, factors such as variation in resource availability (Briones, Montana et al. 1998; Brooks 2000; DeFalco, Fernandez et al. 2007; Brooks 2009), ontogeny (Miriti 2006; Schiffers and Tielborger 2006; Valiente-Banuet and Verdu 2008), and spatial heterogeneity (Brooks 1999; Titus, Nowak et al. 2002; Sears and Chesson 2007) alter the competition/facilitation relationship both temporally and spatially, especially at small scales. Vegetation dynamics in southwestern deserts, such as the Mojave, are defined by a spatial aggregation of large perennials, such as *Larrea tridentata*, that can act as “nurse plants, ” facilitating annual species that benefit from an ameliorated aboveground environment as well as enriched soil resources (Fowler and Whitford 1996). Between shrubs, the interspaces are comparatively harsh and barren, with fewer soil resources and increased exposure (Brooks 1999; Titus, Nowak et al. 2002). Most research to date has compared plant communities between shrubs and interspaces, or studied the interactions between perennials and annuals. Very little research has explored the dynamics among ephemerals in the resource-poor interspaces.

Brassica tournefortii (Gouan) is a non-native annual forb native to the Middle East that was introduced to the western United States in the early 1900’s (Minnich and Sanders 2000). It invaded the Aeolian sand habitats of the Coachella Valley as early as 1927, and has since spread throughout much of the Mojave and Sonoran deserts (Minnich and Sanders 2000; McCasland 2005; Renz 2005; Trader, Brooks et al. 2006; Barrows, Allen et al. 2009). Although considered weedy, *B. tournefortii* was mostly disregarded as an invasive species of major ecological concern until major rain events in the 1980’s and 1990’s revealed the extent and dominance of the invasion (Minnich and Sanders 2000; Barrows, Allen et al. 2009). Because *B. tournefortii* has seldom been studied as an invasive species, little is known about its ecology or status in desert communities. In the Mojave and Colorado deserts, *B. tournefortii* is known to benefit from disturbance (Trader, Brooks et al. 2006; Brooks 2009), exhibits rapid phenology (Marushia, Ch. 1), produces ample seed (Trader, Brooks et al. 2006), and has broad seed germination requirements (Bangle, Walker et al. 2008). Ecologically, *B. tournefortii* has been shown to impact native annual reproduction and reduce abundance of sensitive fringe-toed lizards in threatened dune habitats (Barrows, Allen et al. 2009). However, nothing is known about the interactions of *B. tournefortii* with functionally similar ephemeral native annual forbs. Flowering forbs are considered one of the greatest ecological and cultural assets of southwestern deserts, and impacts on ephemeral native species by *B. tournefortii*, as well as other invasive annuals, are a major source of concern.

This research sought to characterize the interaction of *B. tournefortii* with a community of native annual forbs in the Mojave Desert, U.S.A. Because *B. tournefortii* shares a similar ecological niche as most desert ephemeral native plants, and because Barrows et al.(2009) found negative associations of *B. tournefortii* with native annual forbs in dunes, we hypothesized that increasing *B. tournefortii* density and/or cover would have a negative relationship with native annual forb richness, density, cover, and survival. Because the desert landscape is defined by resource-rich undershrub areas *vs.* resource-poor shrub interspaces, we limited our observations to the forb communities in the interspaces to separate the effects of precipitation as a soil water resource from the multiplied resource benefits in undershrub communities. Interactions were studied over the course of two contrasting years to study the relationship of resource availability to interactions between *B. tournefortii* and the native forb community.

Materials and Methods

Correlations between *B. tournefortii* density and success were compared with native density and success by sampling the density, diversity, growth, and phenology of annual vegetation at site in the central Mojave Desert. Research was conducted over two winter growing seasons, from November 2004 through April 2006. The site is located at 35.07.740 °N, 116.13.220 °W, near the Rasor Rd. exit on Interstate 15 in Riverside County in southeastern California. The site is a typical creosote scrub shrubland dominated by *Larrea tridentata* and annual species, including *B. tournefortii*. The site receives an annual average rainfall of ~15 cm/year in winter precipitation (Western Regional Climate Data Center 2009). The site is bordered on the eastern side by Rasor Rd., a little-used gravel access road, and on the north side by an alluvial wash. Temperature and precipitation data were recorded from the nearest national weather station at Baker, CA (Station # 40436). Data was downloaded from the Western Regional Climate Data Center at http://www.ncdc.noaa.gov. Where missing data occurred, data were supplemented with records from the next nearest city, Barstow, CA (Station # 40521). Temperatures were also recorded onsite in 2005-2006 with HOBO temperature recorders (Onset Computer Corporation, PO Box 3450, Pocasset, MA 02559-3450). Data from the HOBOS closely matched temperature records from Baker and Barstow weather stations.

Year 1, 2004-2005

In the first year the field site was sampled along 6 transects laid 30 m to 45 m apart parallel to Rasor Rd., placed to avoid off-road vehicle tracks and parallel to a steady gradient of disturbance with distance from the road. Each transect measured 30 m in length. A preliminary analysis of the annual community was conducted by using a line-transect intercept method on December 15, 2004. The results of the analysis showed that the annual plant community was patchy and dispersed (data not shown). To census the natural patterns of patches across the annual community, 10 plots measuring 0.5 m^2 were placed at regular 3 m intervals along each transect, producing 60 plots placed along a gradient of disturbance near and far from Rasor Rd. The nearest transect was placed ~10 m from the road edge in highly disturbed soil, while the furthest transect was ~300 m from the road in undisturbed shrubland. Although the regular plot placement did not avoid shrubs, only 7 plots ended up beneath shrubs. These 7 plots were excluded from analyses to keep results consistent for interspace vegetation. Density, cover, and richness of species were recorded for all 60 plots once per month from December 2004 to April 2005. Cover was visually estimated in year 1 using Daubenmire cover categories in an effort to keep data collection consistent and rapid across teams of workers with various levels of training. In year 2, however, lack of precision in the data prompted a switch to straight visual estimation without categories.

Initial species counts in December 2005 were analyzed and used to select 20 plots for analysis of phenology. Plots had a range of *B. tournefortii* densities but a relatively consistent total species density, such that initial densities of *B. tournefortii* varied independently of total density. The minimum total number of plants per plot was 50, the maximum was 128, and the average total number was 94.7 with a standard deviation of 22.4. The three native forbs with the highest densities in all 20 plots were chosen for phenology and growth measurements, including *Camissonia claviformis* (brown-eyed primrose), *Chaenactis stevioides* (desert pincushion), and *Cryptantha angustifolia* (popcorn flower). *Plantago ovata* (desert indianwheat), while plentiful, did not have a rosette growth form like the other native forbs and *B. tournefortii,* and was not chosen because it was less comparable. Ten individuals of each species were arbitrarily chosen within each plot and individually labeled with small color-coded flags. Growth was measured twice per month from January through April 2005 by recording two rosette widths and the height of each labeled plant. Life stages were also recorded, including vegetative rosette, flowering, seed set, dispersal, and/or senescence. *Camissonia claviformis* suffered massive, early mortality and was excluded from analyses. For *Cryptantha angustifolia,* bolting was equivalent to showing buds, and was very difficult to see given the size of the plants. Seed set in *C. angustifolia* either failed or was not apparent in most plants observed. Hence, only flowering was used as a measure of phenology for statistical tests. In addition, 2 of the 20 phenology subplots occurred under shrubs, and these were also excluded from final analyses.

Year 2, 2005-2006

Data analysis from year 1 revealed that, although initial densities of *B. tournefortii* were high in a small number of plots, most plots fell at the low end of *B. tournefortii* densities and the denser patches were not adequately represented. Also, nearly all *B. tournefortii* occurred in the disturbed areas nearer to the road. Therefore, the sampling design was modified in year 2. The number of transects was limited to 3, and all 3 were placed within 40 m of the road. Transects were 80 m long instead of 60, and a random stratified sampling design replaced the evenly-distanced sample plots. Using the line transect data from the previous year, density categories of 0-30, 30-60, 60-90, and 90-120 *B. tournefortii* plants were chosen before sampling. Transects were established and plots in each category were laid on November 11, 2005, immediately after the first flush of germination. The categories were randomly drawn before each plot was placed, and while walking along each transect the next suitable area with an estimation matching the required density category was used to set the plot. A total of 60 plots was placed along the 3 transects with a minimum of 1 m between them to minimize edge effects and disturbance. The same methods as in year 1 were again used to pick 20 plots for subsampling, and the same phenology and growth criteria were collected on the two successful species, *Chaenactis stevioides* and *Cryptantha angustifolia*. Fifteen soil samples were collected at 5 arbitrarily chosen sites next to plots across the sampled area on February 7 2006. Soils were analyzed for ammonium (NH_4), nitrate (NO_3), phosphorous (Olsen P), and particle size by the University of California Agriculture and Natural Resources Lab (Hoagland Annex, University of California, One Shields Avenue, Davis CA 95616-5270).

Data analysis

Data were analyzed by grouping the dataset into community data (species richness and cover of all species per plot) and phenology data (growth measurements and life stages for *B. tournefortii, Chaenactis stevioides*, and *Cryptantha angustifolia*). Community and phenology data were analyzed for each date of collection. Daubenmire cover data from year 1 was converted from categories to percent cover values by substituting the median value of each category. Height provided the most consistent fit for growth across species and was used instead of width or volume. Most density and cover data were skewed to low values in both years; therefore, both native species and *B.*

tournefortii data were log-transformed for normality and to detect trends in the data. Richness data were normally distributed and were not log-transformed. Growth data per species in each plot were averaged and log-transformed, then regressed on log-transformed *B. tournefortii* density and cover per plot. Phenology data was analyzed by averaging the number of sampled plants at each life stage per plot and regressed on the density and cover of *B. tournefortii* per plot. An α of 0.10 is shown for figures to show the changing nature of relationships over time.

Results

Site characteristics

The experimental site received more precipitation in 2005 than in 2006, and precipitation occurred at different times in the winter season, which in turn had strong effects on growth and interactions of annual species (Figure 2.1). According to records at nearby Baker, CA, the site received a total of about 222 mm of precipitation from October 2004 to July 2005 but received less than half as much, about 74 mm, in the same period in 2005-2006. The total for 2005 was twice the average precipitation of 102 mm for Baker, CA, but the total for 2006 was below average (National Climate Data Center 2009). Precipitation was plentiful throughout the growing season of January – March 2005 (Figure 2.1a), while the largest precipitation event in 2006 occurred in October 2005, and was supplemented by events in March and April after many annuals had senesced (Figure 2.1b). The average daily high temperature in 2005 was 24.2 C and was warmer in 2006 at 27.5 C. The average daily low temperatures were 9.9 C in 2005 and

8.6 C in 2006 (National Climate Data Center 2009). The winter of 2006 also had more days with higher temperatures than in 2005 (Figures 2.1a and 2.1b).

Soils were sandy, with an average of 13% (SD +/- 6.2) gravel (>20 mm particles). Soils contained an average of 1.1 (+/- 0.26) µg/g extractable N as ammonium, 0.8 (+/- 0.17) µg/g extractable N as nitrate, and 1.7 (+/- 0.18) µg/g extractable phosphorous. A total of 27 plant species was found in all interspace plots sampled in 2005 and 2006 (Table 2.1). Only two of the species were perennials (*Larrea tridentata* and *Atriplex confertiflora*), and these were infrequent. *Brassica tournefortii* and *Schismus* spp. were the only non-native species (Table 2.1). All native annuals identified are considered common in the Mojave Desert, although not all species found could be identified to the species level due to early mortality.

Annual community responses to Brassica tournefortii:

Densities of both native and non-native annuals were comparable overall in 2005 and 2006, ranging from 0 plants up to 300 plants for natives or *B. tournefortii* in plots (Figure 2.2). However, differences in sampling designs in 2005 and 2006 resulted in different distributions of density in plots among native annuals *vs.* non-native *B. tournefortii*. In 2005, the regular plot spacing design produced a relatively even sample of native annual densities throughout the growing season but sampled plots with lower densities of *B. tournefortii* (Figures 2.2a and 2.2b). The resulting skew in the *B. tournefortii* data prompted the change to a random stratified sampling design in 2006. This design sampled natives evenly early in the season, but drought-induced mortality created a skew to low-density plots for natives late in the season (Figure 2.2c). The new sampling design produced a more even distribution of *B. tournefortii* densities across plots, with some skew to low densities occurring only late in the season (Figure 2.2d).

Annual plant cover was higher overall in 2005 than in 2006 (Figure 2.3). Total cover of native plants in plots was as high as 60 – 70% in 2005, especially early in the season, but most plots had a total native cover of 10 – 40% (Figure 2.3a). *B. tournefortii* cover in 2005 was 0 – 30% in most plots, but a few plots had as much as 50% cover by the end of the season (Figure 2.3b). In contrast, most plots had comparatively low cover of natives in 2006, with less than 10% native cover in most plots during February and March (Figure 2.3c). *B. tournefortii* plots were similar to natives in cover distribution in 2006 (Figure 2.3d).

Richness was greater in plots overall in 2005 than in 2006 (Figure 2.4). The majority of plots in 2005 had between 4 and 7 species total, which was maintained late in the season (Figure 2.4a). In 2006 plots usually had between 1 and 5 species, and the number of species declined in many plots as the season progressed (Figure 2.4b). Although 27 species in total were found over two years (Table 2.1), the maximum richness in individual plots was about 10 species for 2005 and 2006 (Figure 2.4).

The total density of native plants declined with increasing *B. tournefortii* density in 2005, but increased in 2006 (Figure 2.5, Tables 2.2 and 2.3). The correlations were significant at $\alpha = 0.05$ in January and February in 2005 (Figure 2.5a, Table 2.2) and from January to March in 2006 (Figures 2.5b, Table 2.3). The average number of native plants per plot followed the same trend, showing a negative relationship with *B. tournefortii* density in January and February in 2005 (Figure 2.5c, Table 2.2), and a positive relationship from January to March in 2006 (Figure 2.5d, Table 2.3). Correlations were consistently stronger in 2006 than in 2005 (Tables 2.2 and 2.3). Richness was not correlated with *B. tournefortii* cover in 2005 (data not shown), but was positively correlated with *B. tournefortii* density in January 2006 and with both density and cover of *B. tournefortii* in February and March 2006 (Table 2.3).

The total and average per species cover of native plants were positively correlated with *B. tournefortii* cover in both 2005 and 2006 (Figure 2.6, Table 2.2). Positive correlations in total cover occurred only in February and March in 2005 (Figure 2.6a, Table 2.2), but throughout the season in 2006 (Figure 2.6b, Table 2.3). Average cover of native plants per species also increased with *B. tournefortii* cover, but only in March 2005 (Figure 2.6c, Table 2.2) while it consistently increased with *B. tournefortii* cover in 2006 (Figure 2.6d, Table 2.3). In fact, strong, positive correlations of native density and cover with *B. tournefortii* density and cover occurred in December and April of 2006, as well (data not shown). The weaker correlations of native cover with *B. tournefortii* cover in 2005 are likely the product of the Daubenmire cover categories used to collect cover data in 2005 rather than an ecological trend. Cover categories included more error than estimation methods and concealed trends in the data. Therefore, cover data from 2005 should be interpreted cautiously, while cover data from 2006 probably more accurately reflected actual cover since values were estimated more precisely.

Native species responses to Brassica tournefortii:

Chaenactis stevioides and *Cryptantha angustifolia* responded differently to *B. tournefortii* in both 2005 and 2006 (Figures 2.7 and 2.8, Tables 2.2 and 2.3). *C. stevioides* density had a consistently positive relationship with *B. tournefortii* density in both 2005 and 2006 (Figures 2.7a, 2.7b, Tables 2.2 and 2.3). *C. angustifolia* density, in contrast, had a negative relationship with *B. tournefortii* density in January and February of 2005 and no relationship with *B. tournefortii* density in 2006 (Figures 2.7c and 2.7d, Tables 2.2 and 2.3). *Chaenactis stevioides* had lower densities than *C. angustifolia* in many plots in 2005, but the two species were comparable in 2006 (Figure 2.7).

As with density, positive correlations were consistent for *C. stevioides* cover with *B. tournefortii* cover in February of 2005 and throughout the growing season in 2006 (Figures 2.8a and 2.8b, Tables 2.2 and 2.3). Unlike density, however, cover of *C. angustifolia* was also positively correlated with *B. tournefortii* cover in February 2005 and both January and February 2006 (Figures 2.8c and 2.8d, Tables 2.2 and 2.3). Cover values for both *C. stevioides* and *C. angustifolia* were generally less than 5% even in the wet year, 2005. Cover values were even lower for *C. angustifolia* in 2006, while *C. stevioides* maintained cover similar to 2005 in 2006 (Figure 2.8). *C. stevioides* growth was always positively correlated with *B. tournefortii* when responses occurred. *C. angustifolia* growth had strong, positive growth correlations with *B. tournefortii* in 2005, but weak negative correlations with *B. tournefortii* density and cover in February and March of 2006.

B. tournefortii density, cover, growth and reproduction consistently showed conspecific positive correlations with density and cover in 2005 and 2006 (Tables 2.2 and 2.3). The one exception was number of flowering plants in February 2005, since most plants had flowered earlier in December or January (Tables 2.2 and 2.3). Mortality of *B.*

tournefortii was not correlated with conspecific density or cover in 2005 (data not shown), but was negatively correlated in 2006, since plants in higher *B. tournefortii* density and cover areas experienced a lower rate of mortality than those in areas with less *B. tournefortii* (Tables 2.2 and 2.3).

Survival and phenology of *B. tournefortii*, *C. angustifolia*, and *C. stevioides* differed between species and years (Figure 2.9). In general, *B. tournefortii* was taller than either native species (Figures 2.9a and 2.9b), bolted sooner and/or more successfully than either native species (Figures 2.9c and 2.9d), and reproduced more successfully than either native species (Figures 2.9e, 2.9f, 2.9g, 2.9h) in both years. Finally, *B. tournefortii* survived longer than either native species in 2005 and 2006 (Figures 2.9i and 2.9j). In 2005, *C. stevioides* was taller than *C. angustifolia* (Figure 2.9a) and the more successful of the two native species in terms of bolting and senescence (Figures 2.9c and 2.9i) in 2005. *C. stevioides* also survived longer and flowered later than either *B. tournefortii* or *C. angustifolia* in the wet year, 2005 (Figures 2.9e and 2.9i), and in fact survived and flowered a month after most other native annuals had senesced (data not shown). However, *C. stevioides* and *C. angustifolia* had similarly low reproductive success and early mortality in the dry year, 2006 (Figures 2.9f, 2.9h, and 2.9j).

Discussion

Research on interactions within annual plant communities in arid environments is scarce, especially in the context of plant invasions. The literature on these systems focuses largely on the influences of nurse plants, particularly shrubs (Fowler and Whitford 1996; Brooks 1999; Brittingham and Walker 2000; Flores and Jurado 2003;

Thompson, Walker et al. 2005), while less attention has been paid to plant interactions outside shrub canopies. Soil resources are generally higher beneath shrubs compared to interspaces, making the latter less amenable to plant invasions (Brooks 1999). Exotic annual invasions between shrubs, however, have created a continuous fine fuel layer that carries fire across desert communities that are ill-adapted to recover (Brooks 2002; Brooks and Matchett 2006; Steers 2008). Here, we studied the interactions of a non-native annual forb with native ephemeral plants in a low-resource, high stress microenvironment (shrub interspaces) within a low-resource, high-stress ecosystem (the Mojave Desert). We observed positive correlations between *B. tournefortii* presence and native annual success during a dry year (2006), but many negative correlations with native annual success during a wet year (2005). Thus, precipitation and resulting soil moisture are large-scale drivers of both non-native and native annual success (Beatley 1966), but may also determine the biotic interactions that occur in marginal interspace microsites.

Both non-native and native annuals may preferentially grow in beneficial microsites or patches (Guo 1998; Titus, Nowak et al. 2002) with higher organic matter, improved soil water retention, and/or greater soil nutrients, which can result from abiotic soil patterns or from biotic influences such as prior shrub growth or human and animal disturbances (Guo 1998; Brooks 1999; Titus, Nowak et al. 2002). We attempted to control for differences in soil resources by limiting the sampling area to interspaces and avoiding any obvious disturbances or irregularities. However, the positive correlations in this research may have resulted from unrecognized microsite benefits within interspaces that were common to both non-natives and natives, such as higher productivity in washlet compared to hummock micro-topography (Brooks 1999). A similar positive relationship between an non-native species, *Bromus rubens*, and native annuals was observed by Beatley (1966), who hypothesized that *B. rubens* might invade sites that were optimal for natives. However, absence of *B. rubens* was not correlated either positively or negatively with native annuals, and Beatley concluded that distribution patterns of both *Bromus* and natives were driven by soil moisture (1966). In that case competition between species would be outweighed by the benefits of microsites with more soil water and/or nutrients.

If years and microsites with enhanced growing conditions benefited all annuals, one would expect both the annual community as a whole as well as individual species to show positive responses. In our results, however, this was not the case. The native annual community was negatively correlated with *B. tournefortii* density when soil water was plentiful in 2005, yet within species, *Chaenactis stevioides* (hereafter *Chaenactis*) was always positively correlated with *B. tournefortii* regardless of precipitation. In contrast, *Cryptantha angustifolia* (hereafter *Cryptantha*) had different responses both within and between years. In the wet year, *Cryptantha* density was reduced with increasing *B. tournefortii*, yet plants were consistently taller and flowered more with high *B. tournefortii* density late in the season (February). *B. tournefortii* density and cover also reduced *Cryptantha* mortality late in the season. Many of the relationships were opposite in a dry year; *Cryptantha* had higher densities and cover, but were smaller and experienced increased mortality in February. Although *B. tournefortii* may invade the same optimal microsites that benefit native annuals, our data suggest that *B. tournefortii* also has complex biotic interactions with native annuals based on resource stress level.

Research on the relationships of non-native and native species in most ecosystems has focused primarily on competition and negative impacts, while positive relationships between non-natives and natives are seldom addressed (Rodriguez 2006). In desert ecosystems, the interplay of positive and negative interactions between perennials as benefactors and annuals as beneficiaries has often been studied (Holzapfel and Mahall 1999; Tielborger and Kadmon 2000; Flores and Jurado 2003; Weedon and Facelli 2008). It is now commonly accepted that facilitation is one of the primary ecological forces driving patterns of community structure and function in high-stress environments (Lortie and Callaway 2006; Callaway 2007; Brooker, Maestre et al. 2008; Eranen and Kozlov 2008; Maestre, Callaway et al. 2009). Positive relationships are globally observed in arid or desert regions (Holmgren, Scheffer et al. 1997; Tielborger and Kadmon 2000; Tewksbury and Lloyd 2001), and throughout the Mojave Desert, as well (Brittingham and Walker 2000; Miriti 2006), but relationships change under differing resource regimes (Weedon and Facelli 2008). *Larrea tridentata* and other perennial shrubs likely facilitate the invasion of *B. tournefortii* underneath shrubs (Flores and Jurado 2003), but relationships between *B. tournefortii* and native annuals in shrub interspaces have not been addressed.

Because impacts by *B. tournefortii* have been shown in previous research, we expected that biotic interactions would dominate the relationships between non-native and native species. We hypothesized that *B. tournefortii* would show characteristics that could confer competitive advantages over native species, and as *B. tournefortii* density and/or cover increased it would have increasingly negative effects on native annuals. Data from this research demonstrated that *B. tournefortii* was larger and faster growing than native annuals, usurping resources early in the season. *B. tournefortii* also had a higher fecundity in both high and low precipitation years than either *Chaenactis* or *Cryptantha*. In fact, *B. tournefortii* managed to set seed in the drier year when both the native species failed even to flower. These characteristics make *B. tournefortii* more likely to build a seedbank and spread even in years with very little precipitation. *B. tournefortii* also had a higher rate of survivorship in both years, similar to Beatley's observations of *Bromus rubens,* another non-native annual species that has impacted southwestern deserts (1966). However, the ease at which *B. tournefortii* germinates (Bangle et al. 2008) can also be a weakness. The implications of this was observed in the southern Mojave Desert during a year when rainfall sufficient for germination did not occur until February, *B. tournefortii* geminated and emerged in large numbers during the subsequent weeks, but then most plants died before setting seed the following month because there was no followup rainfall and hot windy conditions became prevalent (M. Brooks pers. obs.)

However, our hypothesis that *B. tournefortii* would have negative impacts on the ephemeral desert community was not consistently supported by the data. Many correlations between natives and *B. tournefortii* density and cover were positive, although the strength and timing of these correlations differed in years with different precipitation, and therefore soil water availability. Relationships were consistently positive in a low precipitation year (2006), but native density was lower with increasing *B. tournefortii* in a high precipitation year (2005). Interestingly, the relationship of native cover to *B. tournefortii* density and cover was positive in the same wet year, but only late in the season when native cover increased as their density decreased. This suggests that high densities of *B. tournefortii* suppressed native germination, or that native seedlings experienced greater mortality early in the season.

Many desert annual species in the southwestern U.S. are known to have density-dependent germination, with greater seedling numbers suppressing native germination (Inouye 1980; Tielborger and Valleriani 2005). This phenomenon could be one of the largest yet most overlooked impacts of invasive species in deserts. As the number of *B. tournefortii* seedlings increases, fewer native plants may germinate even when the native seedbank is present and healthy. However, this effect may only be important during high precipitation years since we did not find a similar negative correlation in annual plant community density during a dry year. Interference competition has been shown to strongly regulate similar desert annual communities at the seedling establishment stage in Israel (Goldberg, Turkington et al. 2001). In the Mojave Desert, *Bromus rubens* acquires resources more rapidly than two native annual species and has the potential to outcompete native seedlings (DeFalco, Bryla et al. 2003). *B. tournefortii* exhibits a similarly rapid phenology (Marushia, Ch.1) and may impact desert native annual seedlings through similar processes.

Although native densities decreased with *B. tournefortii* density and cover in a wet year, those plants that survived were larger in dense than in sparse populations of *B.*

tournefortii. This change in relationship is similar to other ontogenetic shifts that occur between competition and facilitation (Miriti 2006; Schiffers and Tielborger 2006). For example, in the Colorado Desert in southern California, adult shrubs facilitate juveniles whereas adults are competitively constrained by one another (Miriti 2006). In desert annuals however, the effect is opposite; *B. tournefortii* appears to suppress natives at a seedling or juvenile stage during high precipitation years, but those natives that survive are facilitated or experience lower competition later. This contrasts to findings in Israel where native annuals facilitated each other as seedlings but competition increased in adults (Schiffers and Tielborger 2006).

There was no inverse conspecific effect of density and cover found for *B. tournefortii*. Instead, *B. tournefortii* appeared to facilitate itself in that higher densities had lower individual mortality and higher numbers of plants bolting, flowering, and setting seed. The conspecific facilitation was especially strong late in the season during the dry year (2006). Invasion facilitation by a species for its own has been a popular subject of study in recent years (Conway, Smith et al. 2002; Jordan, Larson et al. 2008), as has the facilitation of other non-native species by invasives (Simberloff 2006). In *B. tournefortii*, such self-facilitation during drought may improve its ability to reproduce even under stress. *B. tournefortii* has broad germination requirements and little observed dormancy (Bangle, Walker et al. 2008), and self-facilitation could be an important mechanism to maintain and spread a viable seedbank during drought years that might otherwise cause a population crash (DeFalco, Bryla et al. 2003; Simberloff and Gibbons 2004). Improved reproduction at higher densities has also been found in *Lesquerella* *fendleri*, a related annual mustard native to southwestern deserts (Roll, Mitchell et al. 1997).

A possible explanation for the observed positive correlations in the data is that native annuals and *B. tournefortii* may facilitate each other under moderate drought or average rainfall, but compete when resources are plentiful (e.g. Briones, Montana et al. 1998; Brooks 2000). This is in agreement with current theory on the balance of competition and facilitation in many ecosystems; when resources are plentiful, plants compete, but as the habitat becomes more stressful, plants facilitate each other (Bertness and Callaway 1994; Callaway and Walker 1997; Choler, Michalet et al. 2001; Maestre, Callaway et al. 2009). Maestre et al. (2009) built a predictive framework for the expected direction of interaction depending on resource stress level. With annuals defined as "competitive" species, interactions between competitive species as both facilitators and beneficiaries are expected to be negative at high and low stress levels, and positive only at medium levels (Maestre, Callaway et al. 2009). In this case, we might categorize *B. tournefortii* and native species as all competitive species but *B. tournefortii* as a more successful competitor. Our data agree with the hypothesized relationships in that the native annual community had a negative density relationship with *B. tournefortii* in 2005, which was undoubtedly a low-stress year in terms of precipitation. However, when individual species were studied, responses varied between species and between the factors measured within species. The year 2006 could be characterized as a medium to high stress year based on precipitation, and nearly all relationships were positive.

It would be erroneous to interpret our data to mean that *B. tournefortii* benefits the native annual community. *B. tournefortii* exhibits several biological and phenological characteristics such as large size, high survivorship, and consistent fecundity that suggest that it could become an increasingly dominant member of desert annual communities. Even in a drought year when native plants and *B. tournefortii* were positively correlated, removal of *B. tournefortii* might have resulted in comparatively greater native success. Future work should measure the relative success of native annual forbs with and without *B. tournefortii* at increasing densities under different resource levels to determine the tradeoffs between competition and facilitation and the critical density for *B. tournefortii* impacts, if it exists.

Precipitation varies widely in the Mojave desert (Hereford, Webb et al. 2006), and large precipitation events represent rare opportunities for native annual fecundity (Bowers 1987; Bowers 2005). *B. tournefortii* also experiences population explosions during wet years and has especially high fecundity under moist conditions, posing an especial threat for further invasion (Bangle, Walker et al. 2008; Barrows, Allen et al. 2009). Competition during these highly productive years may disproportionately reduce the native seedbank if more native seeds germinate than are replaced by native seedbank additions (Barrows, Allen et al. 2009). Management of *B. tournefortii* in desert ecosystems should involve major *B. tournefortii* removal efforts in high-precipitation years, especially in areas with sensitive annual forbs. Similar recommendations have been made for *Bromus rubens* (Salo 2004), providing opportunities to control more than one invasion simultaneously. However, because *B. tournefortii* exhibits the ability to set more seed than native species even under drought conditions, populations are likely to increase more than natives. In years with average or below-average precipitation, management should focus on satellite populations or population edges to prevent reproduction and spread of this species from invasion foci.

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Figure Legends

Figure 2.1: Maximum daily temperature, minimum daily temperature, and precipitation from October 1 to July 1 in a) 2004-2005 and b) 2005-2006.

Figure 2.2: Histograms of native plant density and *Brassica tournefortii* density in plots during January, February, and March of a,b) 2005 and c,d) 2006.

Figure 2.3: Histograms of native plant cover and *Brassica tournefortii* cover in plots during January, February, and March of a,b) 2005 and c,d) 2006

Figure 2.4: Histograms of species richness in plots during January, February, and March of a) 2005 and b) 2006

Figure 2.5: Total and average density of native plants in plots *vs.* density of *Brassica tournefortii* in January, February, and March 2005 and 2006. Regressions are shown only if $P < 0.10$ in log-transformed analyses as shown in Tables 2 and 3. Axes are drawn on untransformed scale for presentation; therefore, regressions shown are not those that produced the R^2 and P values in Tables 2 and 3. a) Total native density *vs. B. tournefortii* density, 2005, b) total native density *vs. B. tournefortii* density, 2006, c) average density per native species *vs. B. tournefortii* density, 2005, d) average density per native species *vs. B. tournefortii* density, 2006.

Figure 2.6: Total and average cover of native species in plots *vs.* cover of *Brassica tournefortii* in January, February, and March 2005 and 2006. Regressions are shown only if $P < 0.10$ in log-transformed analyses as shown in Tables 2 and 3. Axes are drawn on untransformed scale for presentation; therefore, regressions shown are not those that

produced the R^2 and P values in Tables 2 and 3. Axes here are absolute values provided to show original data; therefore regressions shown are not those that produced the R^2 and P values in Table 2 and 3. a) Total native cover *vs. B. tournefortii* cover, 2005, b) total native cover *vs. B. tournefortii* cover, 2006, c) average cover per native species *vs. B. tournefortii* cover, 2005, d) average cover per native species *vs. B. tournefortii* cover, 2006.

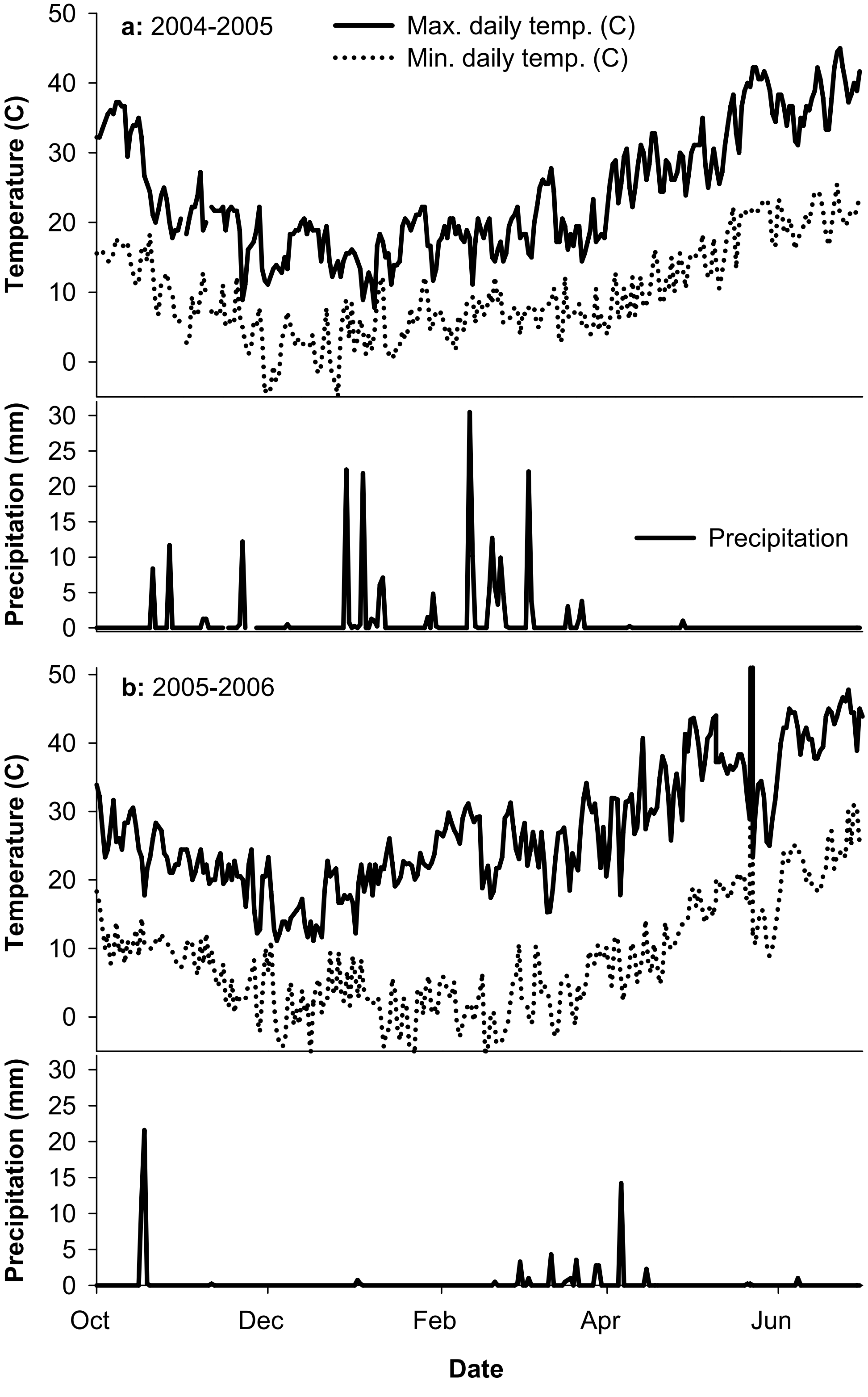
Figure 2.7: Density of *Chaenactis stevioides* and *Cryptantha angustifolia vs.* density of *Brassica tournefortii* in January, February, and March in 2005 and 2006 in a subsample of 20 plots. Regressions are shown only if $P < 0.10$ in log-transformed analyses as shown in Tables 2 and 3. Axes are drawn on untransformed scale for presentation; therefore, regressions shown are not those that produced the data in Tables 2 and 3.Axes here are absolute values provided to show original data; therefore regressions shown are not those that produced the R^2 and P values in Tables 2 and 3. a) *C. stevioides* density *vs. B. tournefortii* density, 2005, b) *C. stevioides* density *vs. B. tournefortii* density, 2006, c) *C. angustifolia* density per native species *vs. B. tournefortii* density, 2005, d) *C. angustifolia* density per native species *vs. B. tournefortii* density, 2006.

Figure 2.8: Percent cover of *Chaenactis stevioides* and *Cryptantha angustifolia vs.*. cover of *Brassica tournefortii* in January, February, and March 2005 and 2006 in a subsample of 20 plots. Regressions are shown only if $P < 0.10$ in log-transformed analyses as shown in Tables 2 and 3. Axes are drawn on untransformed scale for presentation; therefore, regressions shown are not those that produced the R^2 and P values in Tables 2 and 3.Axes here are absolute values provided to show original data; therefore regressions shown are

not those that produced the R^2 and P values in Tables 2 and 3. a) *C. stevioides* cover *vs. B. tournefortii* cover, 2005, b) *C. stevioides* cover *vs. B. tournefortii* cover, 2006, c) *C. angustifolia* cover per native species *vs. B. tournefortii* cover, 2005, d) *C. angustifolia* cover per native species *vs. B. tournefortii* cover, 2006.

Figure 2.9: Phenology of *Brassica tournefortii, Cryptantha angustifolia,* and *Chaenactis stevioides* during a,c,e,g,i) 2005 and b,d,f,h,j) 2006. Bars represent standard error.

2.1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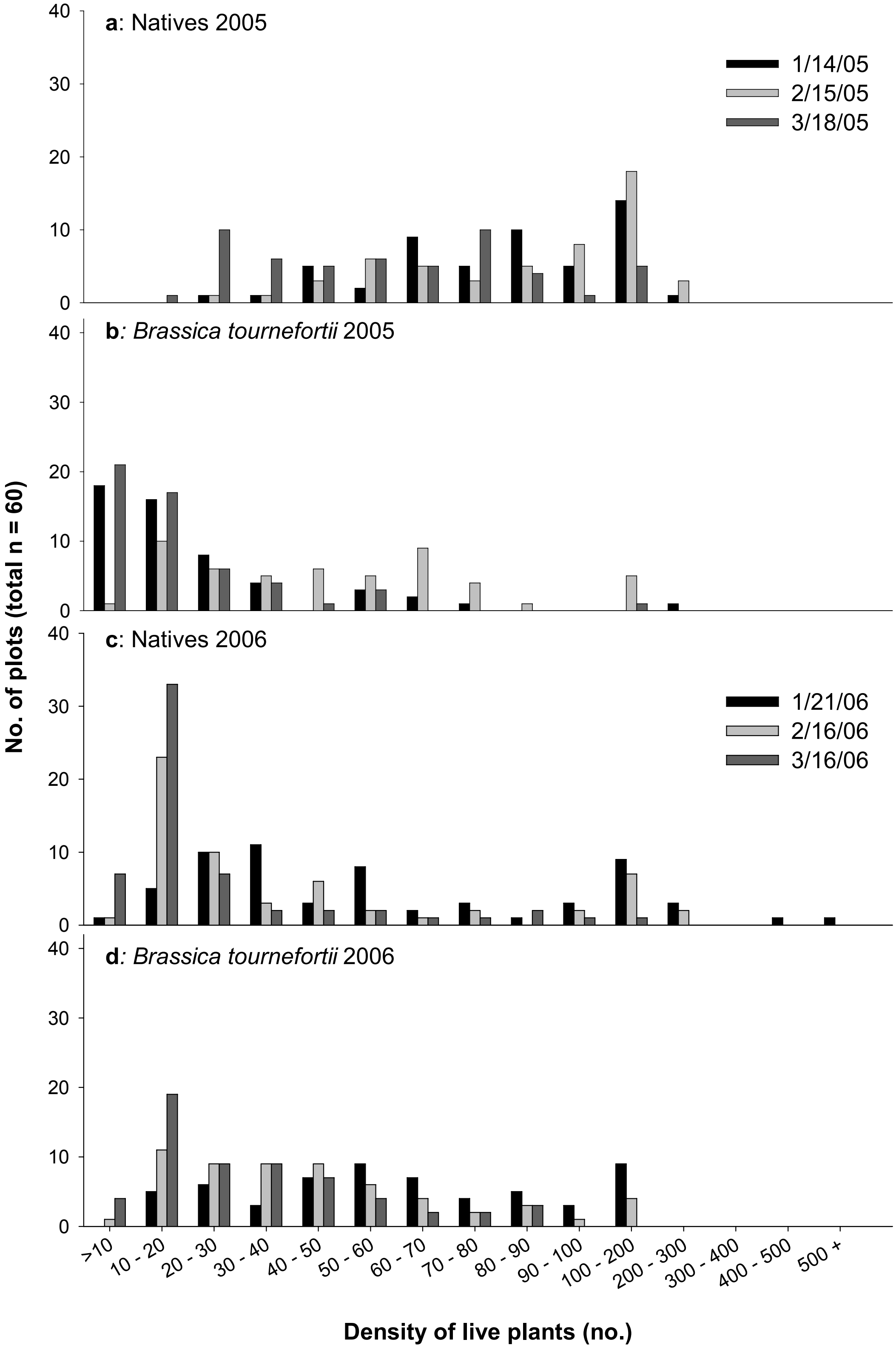
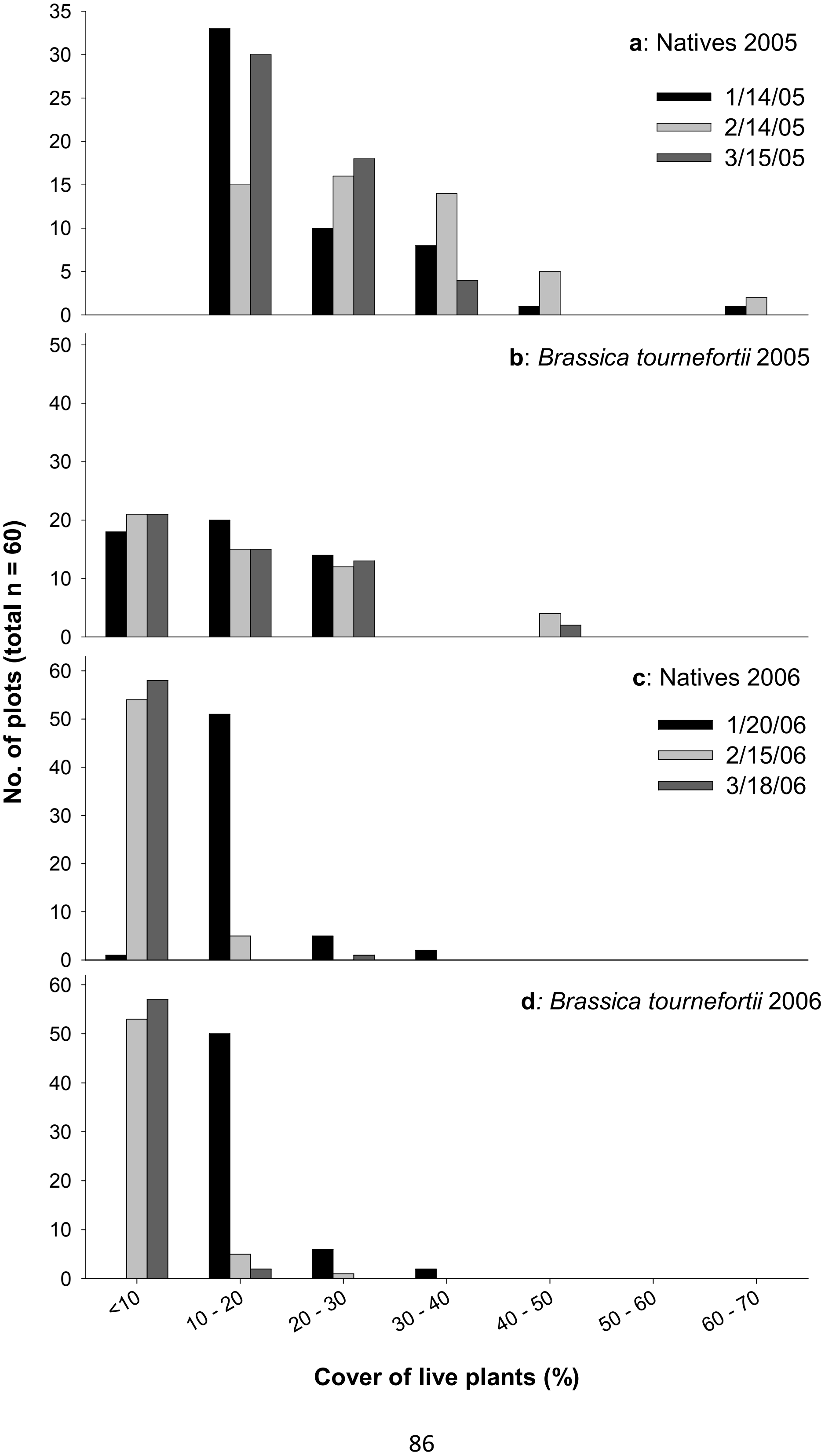
Max. daily temp. (C)
Min. daily temp. (C)
Temperature (C)
50
40
30
20
10
0
Precipitation (mm)
30
25
20
15
10
5
0
Precipitation
b: 2005-2006
Temperature (C)
Precipitation (mm)
Oct
Dec
Feb
Apr
Jun
Date

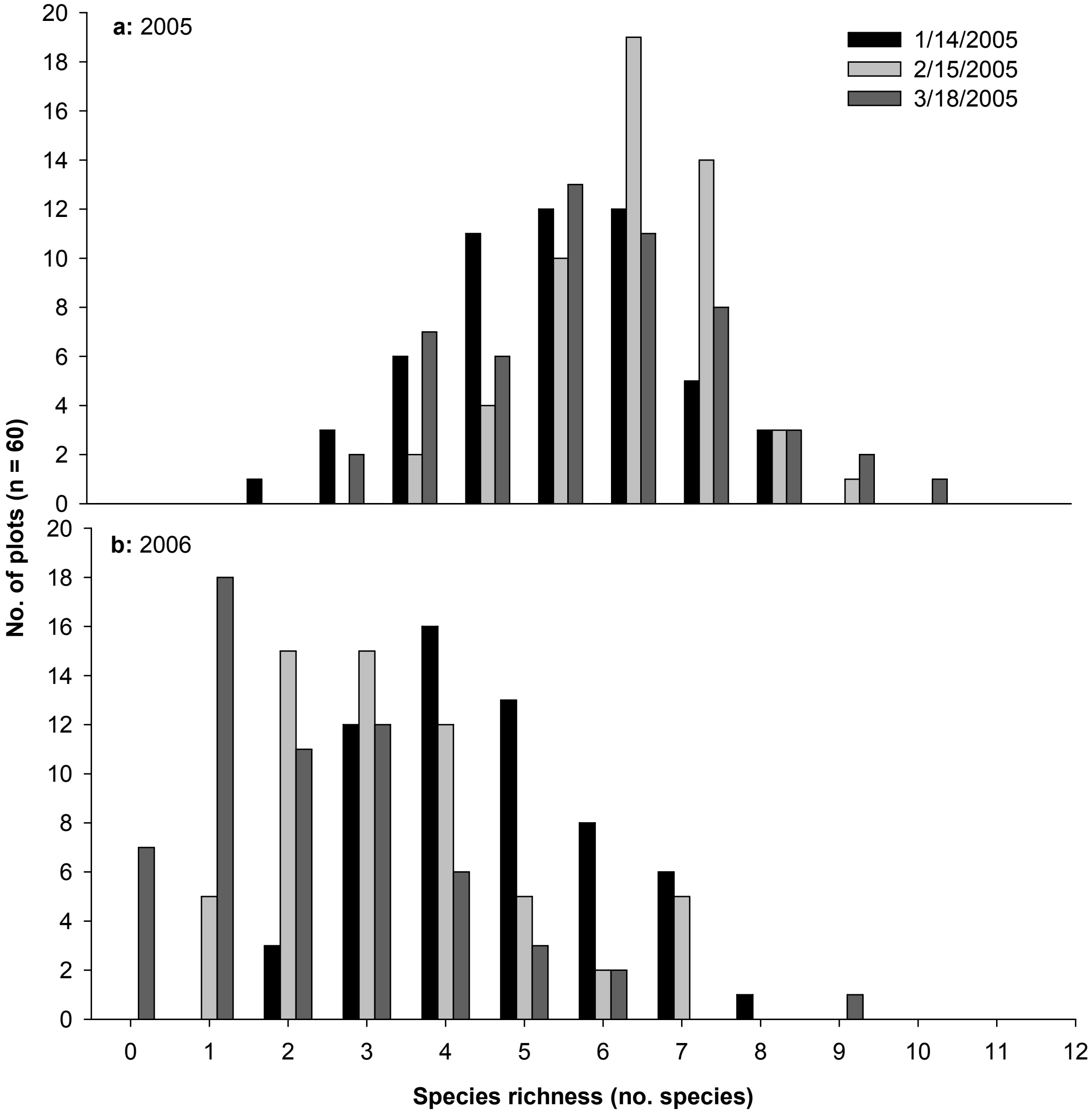
2.2


a: Natives 2005
1/14/05
2/15/05
3/18/05
b: Brassica tournefortii 2005
c: Natives 2006
1/21/06
2/16/06
3/16/06
d: Brassica tournefortii 2006
0
10
20
30
40
No. of plots (total n = 60)
>10
10 - 20
20 - 30
30 - 40
40 - 50
50 - 60
60 - 70
70 - 80
80 - 90
90 - 100
100 - 200
200 - 300
300 - 400
400 - 500
500 +
Density of live plants (no.)

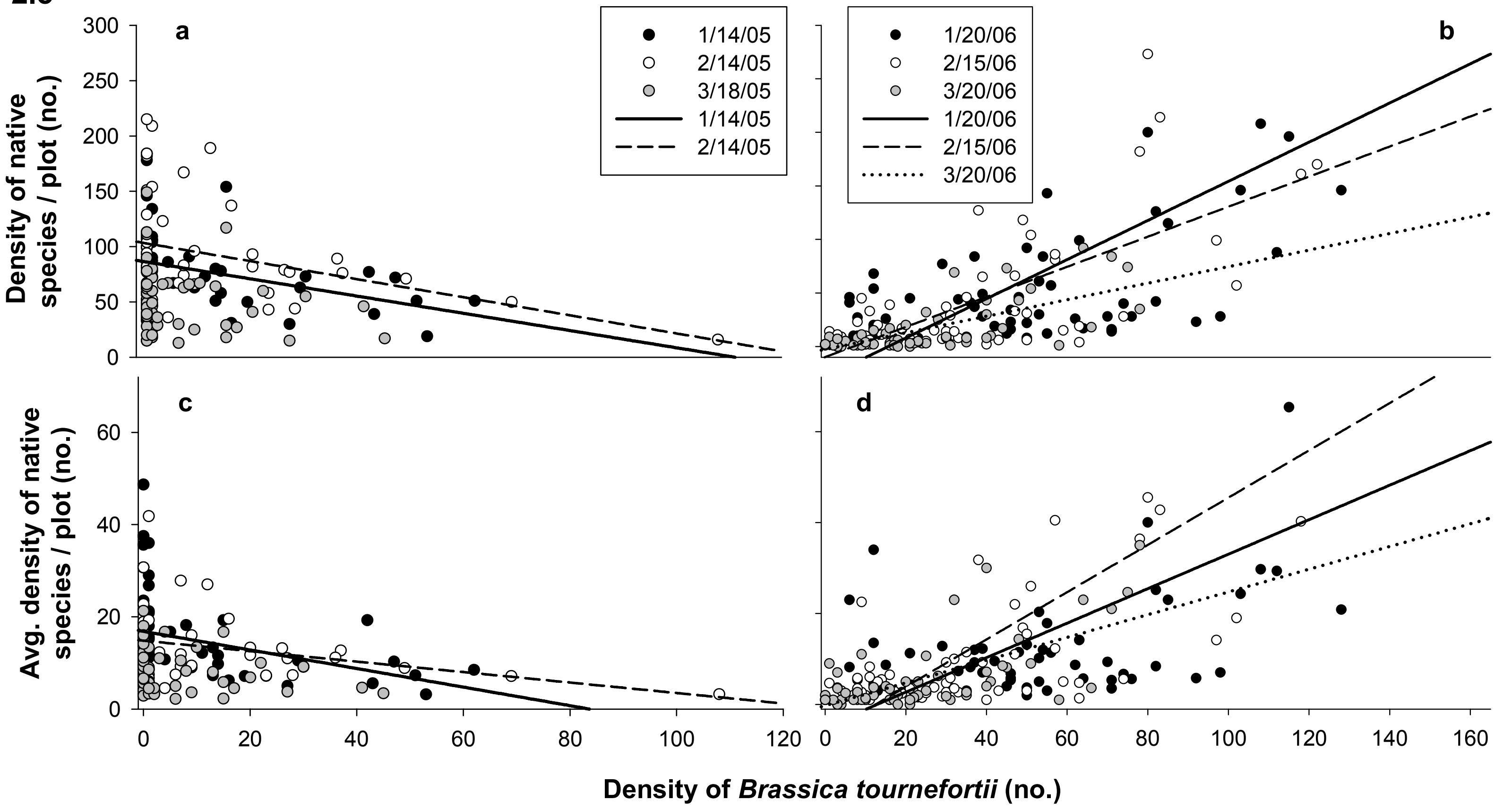
2.3


a: Natives 2005
1/14/05
2/14/05
3/15/05
b: Brassica tournefortii 2005
c: Natives 2006
1/20/06
2/15/06
3/18/06
d: Brassica tournefortii 2006
No. of plots (total n = 60)
Cover of live plants (%)
<10
10 - 20
20 - 30
30 - 40
40 - 50
50 - 60
60 - 70
0
5
10
15
20
25
30
35
40
50
60

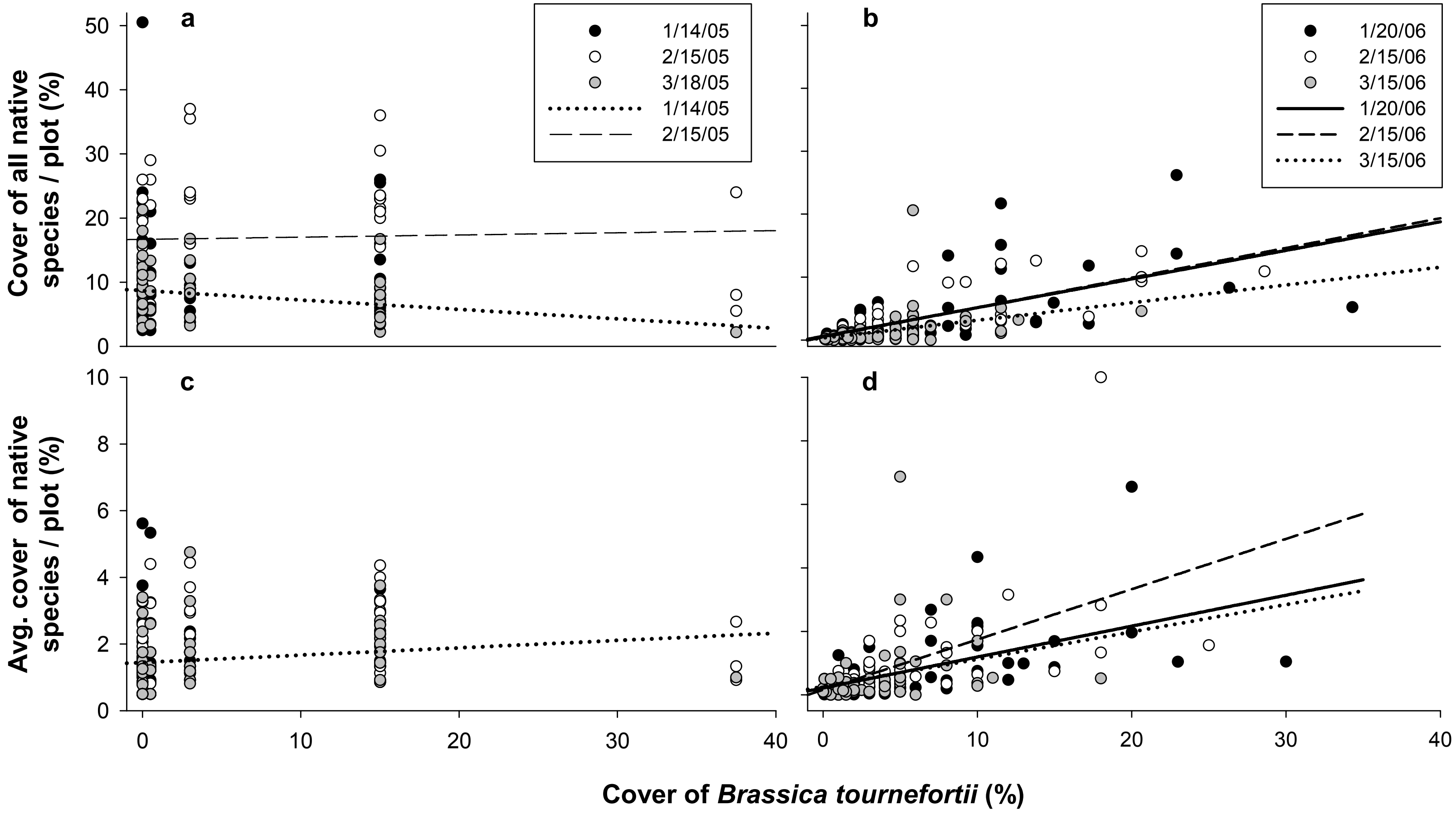
2.4


a: 2005
1/14/2005
2/15/2005
3/18/2005
b: 2006
No. of plots (n = 60)
0
2
4
6
8
10
12
14
16
18
20
0
1
2
3
4
5
6
7
8
9
10
11
12
Species richness (no. species)

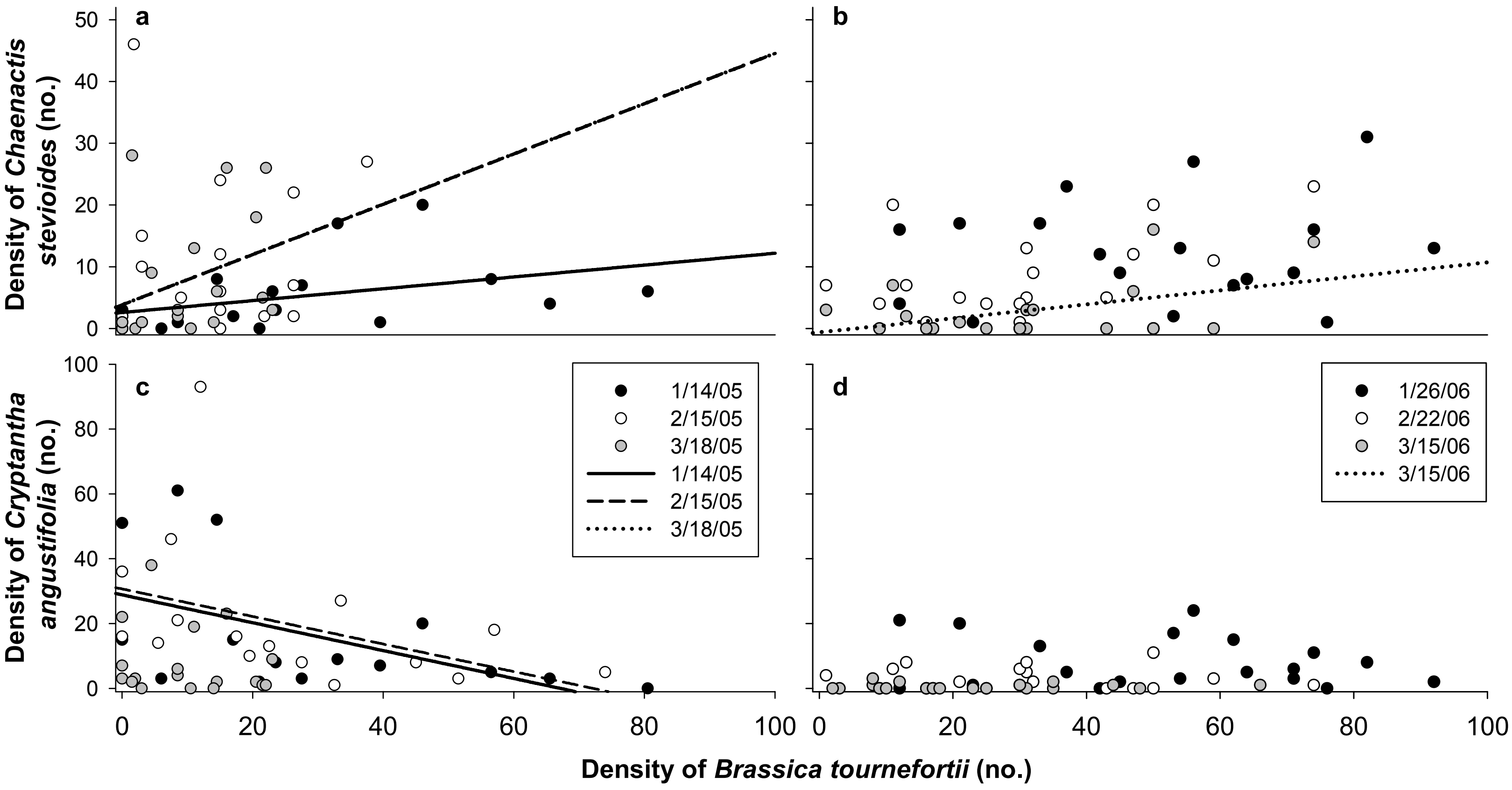
2.5


a
b
c
d
Density of native species / plot (no.)
Avg. density of native species / plot (no.)
Density of *Brassica tournefortii* (no.)
1/14/05
2/14/05
3/18/05
1/14/05
2/14/05
1/20/06
2/15/06
3/20/06
1/20/06
2/15/06
3/20/06
0
50
100
150
200
250
300
0
20
40
60
0
20
40
60
80
100
120
0
20
40
60
80
100
120
140
160

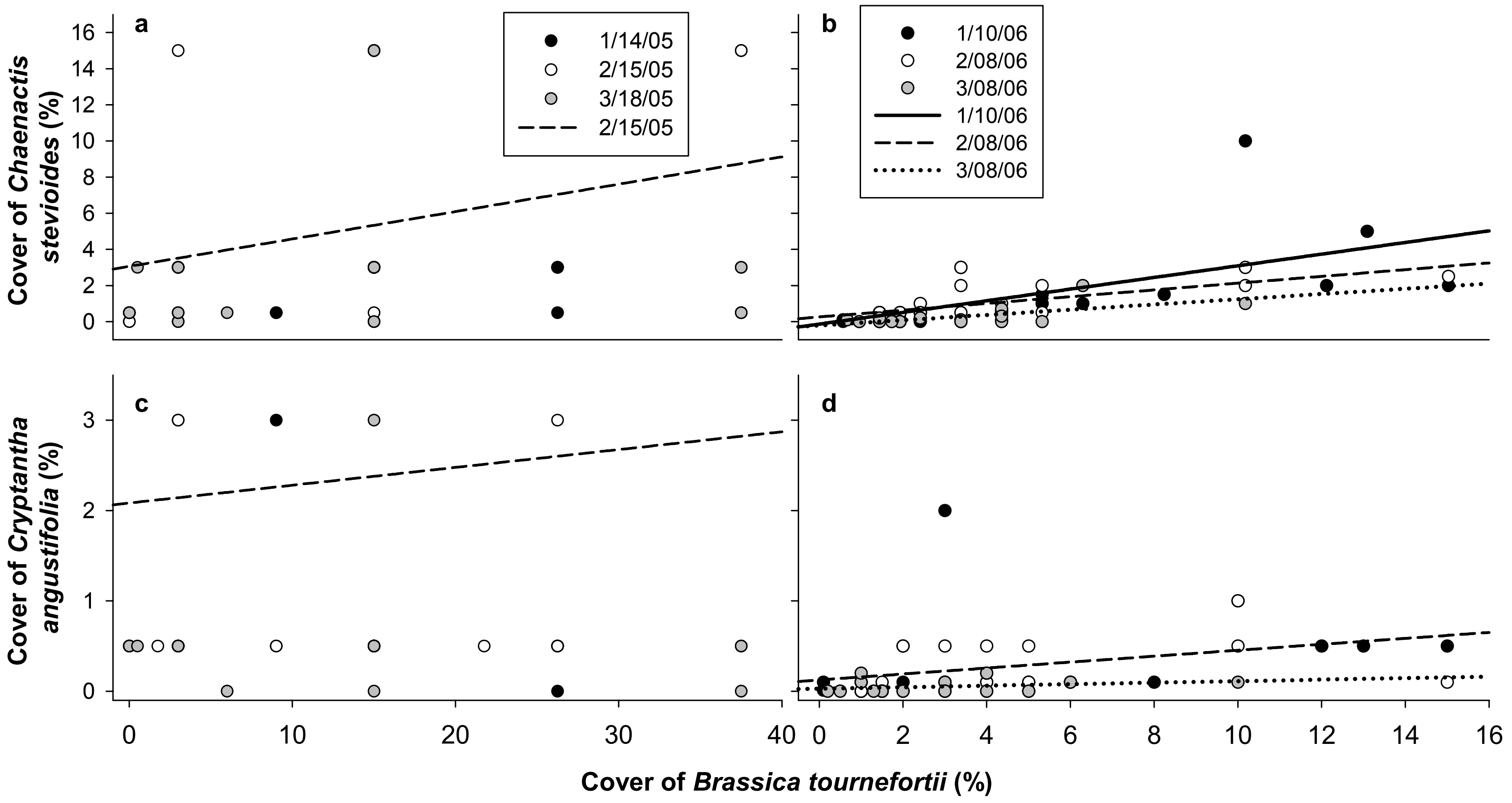
2.6


a
b
c
d
Cover of all native species / plot (%)
Avg. cover of native species / plot (%)
Cover of *Brassica tournefortii* (%)
0
10
20
30
40
50
0
2
4
6
8
10
0
10
20
30
40
1/14/05
2/15/05
3/18/05
1/14/05
2/15/05
1/20/06
2/15/06
3/15/06
1/20/06
2/15/06
3/15/06

2.7


a
b
c
d
Density of *Chaenactis stevioides* (no.)
Density of *Cryptantha angustifolia* (no.)
Density of *Brassica tournefortii* (no.)
0
10
20
30
40
50
0
20
40
60
80
100
● 1/14/05
○ 2/15/05
● 3/18/05
1/14/05
2/15/05
3/18/05
● 1/26/06
○ 2/22/06
● 3/15/06
3/15/06

2.8


a
b
c
d
1/14/05
2/15/05
3/18/05
2/15/05
1/10/06
2/08/06
3/08/06
1/10/06
2/08/06
3/08/06
Cover of *Chaenactis stevioides* (%)
Cover of *Cryptantha angustifolia* (%)
Cover of *Brassica tournefortii* (%)
0
2
4
6
8
10
12
14
16
0
1
2
3
0
10
20
30
40
0
2
4
6
8
10
12
14
16

2.9

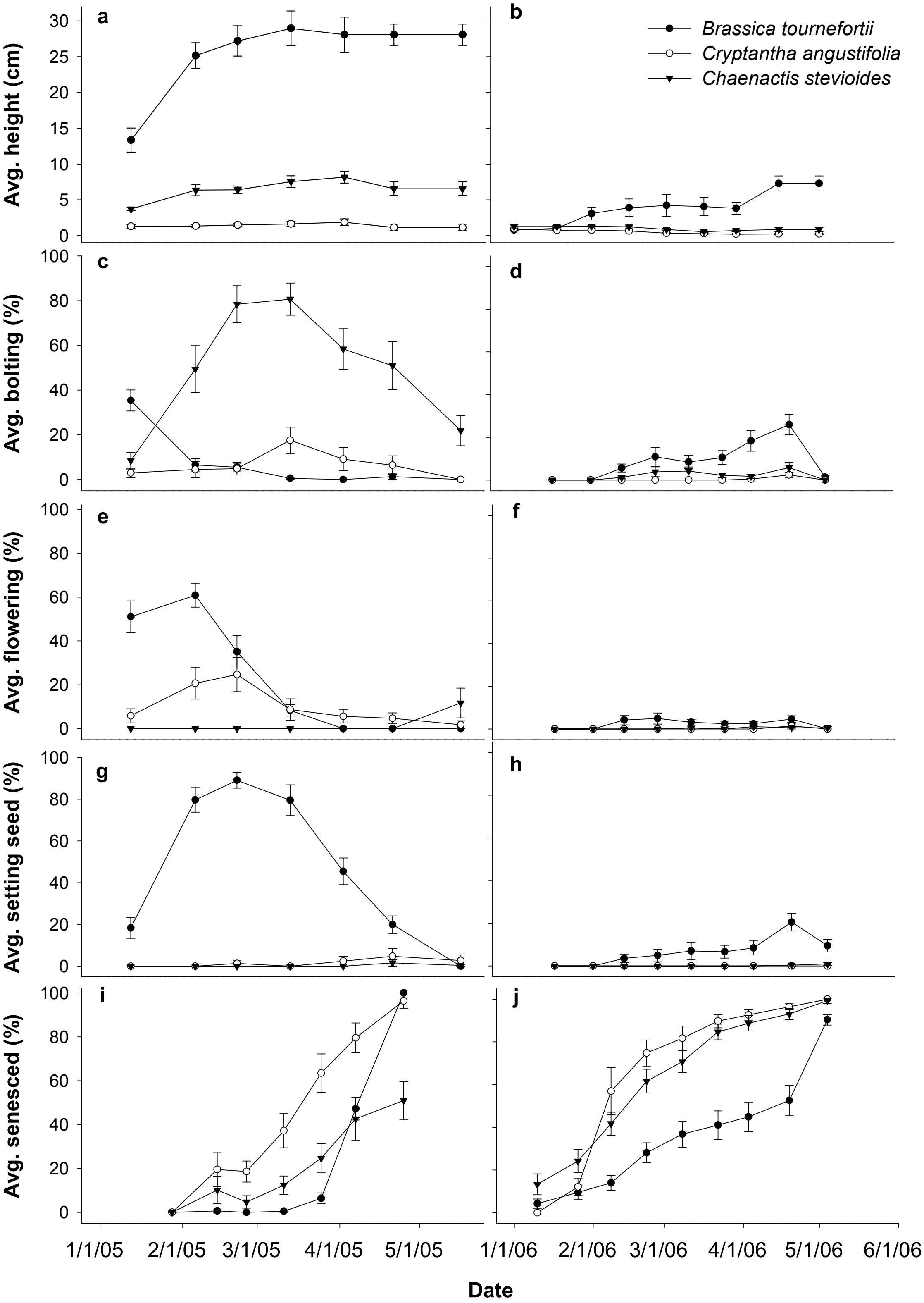

a
b
c
d
e
f
g
h
i
j
Brassica tournefortii
Cryptantha angustifolia
Chaenactis stevioides
Avg. height (cm)
0
5
10
15
20
25
30
Avg. bolting (%)
Avg. flowering (%)
Avg. setting seed (%)
Avg. senesced (%)
0
20
40
60
80
100
1/1/05
2/1/05
3/1/05
4/1/05
5/1/05
1/1/06
2/1/06
3/1/06
4/1/06
5/1/06
6/1/06
Date

Table 2.1: Species present in shrub interspaces at the study site in 2005 and 2006. Exotic species are in **bold**. Perennial species are underlined.

Species List
Abronia villosa
Achronychia cooperii
*Atriplex confertiflora**
Brassica tournefortii
Camissonia claviformis
*Chaenactis fremontii***
Chaenactis stevioides
Chorizanthe brevicornu
Cryptantha angustifolia
*Eriastrum diffusum**
Eriogonum spp.
Gilia spp.
Hesperocallis undulata
Larrea tridentata
Linanthus jonesii
Loeseliastrum schottii
*Lotus strigosus***
Malcothryx glabrata
Mentzelia spp.
*Nama dimissum**
Oenethera deltoides
Pectocarya spp.
Plantago ovata
Schismus spp.
Stephanomeria exigua
Streptanthella langirostris
*Tiquilia plicata***

* 2005 only
** 2006 only

Table 2.2: Correlations of *B. tournefortii, Chaenactis stevioides,* and *Cryptantha angustifolia* to *B. tournefortii* density and cover in 2005. Correlations less than α = 0.10 are reported. Correlations less than α = 0.05 are in **bold**. All values in all regressions were averages within plot by date. All values were log-transformed before regression.

	B. tournefortii																	
	January						**February**						**March**					
	Density			**Cover**			**Density**			**Cover**			**Density**			**Cover**		
	Sign	**R^2**	**P value**	**Sign**	**R^2**	**P value**	**Sign**	**R^2**	**P value**	**Sign**	**R^2**	**P value**	**Sign**	**R^2**	**P value**	**Sign**	**R^2**	**P value**
Total Native Density	**-** [*]	**0.12**	**0.014**	/ [**]	/	/	**-**	**0.09**	**0.035**	**-**	**0.11**	**0.022**	/	/	/	/	/	/
Avg. Native Density	**-**	**0.13**	**0.01**	/	/	/	-	0.06	0.095	**-**	**0.1**	**0.026**	/	/	/	/	/	/
Total Native Cover	/	/	/	/	/	/	/	/	/	+	0.06	0.082	+	0.08	0.053	**+**	**0.11**	**0.02**
Avg. Native Cover	/	/	/	/	/	/	/	/	/	/	/	/	**+**	**0.11**	**0.026**	**+**	**0.13**	**0.013**
B. tournefortii																		
Density	N/A [†]	N/A	N/A	**+**	**0.9**	**<0.001**	N/A	N/A	N/A	**+**	**0.77**	**<0.001**	N/A	N/A	N/A	**+**	**0.75**	**<0.001**
Cover	**+**	**0.85**	**<0.001**	N/A	N/A	N/A	**+**	**0.9**	**<0.001**	N/A	N/A	N/A	**+**	**0.75**	**<0.001**	N/A	N/A	N/A
Growth (Height)	/	/	/	/	/	/	**+**	**0.43**	**0.015**	**+**	**0.55**	**0.004**	**+**	**0.32**	**0.042**	**+**	**0.36**	**0.03**
# Bolting	**+**	**0.4**	**0.0052**	**+**	**0.2**	**0.025**	/	/	/	/	/	/	/	/	/	/	/	/
# Flowering	+	0.23	0.08	/	/	/	-	0.26	0.07	/	/	/	/	/	/	/	/	/
# Setting Seed	**+**	**0.42**	**0.012**	**+**	**0.4**	**0.018**	/	/	/	**+**	**0.39**	**0.023**	+	0.24	0.092	/	/	/
Chaenactis stevioides																		
Density	+	0.19	0.063	/	/	/	**+**	**0.3**	**0.0126**	+	0.17	0.085	**+**	**0.22**	**0.05**	/	/	/
Cover	**+**	**0.31**	**0.015**	/	/	/	**+**	**0.29**	**0.02**	**+**	**0.23**	**0.044**	**+**	**0.24**	**0.039**	/	/	/
Growth (Height)	**+**	**0.54**	**0.003**	**+**	**0.6**	**0.001**	**+**	**0.42**	**0.012**	**+**	**0.41**	**0.013**	+	0.21	0.083	/	/	/
# Bolting	/	/	/	/	/	/	**+**	**0.48**	**0.006**	/	/	/	**+**	**0.37**	**0.016**	/	/	/
# Dead	/	/	/	/	/	/	/	/	/	/	/	/	+	0.2	0.067	/	/	/
Cryptantha angustifolia																		
Density	**-**	**0.23**	**0.025**	-	0.2	0.087	-	0.18	0.0742	/	/	/	/	/	/	/	/	/
Cover	/	/	/	/	/	/	/	/	/	+	0.21	0.058	/	/	/	/	/	/
Growth (Height)	**+**	**0.34**	**0.034**	/	/	/	**+**	**0.56**	**0.012**	**+**	**0.67**	**0.004**	**+**	**0.72**	**0.004**	+	0.43	0.055
# Flowering	/	/	/	/	/	/	**+**	**0.45**	**0.035**	/	/	/	/	/	/	/	/	/
# Dead	/	/	/	/	/	/	/	/	/	/	/	/	**-**	**0.27**	**0.028**	**-**	**0.28**	**0.023**

[*] Signs indicate positive (+) or negative (-) response of row variable to column factor.

[**] / = no significant relationship

[†] N/A = Not applicable or data not available.

Table 2.3: Correlations of *B. tournefortii*, *Chaenactis stevioides*, and *Cryptantha angustifolia* to *B. tournefortii* density and cover in 2006. Correlations less than α = 0.10 are reported. Correlations less than α = 0.05 are in bold. All values in all regressions were averages within plot by date. All values were log-transformed before regression.

	Brassica tournefortii																	
	January						**February**						**March**					
	Density			**Cover**			**Density**			**Cover**			**Density**			**Cover**		
	Sign	**R^2**	**P value**	**Sign**	**R^2**	**P value**	**Sign**	**R^2**	**P value**	**Sign**	**R^2**	**P value**	**Sign**	**R^2**	**P value**	**Sign**	**R^2**	**P value**
Total Native Density	**+**	**0.22**	**<0.001**	**+**	**0.10**	**0.014**	**+**	**0.31**	**<0.001**	**+**	**0.42**	**<0.001**	**+**	**0.36**	**<0.001**	**+**	**0.21**	**<0.001**
Avg. Native Density	**+**	**0.18**	**<0.001**	**+**	**0.07**	**0.044**	**+**	**0.30**	**<0.001**	**+**	**0.32**	**<0.001**	**+**	**0.30**	**<0.001**	**+**	**0.16**	**0.002**
Total Native Cover	**+**	**0.09**	**0.022**	**+**	**0.45**	**<0.001**	**+**	**0.28**	**<0.001**	**+**	**0.54**	**<0.001**	**+**	**0.30**	**<0.001**	**+**	**0.18**	**<0.001**
Avg. Native Cover	**+**	**0.07**	**0.043**	**+**	**0.41**	**<0.001**	**+**	**0.25**	**<0.001**	**+**	**0.22**	**<0.001**	**+**	**0.24**	**<0.001**	**+**	**0.14**	**0.004**
Richness	+	0.05	0.094	/	/	/	**+**	**0.11**	**0.010**	**+**	**0.24**	**<0.001**	**+**	**0.19**	**<0.001**	**+**	**0.13**	**0.005**
B. tournefortii																		
Density	N/A	N/A	N/A	**+**	**0.34**	**0.008**	N/A	N/A	N/A	**+**	**0.28**	**0.025**	N/A	N/A	N/A	**+**	**0.83**	**<0.001**
Cover	**+**	**0.34**	**0.008**	N/A	N/A	N/A	**+**	**0.28**	**0.025**	N/A	N/A	N/A	**+**	**0.83**	**<0.001**	N/A	N/A	N/A
Growth (Height)	/†	/	/	/	/	/	/	/	/	**+**	**0.45**	**0.002**	+	0.20	0.056	**+**	**0.25**	**0.029**
# Bolting	/	/	/	/	/	/	/	/	/	**+**	**0.57**	**<0.001**	**+**	**0.36**	**0.006**	**+**	**0.03**	**0.001**
# Flowering	/	/	/	/	/	/	/	/	/	**+**	**0.53**	**0.001**	/	/	/	**+**	**0.23**	**0.036**
# Setting Seed	/	/	/	/	/	/	/	/	/	**+**	**0.44**	**0.003**	/	/	/	**+**	**0.26**	**0.025**
# Dead	/	/	/	/	/	/	-	0.19	0.070	**-**	**0.37**	**0.016**	**-**	**0.47**	**0.001**	**-**	**0.38**	**0.005**
Chaenactis stevioides																		
Density	/	/	/	**+**	**0.23**	**0.037**	/	/	/	**+**	**0.41**	**0.004**	**+**	**0.24**	**0.038**	**+**	**0.22**	**0.049**
Cover	/	/	/	**+**	**0.54**	**<0.001**	/	/	/	**+**	**0.35**	**0.009**	/	/	/	/	/	/
Growth (Height)	/	/	/	/	/	/	/	/	/	**+**	**0.42**	**0.005**	/	/	/	/	/	/
# Bolting	/	/	/	/	/	/	/	/	/	/	/	/	**+**	**0.25**	**0.034**	**+**	**0.30**	**0.019**
Cryptantha angustifolia																		
Density	/	/	/	/	/	/	/	/	/	**+**	**0.38**	**0.007**	/	/	/	/	/	/
Cover	/	/	/	**+**	**0.22**	**0.043**	/	/	/	**+**	**0.49**	**0.001**	/	/	/	/	/	/
Growth (Height)	/	/	/	/	/	/	-	0.34	0.095	/	/	/	-	0.36	0.086	-	0.37	0.084
# Dead	/	/	/	/	/	/	**+**	**0.22**	**0.047**	/	/	/	/	/	/	/	/	/

* Signs indicate positive (+) or negative (-) response of row variable to column factor.

**N/A = Not applicable; data not collected.

† / = no significant relationship

CHAPTER 3

Phenology as a Basis for Control of Exotic Species in Southwest US Deserts

Exotic annual species are an increasing ecological issue in desert ecosystems, particularly the invasive mustard *Brassica tournefortii*. Few options for controlling such species exist, but hand weeding *B. tournefortii* is the most common method employed. Weeding is inadequate and expensive for large-scale invasions, however, and new methods must be developed. Exotic annuals have general germination requirements and rapid phenology compared to natives, suggesting that a window for selective control of exotic annuals may exist immediately after seedling emergence. This hypothesis was tested by comparing a cotyledon-stage glyphosate application to a bolting-stage herbicide application and to hand weeding *B. tournefortii*, plus an untreated control. Treatments were tested at two sites dominated by either exotic or native species. Cover and species richness data were collected during peak flowering underneath and between shrubs. Results show that early glyphosate did not reduce or increase native cover, but did reduce exotic cover both between and beneath shrubs. Late herbicide impacted exotic cover more than native cover, but often reduced native richness. Natives responded positively only at the native-dominated site, and only through weeding under shrubs. The same treatment caused an increase in *E. cicutarium* under shrubs at the exotic-dominated site. Both herbicide treatments changed the dominance of exotic and native species, especially at the native site. Results show that rapid phenology may be exploited to control exotics in desert annual communities, but that tradeoffs exist for all control methods.

Introduction

Invasive exotic annual plants are of increasing concern in desert ecosystems. Although exotic annuals have been shown to have negative impacts on native annual species (Brooks 2000; Salo, McPherson et al. 2005; Barrows, Allen et al. 2009), and are a major cause of vegetation conversions (Schiermeier 2005), land managers are generally concerned that control methods will impact the native species more than competition with exotics. Furthermore, few options are available for controlling these species in natural landscapes and most methods have not been rigorously tested. However, neglecting control of exotic species increases invasive populations, perpetuating the risk of widespread invasion and altered landscapes.

Impacts on native forbs in southwest deserts of the U.S.A occur from a small group of exotic species. These include annual grasses, especially *Bromus* spp. (*B. rubens* and *B. tectorum)* and *Schismus* spp. (*S. barbatus* and *S. arabicus*), and annual forbs, especially *Brassica tournefortii* and *Erodium cicutarium*. *Bromus* spp. are widespread throughout the western U.S., while *Schismus* spp. and *B. tournefortii*, introduced in the early 1900s (DiTomaso 2007), are still expanding in that region. *E. cicutarium* was introduced into California in the mid 1700s (Mensing and Byrne 1998) and is common throughout most of North America, although it has only recently been studied as an invasive species in California’s deserts (Brooks 1999; Brooks 2000; Brooks and Berry 2006; Steers 2008). *Schismus* spp. and *E. cicutarium* are generally not controlled because they are ubiquitous, but *B. tournefortii* is still uncommon or absent in many areas across the southwestern deserts, offering a unique opportunity to prevent *B. tournefortii* from further impacting desert ecosystems. Management of *B tournefortii* is essential to remove it from sensitive areas, such as the critical sand dune habitat of the Coachella Valley of California (Barrows, Allen et al. 2009). Barrows et al. (2008) found that *B. tournefortii* had negative effects on all native annual plants measured in dunes, including an 80-90% reduction of flowers and fruits in native forbs.

Hand weeding is currently used to control small infestations of *B. tournefortii* in desert ecosystems. Rosettes are relatively easy to pull once they have bolted and weeding is highly selective. Hand weeding has also been used as an experimental tool to study the effects of *B. tournefortii* on native populations, communities, and ecosystem processes in the Coachella Valley (Barrows, Allen et al. 2009). However, hand weeding is labor-intensive, expensive, and cannot easily be applied to large (> 1 hectare) areas. Moreover, hand-weeding produces an overwhelming amount of biomass that requires disposal elsewhere to prevent reseeding the site. Finally, only *B.* tournefortii can be hand-weeded effectively because other exotics, such as *E. cicutarium* or *Schismus* spp., are too small and widespread. For these reasons, hand weeding is not appropriate for large-scale weed control in the desert.

Herbicides are consistently more cost-effective than hand-weeding but their use in desert wildlands is limited. Nonselective herbicides may impact sensitive animal or plant species (California Native Plant Society 2008). However, herbicides disturb the soil less than hand weeding. Since soil disturbance can often promote invasive exotic plants, hand weeding can encourage rather than discourage some exotic species (Hobbs and Huenneke 1992). Impacts from human trampling during hand weeding can be substantial, especially with the large teams needed to control entire populations of exotic species. Invasive plant control projects are often limited by budgets and, especially with ephemeral desert annuals, time. Herbicides are both cost efficient and effective, especially for large (>1 hectare) areas. While herbicides may impact native species, they can have a lasting effect and reduce exotic species in the desert for years following application (Allen, Cox et al. 2005).

Exotic annuals, such as *Erodium* spp., in desert ecosystems generally have more rapid phenology than native annual species (Burk 1982; Jennings 2001; DeFalco, Bryla et al. 2003). They often germinate rapidly (Bartolome 1979) and emerge before most native forbs (DiTomaso 2007), subject to temperature and precipitation patterns. In addition, native annual forbs in the desert often have particular daylength, temperature, and cumulative precipitation requirements to allow germination (Beatley 1967; Beatley 1974; Venable, Pake et al. 1993; Adondakis and Venable 2004). In contrast, invasive species that are not native to the desert may have general germination requirements (Blackshaw 1992; Gutterman 1996; Gutterman 2001; Bangle, Walker et al. 2008, Holt and Tayyar unpublished data). For instance, Beatley (1966) found that *Bromus rubens*, a highly invasive annual exotic grass, required less rain to germinate than native annuals, and Inouye et al. (1980) found that *Erodium cicutarium* was among the first cohort to germinate and contributed to a large, early proportion of biomass. This difference in phenology between exotic and native species could create a window of opportunity for management during the period between exotic and native emergence. Removing exotic species just after emergence would prevent impacts on natives from competition and reduce the number of exotic plants overall, even if later rain events produced new cohorts.

Steers (2008) used early raking to preferentially remove exotic annuals in the desert two weeks after the first major rain event in 2006 and 2008. Exotic grasses were removed with this treatment but raking also negatively impacted native annual forbs. Soil disturbance caused by raking could encourage more exotic species than native forbs (Hobbs and Huenneke 1992; Brooks, Draper et al. 2006; Steers 2008), and Steers suggested that herbicides might be a better means of using differential phenology for control of exotic annual species (2008). In comparison to hand weeding, which would remove only *B. tournefortii*, or Fusilade II ®, which would remove only grasses, an early glyphosate application might have the added benefit of removing several exotic species at once.. Since previous research suggests that removal of all exotic species promotes the greatest native forb success (Steers 2008; Cox and Allen in press), a nonselective herbicide application that takes advantage of rapid phenology might increase control of all exotic functional groups while decreasing labor and cost.

The purpose of this research was to test the most common method of *B. tournefortii* control, hand weeding, against two herbicide application methods using glyphosate. These included an early application intended to take advantage of rapid phenology in exotic species and a bolting-stage application intended to prevent seed set. We hypothesized that early application would preferentially remove most exotic annuals with minimal impact to native annual forbs, but that late application would impact all species equally. We tested the effects of these treatments in one heavily invaded desert community and one less invaded community that had the same exotic species present.

Materials and Methods

Study sites

Two creosote shrub (*Larrea tridentata*) communities were chosen for comparison. Snow Creek is located at the farthest western edge of the Colorado desert in the Coachella Valley (33° 54’04.00” N, 116° 40’42.98” W) and often receives more rainfall than the rest of the low desert, an average of 12 to 23 cm during the wet season from October to April (Western Regional Climate Data Center 2009). Snow Creek also experiences nitrogen deposition at a rate of 12-16 kg N ha^{-1} yr^{-1} downwind from the urbanized Los Angeles basin (Tonnesen et al. 2007). This site is heavily invaded by the exotic species *Schismus* spp., *Erodium cicutarium,* and *B. tournefortii.* The second site, Willow Hole (33° 53’29.76” N, 116° 27’31.63” W) is farther east in the Coachella Valley; its average precipitation is 11 cm during the winter season (Western Regional Climate Data Center 2009). Willow Hole experiences less nitrogen deposition than Snow Creek, about 5 kg N ha^{-1} yr^{-1}. Willow Hole is dominated primarily by native species and *B. tournefortii*, with varying cover of *Schismus* spp. and patches of *E. cicutarium*. Both sites are essentially flat, located in stabilized dunes with sandy soils, and experience some human disturbance from casual litter dumping, off-road vehicles, and nearby wind farms.

Plots were established at each site in the winter of 2006-07, but due to lack of rainfall no experiments were conducted until the winter of 2007-08. Temperature and rainfall were recorded in 2007-08 at Snow Creek with two HOBO temperature sensors

(Onset Computer Corporation, PO Box 3450, Pocasset, MA 02559-3450) and two tipping-bucket rain gauges connected to a HOBO event recorder. Data for Willow Hole in 2007-08 was collected from the nearby north Palm Springs NOAA weather center (Western Regional Climate Data Center 2009).

Experimental design

Exotic weed control experiments were conducted at each site in 2007-08. The experiments were arranged as randomized complete designs with four treatments (including an untreated check) in 12 blocks for a total of 48 plots per site. Treatments included hand weeding, early herbicide application, and late herbicide application. Blocks consisted of four loosely grouped 8 m^2 plots, each centered on an individual creosote shrub and laid with all sides parallel to the compass directions. Plots within each block were a minimum of 2 m from each other on a parallel side and within approximately 15 m of each other, but could be as much as 50 m from each other at Willow Hole. Plots were established before the first fall rains to avoid bias due to differences in the annual plant community that might be present.

Previous research has shown differences between annual communities underneath creosote shrubs *vs.* between shrubs (interspaces) (Brooks 1999; Brooks 2000); therefore, these two microhabitats were sampled and analyzed separately. In each plot, four 1 m x 0.5 m subplots were used to sample the interspace and undershrub regions (two in the interspace and two under shrubs) following application of treatments. Wind direction, and thus the longest shrub axis, was generally west to east, so in the undershrub regions the two subplots were placed on the north and south sides of the creosote to control for solar angle. Subplots were placed at the edge of the canopy with some overhanging creosote cover. Shrub interspaces are heterogeneous with patchy plant growth at a small scale, so subplots were established where seedlings and/or litter were present in order to record the maximum possible response to treatments. Microsites that contained senesced shrubs, rodent or insect mounds, offroad vehicle tracks, or any other obvious disturbances were avoided. For late herbicide and hand weeded treatments, only the original two marked subplots were measured. However, plots were sometimes sparse and heterogeneous in untreated and early herbicide treatments plots; therefore, randomly placed subplots were added at the time of data collection to reduce variation. Random subplots were added by tossing a plot frame into the interspace within the plot and orienting the frame to the nearest microsite that was not bare. For untreated plots, one subplot was added for a total of three subplots. For early herbicide treatments, two subplots were added for a total of four subplots.

Management treatments

The first major rainfall of the 2007-2008 season occurred on November 30, 2007 and *B. tournefortii* seedlings were observed as early as December 16 at Snow Creek. Early herbicide treatments were applied on December 21 and 22 at Willow Hole and Snow Creek, respectively. Glyphosate (Roundup Pro, 41% a.i.) was mixed at 21 ml/liter water with a blue dye added to mark the spray pattern. Hand-pump sprayers (Solo 456 sprayers, 5100 Chestnut Ave., Newport News,VA 23605) were used to apply a light, even mist over the entire treated plot, avoiding shrubs but spraying underneath them. At Snow Creek, one block was omitted due to lack of herbicide; the 11 treated plots received a total of 2,589 ml a.i./ha. An identical mix of glyphosate was applied at Willow Hole using the same hand-pump sprayer, avoiding large patches of bare ground and shrubs. Spot-spraying halved the quantity of herbicide used for 12 blocks to only 1,288 ml a.i/haat Willow Hole. Herbicide rate estimates are somewhat conservative since the entire fertile island underneath each shrub was not sprayed, only the open edges beneath the canopy, subtracting a varying amount of area from each sprayed plot.

Hand weeding of *B. tournefortii* occurred when rosettes were flowering and beginning to set seed, but before seed were mature and viable. Hand weeding treatments were limited to the marked subplot areas in both interspace and undershrub areas, and included a 0.5 m^2 weeded buffer zone. Willow Hole was weeded on February 21, while Snow Creek was weeded on February 22, 2008.

Late herbicide application took place at the same flowering stage as hand-weeding, which is the typical stage recommended for spraying annual forbs with glyphosate. All *B. tournefortii* and *E. cicutarium* were bolting, flowering, and/or beginning to set seed, but seed was immature and not yet viable. Plants were sprayed with the same concentration of glyphosate as the early herbicide treatment using a pressurized gas backpack sprayer (R&D Sprayers, model C. 419 Hwy 104 Opelousas, LA USA 70570). The gas sprayer delivered a finer, more consistent mist of 3,955 ml a.i./ha. Willow Hole was sprayed with 2, 589 ml a.i./ha. At Snow Creek the entire 8 m^2 plot area was sprayed, while at Willow Hole only the patches with exotic annuals were sprayed, again avoiding large bare patches. Both sites were sprayed on February 23 2008.

Data collection and analysis

Richness and percent cover of all species, plus cover of bare ground, litter, and rock were collected on all subplots at the peak of native annual forb flowering. Data was collected at Willow Hole on March 6 and 7, 2008 and at Snow Creek on March 10, 11 and 13, 2008. Plots with the late herbicide treatment were left undisturbed until mortality was complete, and late herbicide data for both sites was collected on March 15. Cover of litter resulting from late herbicide application was collected in addition to live plant richness and cover data.

Data at each site were analyzed separately, and within each site data for interspace and undershrub subplots were analyzed separately. Cover was calculated as relative values by cover type (native, exotic, herbicide kill, litter, and bare ground) and as absolute values by species for exotic annuals. Interspace and undershrub subplot cover values were averaged within a treatment and compared across treatments using analysis of variance (ANOVA). Average richness of natives and exotics was compared by treatment using ANOVA. Mean separations between plant types and treatments were tested using Tukey's HSD test. Dominance was assessed by ordering the average absolute cover values among treatments from greatest to least.

Results

Site:

Snow Creek received 22 cm of rain from December to April in 2007-2008. The first rain event was ~4 cm of precipitation on Nov.30. Precipitation at this site was likely above normal; however, no long-term data for this site exists. Temperatures ranged between -6.7°C and 44.5°C, but averaged 14°C during the period of study. Willow Hole received 10.6 cm of rain, beginning with ~2.8 cm on Nov. 30, which was slightly above normal. Temperatures ranged between 2.2°C and 36.1°C, with an average temperature of 17.7°C (Figure 3.1).

At the time the early glyphosate treatment was applied, seedlings were smaller and fewer at Willow Hole and larger and more abundant at Snow Creek. All seedlings were at the cotyledon stage, although some *B. tournefortii* at Snow Creek had the first two true leaves. Some native seedlings were observed at that site, primarily *Pectocarya* spp., although a formal census of native seedlings present was not taken. Seedlings of *Erodium* and *Schismus* spp. were also observed during the early herbicide application at Snow Creek. At Willow Hole, the majority of exotic seedlings consisted of *B. tournefortii*, although a few native seedlings were noted. Very few *B. tournefortii* seedlings had their first true leaves. The difference in phenology between sites may have been due to reduced rainfall at Willow Hole.

After all treatments, at the time of peak native flowering and data collection, exotics were the dominant ground cover at Snow Creek, while bare ground and native cover were dominant at Willow Hole (Figures 3.2a and 3.2b, Tables 3.1 and 3.2). Both sites were heavily invaded underneath shrubs (Figures 3.3a and 3.3b, Tables 3.1 and 3.2). Of the exotic species present at each site, Snow Creek interspaces were dominated by *Schismus* spp. and *Erodium cicutarium* as much or more than *Brassica tournefortii* (Figure 3.4a), but underneath shrubs *B. tournefortii* was the dominant exotic species (Figure 3.4c). In contrast, *B tournefortii* was the dominant exotic species at Willow Hole both underneath and between shrubs, with very little *Schismus* spp. cover and almost no *E. cicutarium* at the site (Figures 3.4b and 3.4d). Native richness was equal to or less than exotic richness at Snow Creek (Figures 3.5a and 3.5c), but was comparatively high at Willow Hole, especially in shrub interspaces (Figures 3.5b and 3.5d).

Labor:

One of the major concerns of land management organizations seeking to control *B. tournefortii* is the time, effort, and cost required for different methods of control. For these experiments, about 16 person-hours (p.h) were used to spray both sites each time an herbicide treatment was performed (16 p.h for early application, 16 p.h for late application). The entire 8 m^2 plot area was sprayed for most herbicide treatments, with the exception of about some early application plots at Willow Hole, which were spot-sprayed where seedlings were distinctly patchy. The maximum total area sprayed was therefore about 1500 m^2 across both sites at each treatment time. Overall, each herbicide treatment required about 100 person-hours per hectare. In contrast, roughly 50 person-hours were required to hand-weed about 290 m^2 total (including buffer zones around subplots), across both sites. Scaling up, about 1,740 person-hours would be required to hand-weed *B. tournefortii* from one hectare.

Interspace plots:

Relative exotic species cover was reduced in all treatments in both sites, except for hand weeding in interspaces at Snow Creek (Figure 3.1a). Interspace subplots at Snow Creek had a layer of *Schismus* spp. and *Erodium cicutarium* underneath the *Brassica tournefortii*; therefore hand weeding *B. tournefortii* had no significant impact on the overall cover of exotic species (Figure 3.2a). Likewise, hand weeding did not increase bare ground at Snow Creek (Figure 3.2a), but did increase bare ground at Willow Hole (Figure 3.2b). Herbicide increased bare ground at both sites, however (Figures 2a and 3.2b).

Relative native cover was not reduced by early glyphosate application at either Snow Creek or Willow Hole (Figures 3.2a and 3.2b). Native cover was not reduced by hand weeding at either site, nor was it increased by any of the exotic control techniques in shrub interspaces (Figures 3.2a and 3.2b). At Snow Creek, native cover was not reduced by late glyphosate application compared to the control but was lower than native cover in hand weeded subplots (Figure 3.2a). Native cover was reduced by late glyphosate application at Willow Hole (Figure 3.2b). *B. tournefortii* hand weeding alone accounted for the same increase in bare ground as late herbicide, but without the herbaceous annual mortality (Figure 3.2b)

All exotic species were reduced by both herbicide treatments at both sites, but early herbicide was less effective than late herbicide in removing exotic species cover (Figures 3.2a and 3.2b). Late herbicide application resulted in the lowest cover of all three exotic species (Figures 3.4a and 3.4b), but also reduced native cover (Figures 3.2a and 3.2b). *E. cicutarium* was best controlled by early glyphosate application, while *Schismus* spp. were best controlled by late glyphosate application (Figure 3.4a). Early glyphosate application did not differ from late application in reducing *B. tournefortii* at Snow Creek, where seedlings were larger and/or fully emerged at the time of early treatment, *B. tournefortii* mortality was greater in late application treatments than early application at Willow Hole, where seedlings were smaller and/or had not fully emerged at the time of early treatment. This suggests that especially small seedlings either escaped herbicide application, or that all seedlings were not yet emerged at Willow Hole, whereas the impacts to seedlings and adults were essentially equivalent at Snow Creek. Late herbicide application consistently reduced both exotic and native richness, but early herbicide application did not (Figures 3.5a and 3.5b). Hand weeding *B. tournefortii* reduced exotic richness at Willow Hole, where *B. tournefortii* was one of two dominant exotic species at the site (Figure 3.5b).

Species responses to hand weeding in shrub interspaces differed between sites. Hand weeding removed only *B. tournefortii* and had no effect on either *E. cicutarium* or *Schismus* spp. at Snow Creek (Figure 3.4a). The same removal treatment at Willow Hole, where *B. tournefortii* was the dominant exotic annual, resulted in a small decrease in *Schismus* spp. as well. The other exotic species present, therefore, had no response to *B. tournefortii* removal at the heavily invaded site (Snow Creek) and a negative response at the less invaded site (Willow Hole).

The ranked dominance of annual species changed with early glyphosate application at both sites. At Snow Creek, *B. tournefortii* and *Schismus* spp. remained highest in cover among annuals in early treatment plots. However, native *Crassula connata* increased over sixfold and replaced exotic *E. cicutarium* in ranking (Table 3.1). Four native species, including one dominant one, were lost from control plots with early glyphosate treatment and two new native species were found (Table 3.1). At Willow Hole, *B tournefortii* cover was reduced but still highest after early herbicide treatment, while *Schismus* spp. had reduced cover (Table 3.2). Five native species had over 5% cover following early herbicide treatment. Natives *Camissonia pallida* and *Cryptantha angustifolia* replaced *Pectocarya heterocarpa* and *P. recurvata* as the annual forbs with the greatest cover. *Pectocarya* spp. still constituted over 5% of the average total cover each in early glyphosate application and were not removed from the native annual community (Table 3.2). Some native species, such as *Eremalche exilis*, saw large increases with early glyphosate treatment, while others, such as *Lotus strigosus,* decreased in cover (Table 3.2). Three native species were found in control plots that were absent in early glyphosate plots, but these were replaced by three species that were not found in control plots (Table 3.2).

Undershrub plots:

Undershrub regions were more similar across sites than were interspaces (Figures 3.3a and 3.3b), and were heavily invaded by *B. tournefortii*, even with other exotic species present (Figures 3.4c and 3.4d). Bare ground under shrubs increased with early herbicide application at Snow Creek, but only increased with hand weeding at Willow Hole (Figures 3.3a and 3.3b). Instead of increasing bare ground underneath shrubs, late glyphosate application produced a high relative cover of new litter from herbicide mortality at both sites (Figures 3.3a and 3.3b)

Undershrub vegetation at both sites responded more strongly to exotic control treatments than in interspace subplots at both sites. As in interspace plots, early glyphosate application reduced exotic cover but did not reduce native cover (Figures 3.3a and 3.3b). Bare ground increased at Snow Creek, and *Schismus* spp. decreased, but the same effects were not found at Willow Hole (Figures 3.3a, 3.3b, 3.4c, 3.4d). Late glyphosate application was again the most effective means of reducing exotic cover at both sites, but also reduced native cover under shrubs at Snow Creek when compared to control and hand-weeded treatments (Figures 3.3a, 3.3b, 3.4c, 3.4d). Late herbicide application also reduced native and exotic richness and both sites (Figures (3.5c and 3.5d). Both herbicide applications were highly successful in controlling *E. cicutarium* and *Schismus* spp. at Snow Creek only. *B. tournefortii* was more successfully controlled by late than by early herbicide treatment (Figures 3.4c and 3.4d).

Early herbicide application did not change the ranking of dominant species at Snow Creek except to remove two exotics, *Bromus rubens* and *E. cicutarium*, as dominant species and reduce cover of one native (Table 3.1). At Willow Hole, however, early glyphosate treatments reduced *B. tournefortii* and *Schismus* spp., and increased native *Camissonia pallida* and *Eremalche exilis* in cover dominance (Table 3.2).

Hand weeding underneath shrubs increased native cover at Willow Hole but not at Snow Creek (Figures 3.3a and 3.3b). At Snow Creek, *E. cicutarium* increased in response to hand weeding (Figure 3.4c). Hand weeding the ample *B. tournefortii* at Snow Creek disrupted the soil, removed the few native plants left under shrubs, and produced stacks of leftover biomass along with noticeable trampling from the weeding team. Unlike the interspaces, hand weeding underneath shrubs at Willow Hole did not correspond with a decrease in *Schismus* spp. cover (Figure 3.4d).

Both early and late herbicide application decreased native richness at Snow Creek (Figure 3.5c), but only late herbicide application reduced native richness at Willow Hole

(Figure 3.5d). Exotic richness decreased at both sites with late herbicide application (Figures 3.5c and 3.5d). As in interspaces, exotic species richness was reduced with hand weeding underneath shrubs at Willow Hole, plus there was a corresponding increase in native richness (Figure 3.5d). Hand weeding beneath shrubs at Willow Hole disrupted soil but *B. tournefortii* plants were less dense and weeders were able to leave the native plant community mostly intact. Trampling was not as apparent at Willow Hole because of the large proportion of bare ground.

Overall, undershrub subplots were more responsive to exotic plant control than interspaces. Undershrub subplots at Willow Hole were the only areas tested to show a positive native response to exotic control treatments.

Discussion

The native and exotic flora studied in this research showed different responses to management techniques depending on invasion level of the site and location of the plot within the site in relation to shrubs. At Snow Creek, the heavily invaded site, high overall cover of exotics corresponded with low cover and richness of native annuals. As a group, native annuals at Snow Creek showed no positive response to any of the management treatments. Results from Snow Creek support previous findings that exotic annuals have strong impacts on the native annual community in desert ecosystems (Brooks 1999; Brooks 1999; Brooks 2000; Brooks, D'Antonio et al. 2004; Steers 2008; Barrows, Allen et al. 2009), and also suggest that one year of exotic control will not increase native annual success at heavily invaded sites. Willow Hole was less invaded overall, but resembled Snow Creek in undershrub *B. tournefortii* invasion. As high-resource islands in the landscape, undershrub annual communities are most prone to invasion (Fowler and Whitford 1996; Brooks 1999; Huston 2004). *B. tournefortii* may compete directly with shrubs (DeFalco, Fernandez et al. 2007), but results show strong competition of *B. tournefortii* with other native and exotic annuals, as well.

At Snow Creek, exotic annuals other than *B. tournefortii* were present and dominant, such as *Erodium cicutarium* and *Schismus* spp. *B. tournefortii* weeding underneath shrubs encouraged the competitive release of the other exotic, rosette forb, *E. cicutarium*. As similar growth forms, these two species may compete directly and replace each other when one is removed (Brooks 2000). Our results show that, as a management choice, hand weeding a heavily invaded site would not have the intended effects of promoting natives or diminishing exotic cover. Instead, it could encourage other exotic species to replace *B. tournefortii*, particularly in a resource-rich site such as underneath shrubs. Similar replacement effects have been found in exotic grass removal experiments in coastal sage scrub, where *E. cicutarium* replaced grasses (Cox and Allen 2008). An herbicide might be a wiser choice for more heavily invaded areas because it would effectively remove all exotic species, not just *B. tournefortii*. Even without positive response from natives, an herbicide could prevent further inputs to the exotic seedbank.

In contrast to hand weeding at Snow Creek, weeding was effective underneath shrubs at Willow Hole, where *B. tournefortii* was the only dominant exotic species. Weeding *B. tournefortii* under shrubs at Willow Hole increased native cover and richness. Willow Hole's high native richness and cover may have created a greater capacity for immediate response to treatment (Lavorel 1999). However, *E. cicutarium* was not a factor at this site, allowing native annuals to benefit from competitive release underneath shrubs instead. Competition is an important factor when resources are high, but plants may not compete directly when resources are low, such as in interspaces (Briones, Montana et al. 1998). Our results agree, since there was no response of native annuals to weeding in interspaces at either site. In fact, rather than competing, cover of all species, including natives, was positively correlated with *B. tournefortii* in interspaces, which may be attributed to beneficial microsites in the landscape, or an overall facilitation effect for all annuals in resource-poor interspaces (Marushia Ch. 2). Weeding *B. tournefortii* from interspaces at Willow Hole actually diminished *Schismus* spp. cover as well, suggesting that facilitation was especially important for *Schismus* spp. in the resource-poor interspaces (Schiffers and Tielborger 2006). This hypothesis is further supported by results from hand-weeding *B tournefortii* underneath shrubs, where *Schismus* spp. neither declined nor increased. Shrubs are known to facilitate some annuals by creating resource-rich islands in the landscape (Holzapfel and Mahall 1999). Shrub facilitation appears to have outweighed both *B. tournefortii* facilitation and competition for *Schismus* spp. in resource-rich undershrub sites.

Hand weeding is promising for targeted areas with *B. tournefortii* as the only invader because it may maximize native response while minimizing native mortality. However, control should not only seek to benefit natives in the short term, but also reduce exotics long-term. *B. tournefortii* is the latest invasive to impact desert ecosystems, but *E. cicutarium, Schismus* spp.*, and Bromus* spp. have all had major impacts on desert ecosystems throughout the western United States (Beatley 1966; Salo

2004; Schutzenhofer and Valone 2006). Selective hand-weeding benefited natives only when exotics other than *B. tournefortii* was not dominant, and therefore would not benefit from competitive release. However, many other landscapes will have two or more dominant exotics and management methods that are efficient at removing many exotics or preventing future impacts will ultimately have the greatest benefits for native communities (Steers 2008).

Herbicide treatment may remove multiple exotic species at the same time, is generally less expensive than mechanical removal, and requires less time and effort, as shown by our labor calculations. Although a bolting-stage herbicide application had clear impacts to the native annual community, cotyledon-stage application did not. This suggests that careful timing of herbicide application can take advantage of rapid phenology to reduce exotic annuals in some desert ecosystems, and may be a useful alternative to hand weeding as a means of exotic annual control. As a nonselective herbicide, glyphosate had the advantage of removing not just *B. tournefortii*¸ but also *E. cicutarium*, and reduced the impacts of multiple exotic annuals. If early herbicide application is further investigated, future research should assess which is greater over several years: impacts to the native annual community from invasive plants, or impacts from early herbicide application.

Efficient management includes reducing the seedbank by encouraging germination and controlling seedlings while preventing seed set and dispersal. Either the early or late herbicide treatments in this research would accomplish this goal, although both application timings allowed some seed production by different species. In the early herbicide treatments, native species may have had greater seed set than in late herbicide treatments, but some *B. tournefortii* and *Schismus* spp. recovered after treatment and reproduced. In contrast, the late herbicide treatment prevented all *B. tournefortii* seed production, but native fecundity was also likely impacted, while *E. cicutarium* and *Schismus* spp. had already produced some seed by the time the herbicide was applied. Particularly at Snow Creek, however, all exotic annuals were reduced or removed by herbicide treatment, and because so little native component remained at the site in the first place, native cover was not reduced relative to untreated controls. Native richness was impacted by exotics underneath shrubs, however, so even at this heavily-invaded site, some impacts to the native community remained. Furthermore, even with herbicide use, the high rate of nitrogen deposition from air pollution may favor exotic annuals over native forbs (Brooks 2003).

Exotic litter is a major fuel source for desert fires, and reducing fuel loads is a goal for land managers (Brooks 1999). Late herbicide application resulted in high cover of litter underneath shrubs in our experiments. An alternative treatment to prevent seed set and fuel buildup would be a rosette-stage herbicide application, after all species have germinated but before or during flowering of the earliest exotic annual species. This would allow for maximum exotic seedbank depletion, but would kill exotics before they can add to the seedbank or create a fuel load. A rosette-stage application would not avoid native annuals, however.

Site-specific characteristics, goals for land management, and ownership policies at each particular site will influence the benefits and tradeoffs for each exotic control technique. The complement of exotic species at the site, in particular, has enormous implications for the response of the annual community. Hand weeding was an acceptable choice for Willow Hole underneath shrubs because there was little exotic cover otherwise to compete with native species; therefore, natives benefited from control. However, shrubs and interspaces were both invaded at this site, and the cost of hand weeding the entire landscape would be prohibitive for many land managers. An acceptable compromise might be to treat the interspaces using an early herbicide application and hand-weed underneath shrubs. Spot-treating the interspaces after early treatment, perhaps during hand weeding, might maximize the benefits of all three techniques, removing as many exotic annuals as possible while promoting native annuals. If a site had rare or endangered native plants, however, management goals and policies might dictate hand-weeding as the only appropriate choice.

Early herbicide treatment retained native cover while reducing exotic cover at both sites. However, exotics were not wholly removed from the system and natives did not show a positive response to early herbicide application. Native annuals may not be able to respond positively except when there is complete removal of all exotic species in the system (Steers 2008). Native annual seedbanks are generally assumed to be healthy and intact in desert ecosystems because invasion and other disturbances have been low overall until relatively recently (Venable, Pake et al. 1993). Native annual forb germination is density-dependent, however, and may be inhibited by increasing densities of exotic annuals (Inouye 1980). Invasions may therefore reduce the occurrence of natives in the annual community by inhibiting germination, even when an intact seedbank exists. In a heavily-invaded site where fire is an issue but native annuals have already been diminished by exotics for several years, the benefits of preventing fuel loads and exotic seedbank inputs by controlling exotics could outweigh impacts of control measures on the native flora. Removing some of the exotic seedbank could, in time, reduce germinating plant densities in the fall and stimulate germination in the native seedbank.

Although results from this research show the potential to exploit exotic species' rapid phenology, further research is required before such a technique could be widely utilized. Rainfall is extremely variable in southwestern deserts (Hereford, Webb et al. 2006), and may be subject to even greater extremes with climate change. Initial rainfall amounts and accompanying temperature regimes may drastically affect emergence patterns between exotic *vs.* native species from year to year (Bowers 1987). For instance, a series of small, warm rainfall events early in the fall could be more likely to produce a well-defined cohort of exotic annuals before native annuals meet germination requirements. In contrast, a large, cold rain event later may cause corresponding germination in both natives and exotics (Beatley 1974), removing the window for selective control. While data on the temperature and precipitation requirements of native annuals exists (Beatley 1974; Bowers 1987), this data should be synthesized and compared to data for exotic annuals to develop a predictive matrix and predict those patterns most likely to produce opportunities for selective control. Combined with further field tests, new herbicide timing techniques could be developed for annual communities.

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Figure Legends

Figure 3.1: Temperature and precipitation as recorded at Snow Creek and Palm Springs. Palm Springs data represents nearby Willow Hole study site.

Figure 3.2: Relative percent (%) cover of all cover types in shrub interspaces at Snow Creek (a) and Willow Hole (b) post-treatment, at the peak of native flowering. Significance was tested within cover type across treatments at each site using Tukey's HSD. Differences are noted by letters at the base of each cover type to the right of each treatment (ABC, natives; abc, exotics; XYZ, litter; xyz, bare ground; NS, no significant differences). Cover types within a site labeled with identical letters are not different at P = 0.05. No comparisons exist within site for herbicide litter.

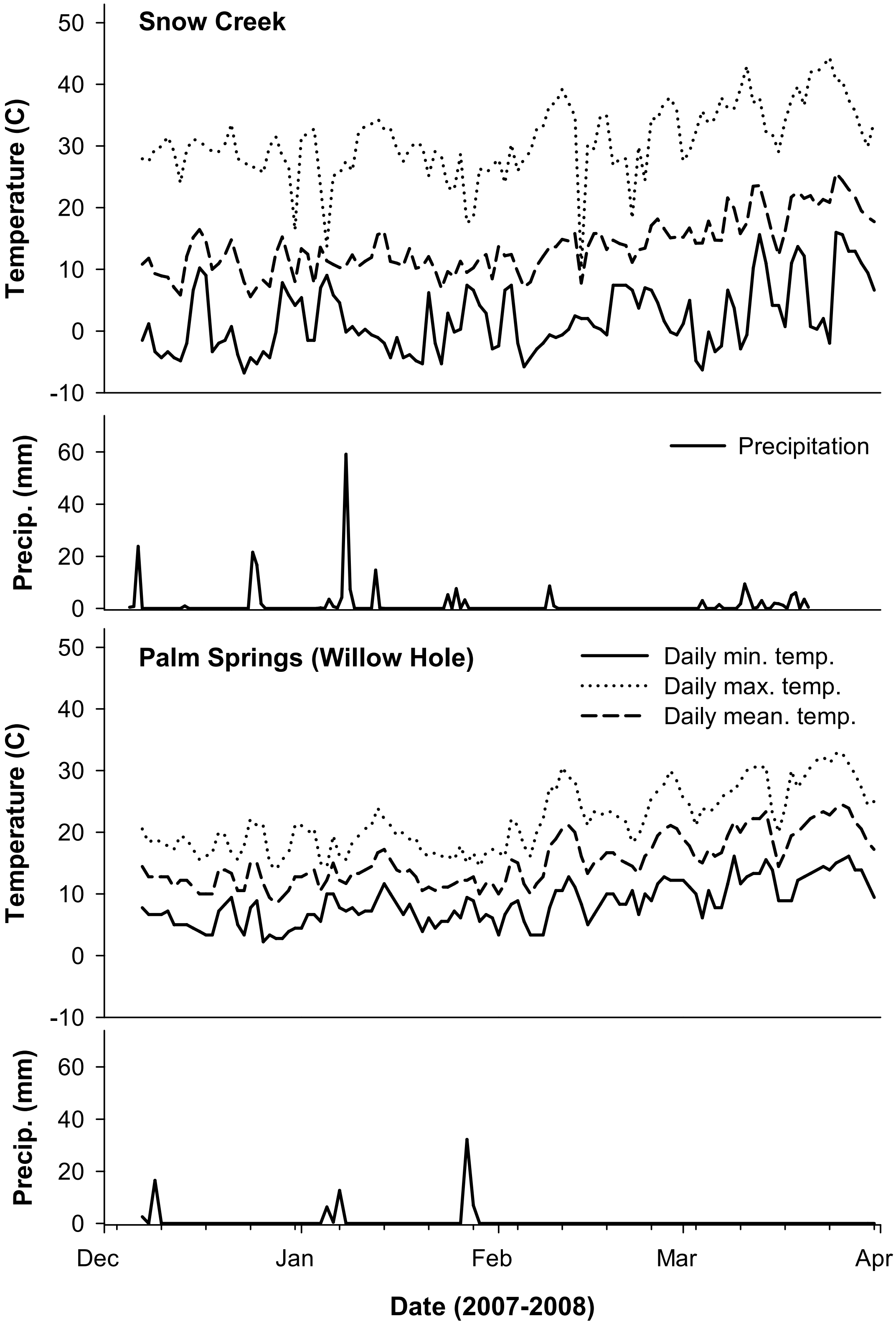
Figure 3.3: Relative percent (%) cover of all cover types underneath shrubs at Snow Creek (a) and Willow Hole (b) post-treatment, at the peak of native flowering. Significance was tested within cover type across treatments at each site using Tukey's HSD. Differences are noted by letters at the base of each cover type to the right of each treatment (ABC, natives; abc, exotics; XYZ, litter; xyz, bare ground; NS, no significant differences). Cover types within a site labeled with identical letters are not different at P = 0.05. No comparisons exist within site for herbicide litter.

Figure 3.4: Absolute percent (%) cover of the three most common exotic species in shrub interspaces and underneath shrubs at Snow Creek and Willow Hole, post-treatment and at the peak of native flowering. Significance was tested within species across treatments at each site using Tukey's HSD. Differences are noted by letters above each

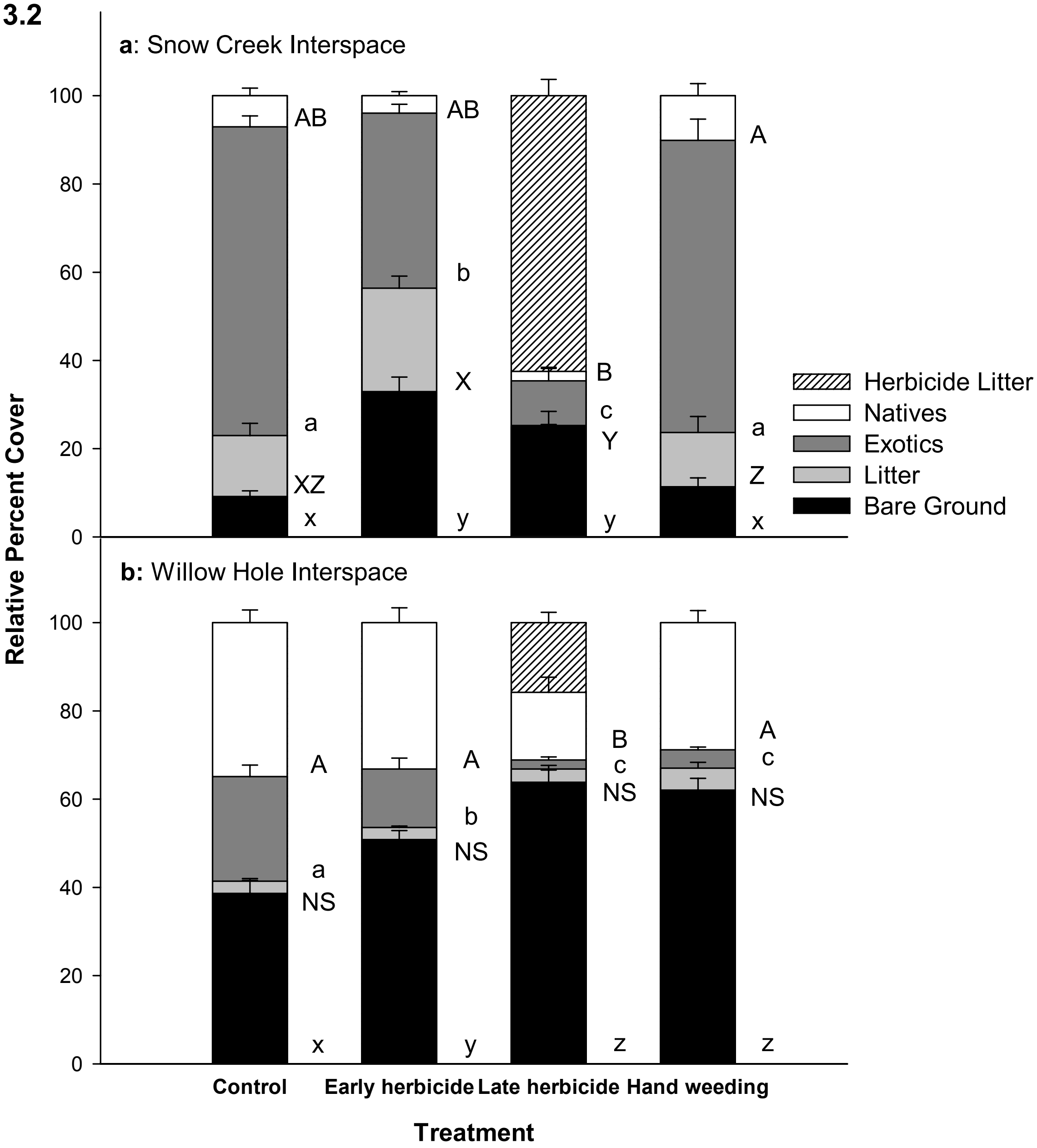
bar (ABC, *B. tournefortii*; abc, *E. cicutarium*; XYZ, *Schismus* spp.; NS, no significant differences). Species within a site labeled with identical letters are not different at P = 0.05. (a) Snow Creek interspace, (b) Willow Hole interspace, (c) Snow Creek underneath shrubs, (d) Willow Hole underneath shrubs.

Figure 3.5: Species richness of native and exotic species in shrub interspaces and underneath shrubs at Snow Creek and Willow Hole, post-treatment and at the peak of native flowering. Significance was tested within species type across treatments at each site using Tukey's HSD. Differences are noted by letters above each bar (ABC, exotic richness; abc, native richness; NS, no significant differences). Species within a site labeled with identical letters are not different at P = 0.05. (a) Snow Creek interspace, (b) Willow Hole interspace, (c) Snow Creek underneath shrubs, (d) Willow Hole underneath shrubs.

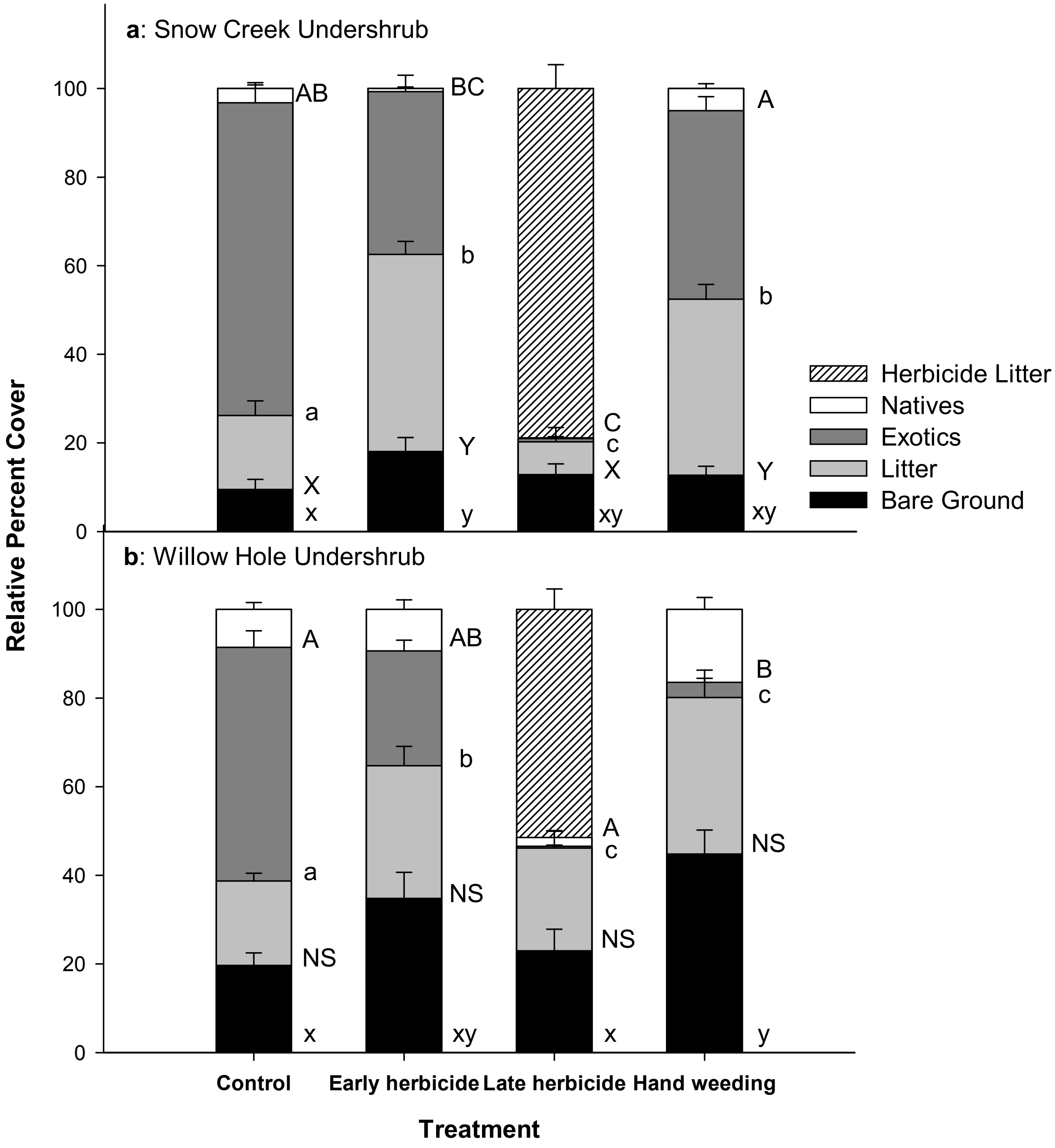
3.1


Snow Creek
Temperature (C)
50
40
30
20
10
0
-10
Precipitation
Precip. (mm)
60
40
20
0
Palm Springs (Willow Hole)
Daily min. temp.
Daily max. temp.
Daily mean. temp.
Temperature (C)
Precip. (mm)
Dec
Jan
Feb
Mar
Apr
Date (2007-2008)

3.2

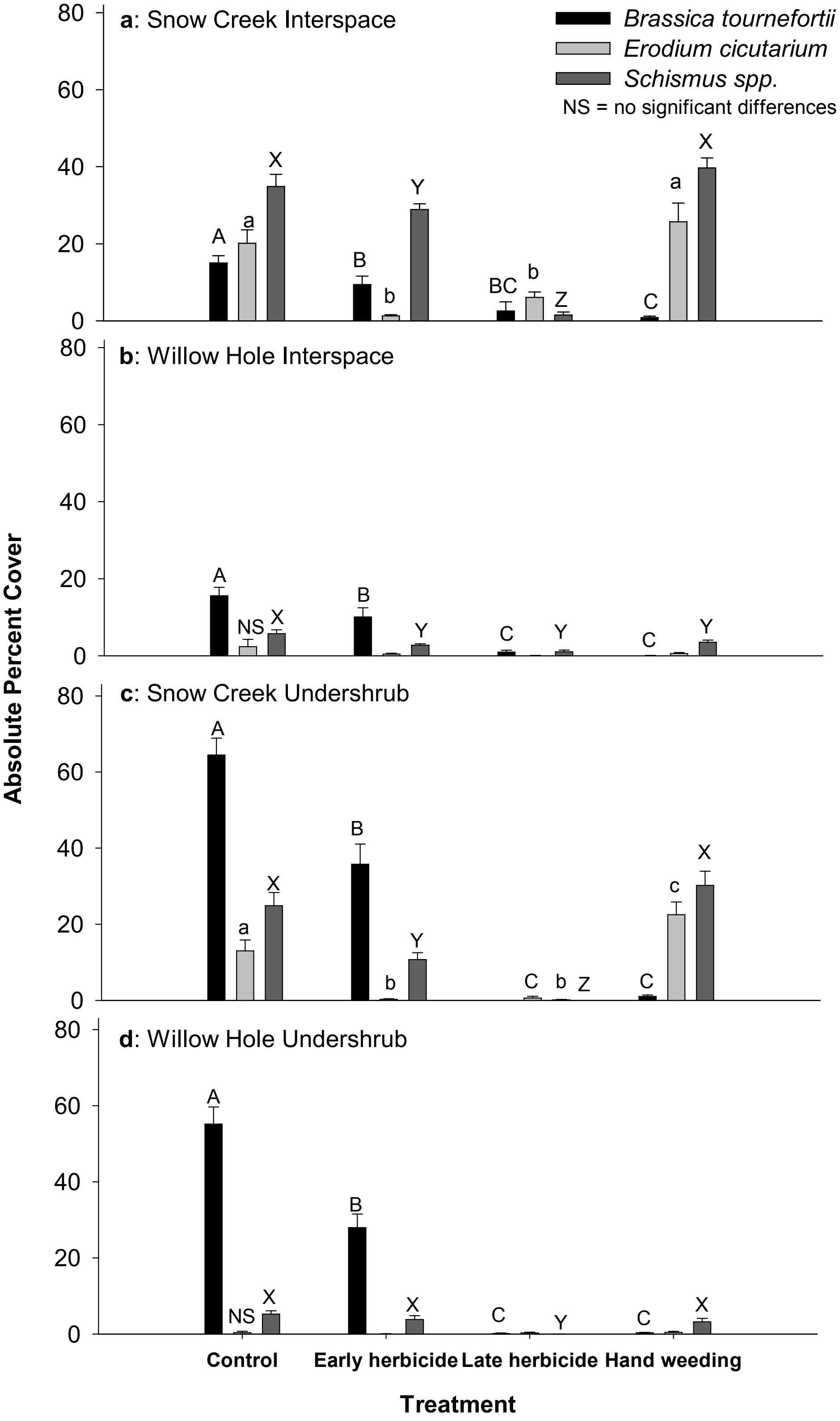

a: Snow Creek Interspace
b: Willow Hole Interspace
Relative Percent Cover
0
20
40
60
80
100
AB
a
XZ
x
AB
b
X
y
B
c
Y
y
A
a
Z
x
A
a
NS
x
A
b
NS
y
B
c
NS
z
A
c
NS
z
Herbicide Litter
Natives
Exotics
Litter
Bare Ground
Control
Early herbicide
Late herbicide
Hand weeding
Treatment

3.3



a: Snow Creek Undershrub
b: Willow Hole Undershrub
Relative Percent Cover
0
20
40
60
80
100
AB
a
X
x
BC
b
Y
y
C
c
X
xy
A
b
Y
xy
A
a
NS
x
AB
b
NS
xy
A
c
NS
x
B
c
NS
y
Herbicide Litter
Natives
Exotics
Litter
Bare Ground
Control
Early herbicide
Late herbicide
Hand weeding
Treatment

3.4


a: Snow Creek Interspace
Brassica tournefortii
Erodium cicutarium
Schismus spp.
NS = no significant differences
80
60
40
20
0
A
a
X
B
b
Y
BC
b
Z
C
a
X
b: Willow Hole Interspace
80
60
40
20
0
A
NS
X
B
Y
C
Y
C
Y
c: Snow Creek Undershrub
80
60
40
20
0
A
a
X
B
b
Y
C
b
Z
C
c
X
d: Willow Hole Undershrub
80
60
40
20
0
A
NS
X
B
X
C
Y
C
X
Absolute Percent Cover
Control
Early herbicide
Late herbicide
Hand weeding
Treatment

3.5

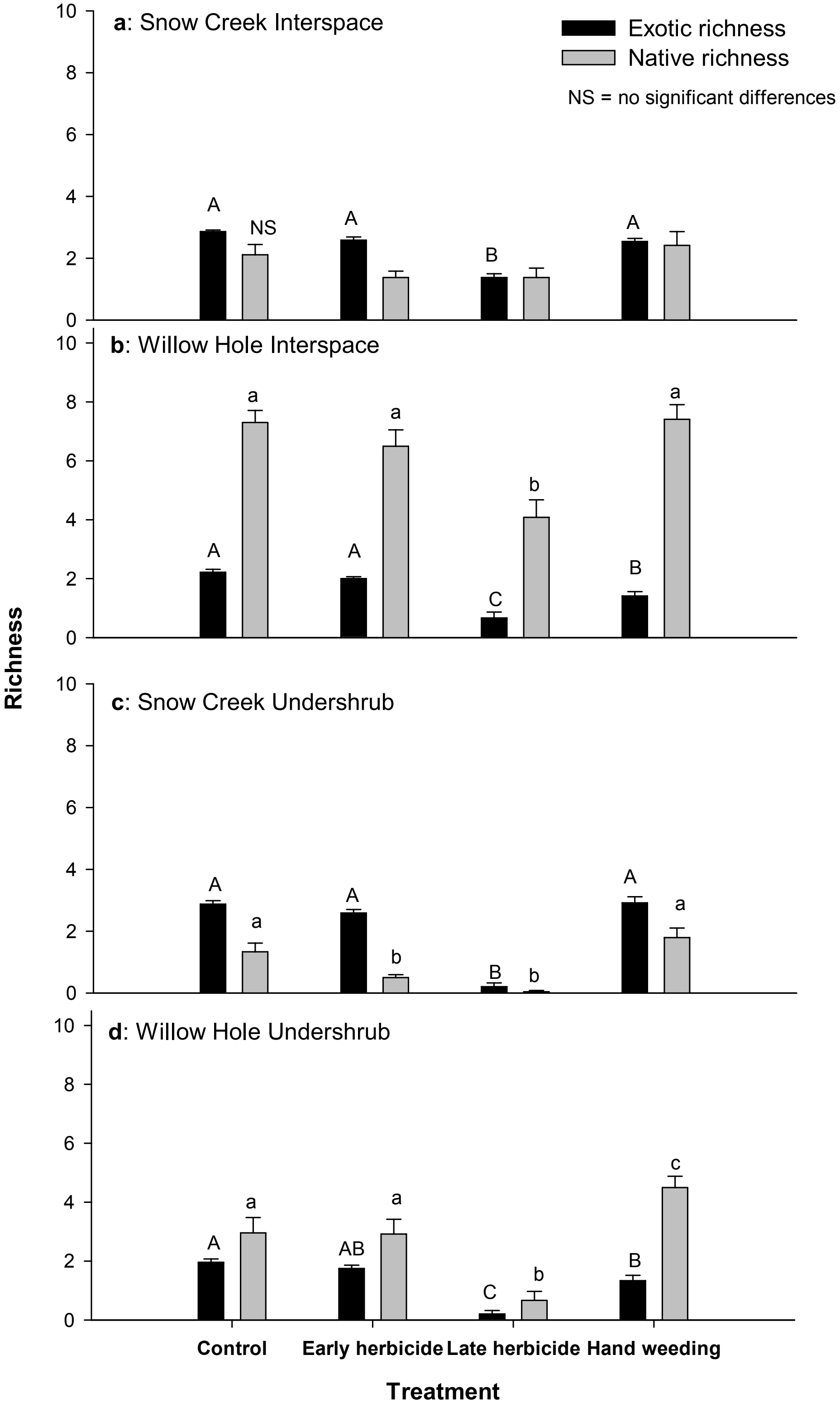

Richness
10
8
6
4
2
0
a: Snow Creek Interspace
Exotic richness
Native richness
NS = no significant differences
A
NS
A
B
A
b: Willow Hole Interspace
a
a
b
a
A
A
C
B
c: Snow Creek Undershrub
A
a
A
b
B
b
A
a
d: Willow Hole Undershrub
a
A
a
AB
C
b
c
B
Control
Early herbicide
Late herbicide
Hand weeding
Treatment

Table 3.1: Average total cover and standard error for all species present in treated plots at Snow Creek. The most dominant species (> 5 % cover) per treatment are highlighted.

	Snow Creek Interspace								**Snow Creek Undershrubs**							
	Control		Early herbicide		Late herbicide		Hand weeding		Control		Early herbicide		Late herbicide		Hand weeding	
Species	Cover (%)	s.e.	Cover (%)	s.e.	Cover (%)	s.e.	Cover (%)	s.e.	Cover (%)	s.e.	Cover (%)	s.e.	Cover (%)	s.e.	Cover (%)	s.e.
Amsinckia tesselata															0.50	0
Brassica tournefortii	22.47	2.94	12.21	2.72	31.50	26.50	2.05	1.02	64.46	4.46	35.77	5.29			2.19	0.94
Bromus rubens			0.80	0.20	0.50	0			25.00	0	3.57	1.06			4.09	1.18
Camissonia pallida	1.65	0.25	2.46	0.63	1.23	0.36	1.19	0.26	1.13	0.63	0.73	0.27			1.30	0.30
Chaenactis fremontii	1.67	0.93	0.50	0.00	1.50	0	1.50	0.22	3.19	1.05					1.48	0.21
Crassula connata	0.75	0.25	6.85	4.78					2.00	0					10.00	0
Cryptantha angustifolia							0.20	0								
Eriastrum diffusum			1.00	0												
Eriastrum wilcoxii	1.50	0.58	0.50	0			0.63	0.13								
Erodium cicutarium	32.63	4.70	2.80	0.62	7.35	1.68	33.36	6.52	14.89	2.76	1.30	0.54	3.75	0.75	24.25	3.62
Larrea tridentata									35.82	6.71	41.82	5.26	50.79	4.78	31.67	4.96
Lastarria coriacea	2.00	0														
Lasthenia californica	2.00	0					0.20	0	0.50	0						
Lepidium spp.													3.00	0	0.50	0
Loeflingia squarrosa	0.30	0	1.31	0.34												
Lotus strigosus	3.16	0.80	0.50	0	2.08	0.60	4.10	1.41	2.60	0.81					3.40	1.20
Lupinus sparsiflorus	4.00	0							1.00	0	0.50	0.00				
Lupinus spp.			1.50	0												
Malacothrix glabrata	3.00	0			1.50	0	5.50	4.50							3.83	0.93
Pectocarya heterocarpa	7.72	2.41	3.46	0.81	2.75	0.52	10.75	3.44	1.88	0.88	0.63	0.13			1.30	0.53
Pectocarya recurvata			1.25	0					2.00	0	0.50	0.00				
Phacelia distans	1.00	0	0.50	0			0.50	0	11.50	10.50	5.00	0.00			2.00	1.00
Plantago ovata			0.50	0												
Schismus spp.	45.75	3.38	32.90	1.86	4.43	2.04	49.67	3.20	25.50	3.23	10.74	1.81			30.21	3.73
Sisymbrium spp.											1.00	0				
Stephanomeria spp.	4.57	0.85	1.39	0.39	0.90	0.24	7.05	2.81	7.50	1.84	4.50	3.50	6.00	0	10.10	4.53

Table 3.2: Average total cover and standard error for all species present in treated plots at Willow Hole. The most dominant species (> 5 % cover) per treatment are highlighted.

	Willow Hole Interspace								**Willow Hole Undershrubs**							
	Control		Early herbicide		Late herbicide		Hand weeding		Control		Early herbicide		Late herbicide		Hand weeding	
Species	Cover (%)	s.e.	Cover (%)	s.e.	Cover (%)	s.e.	Cover (%)	s.e.	Cover (%)	s.e.	Cover (%)	s.e.	Cover (%)	s.e.	Cover (%)	s.e.
Achronychia cooperi	0.82	0.27	3.00	2.67			0.50	0							0.15	0.05
Astragalus spp.			8.00	0	3.25	2.75										
Brassica tournefortii	18.65	2.65	11.42	2.69	4.13	1.53	0.31	0.17	55.17	4.51	27.96	3.59	3.50	0	0.77	0.15
Calyptridium monandrum	3.71	1.27	3.26	0.81	2.34	0.46	2.34	0.90	1.18	0.35	2.30	1.08	0.63	0.13	1.88	0.52
Camissonia claviformis	2.22	0.70	3.07	1.33	2.53	0.65	2.25	0.77	1.57	0.99	4.83	2.21	1.25	0.75	1.03	0.49
Camissonia pallida	7.48	2.08	9.64	1.89	11.20	6.11	5.33	1.36	4.52	1.20	5.34	0.90	4.25	3.88	7.43	2.17
Chaenactis fremontii	0.60	0														
Chorizanthe brevicornu	1.58	0.28	1.26	0.50	2.13	0.66	2.75	1.76	2.37	1.84	0.50	0			1.25	0.43
Crassula connata			0.13	0.03			0.76	0.23			2.00	0	7.00	0.00	6.83	4.46
Cryptantha angustifolia	9.04	1.58	8.33	0.88			4.85	0.70	1.53	0.40	2.81	0.50	0.50		2.71	0.78
Cryptantha maritima	1.00	0			0.50	0										
Cryptantha micrantha	0.10	0	0.20	0.06			0.20	0.10								
Eremalche exilis	0.50	0.3	4.10	2.99			2.55	2.45	4.00	0	9.50	5.50			0.50	
Eriastrum diffusum	4.26	1.38	2.79	0.60	1.00	0	4.75	1.43	1.54	1.00	2.70	1.30	1.81	0.19	2.48	0.69
Erodium cicutarium	8.47	4.22	3.36	0.76	4.25	1.18	1.88	0.44	4.50	0	1.00	0	2.33	0.67	2.63	1.18
Filago arizonica	2.20	0.87	2.23	0.70	1.00	0.38	3.16	0.81	1.75	0.75	1.58	0.62	1.13	0.38	2.09	0.72
Krameria greyi									11.00	0						
Larrea tridentata									59.83	4.85	36.88	5.73	60.46	4.94	35.86	6.77
Loeflingia squarrosa			0.90	0.65			2.04	1.55							0.50	
Loeseliastrum schottii	1.70	0.37	0.59	0.18	0.50		0.31	0.13							0.20	
Lotus strigosus	3.50	2.50	0.60	0.21	3.29	0.94	2.57	1.76			3.00	0				
Lupinus spp.	1.00	0			2.00	0										
Malacothrix glabrata	1.83	0.73	0.50	0	3.00	0.41			1.85	0.98					0.10	
Pectocarya heterocarpa	10.93	4.06	7.29	1.53	3.78	1.53	7.60	1.99	1.84	0.56	3.99	1.29	12.00	0	6.25	2.27
Pectocarya linearis	2.00				3.37	0.96										
Pectocarya platycarpa	0.50	0.30							1.00	0						
Pectocarya recurvata	9.06	3.05	7.38	3.26	4.57	1.03	5.10	1.47	10.75	6.45	2.17	0.83	6.00	0	4.86	3.46
Plantago ovata	0.20	0														
Rafinesquia neomexicana	1.07	0.34	2.14	0.76			0.70	0.30	2.75	1.44					4.33	1.86
Schismus spp.	6.78	1.17	3.07	0.46			3.96	0.53	5.83	0.77	4.91	1.20	0.25	0	4.09	1.04

CONCLUSION

Although this dissertation focuses specifically on *Brassica tournefortii*, the questions and results of this research are broadly applicable to desert invasion ecology. In Chapter 1, I asked, “why has *B. tournefortii* invaded the desert, whereas congeneric invasive mustards have not?” Because *B. tournefortii, B. nigra,* and *Hirschfeldia incana* are closely related species that share many similar traits, the difference in phenology between these species was a distinct finding that may explain the distribution of *B. tournefortii.* However, rapid phenology and consistent reproduction are traits that probably extend to other invasive species in harsh, variable environments.

In Canadian prairies, *Erodium cicutarium*, another desert invader, emerges in as little as 7 days and flowers in 46 days, which is a comparable phenology to *B. tournefortii*. Furthermore, *E. cicutarium* has been present in North America much longer than *B. tournefortii* (Mensing and Byrne 1998; Mensing 1998) and may have had the opportunity to adapt and produce ecotypes suited to various environments. In contrast, *B. tournefortii*, which is native to the Sahara region, was likely already pre-adapted to southern California’s arid climates, where it is currently invasive and exhibits no ecotypes (Chapter 1). *B. tournefortii* may be experiencing natural selection from climate at the fringes of its range, a hypothesis that is currently being explored by other investigators. With increased residence time, *B. tournefortii*’s rapid phenology may grant it the potential for widespread invasion in North America, similar to *E. cicutarium* (USDA NRCS 2009).

B. tournefortii invasion may be aided by chemical aspects as well. Brassicaceae as a group are consistently nonmycorrhizal and produce glucosinolates, which can deter predators and alter soil chemistry (Schreiner and Koide 1993). Other invasive mustards such as *Alliaria petiolata* are known to inhibit native plant by disrupting biotic interactions (Stinson, Campbell et al. 2006; Mueller 2009), but this has not been tested for *B. tournefortii* invasion of desert ecosystems. Glucosinolates and/or alteration of belowground biota may assist *B. tournefortii* in rapid invasion.

Chapter 2 investigated *B. tournefortii* interactions with native annuals, but results were variable. *B. tournefortii* at high densities and cover appears to interfere with native annuals during a high-precipitation year, but some interactions between *B. tournefortii* and native annuals were also positive during a low-precipitation year. These results do not support the hypothesis that *B. tournefortii* consistently impacts native forbs. If interference did occur, the effects might be time, space, or resource-dependent (Briones, Montana et al. 1998; Dickie, Schnitzer et al. 2005; Valiente-Banuet and Verdu 2008; Maestre, Callaway et al. 2009) and may not have been captured by the variables measured in this research. Because shrub interspaces, where this research was conducted, are not limited by aboveground resources such as light, most interactions are likely to occur belowground. The research in Chapter 2 did not correlate belowground resources with *B. tournefortii* density or annual forb success, nor did it measure competition or facilitation directly. Future research should focus on disentangling the effects of microsite soil resources, particularly nutrients and mycorrhizae, from plant-plant interactions. Such research may help explain the changing relationships of native species and/or communities with *B. tournefortii.*

B. tournefortii effects in desert communities are probably context-dependent on larger scales and at many trophic levels. Chapter 2 results indicate that relationships of native forbs to *B. tournefortii* vary with plant species, and Barrows et. al. (2008) found that *B. tournefortii* impacts fringe-toed lizards. This dissertation tested a single site in the central Mojave, and the cover of *B. tournefortii* measured during this work was not as high as can be observed in other areas in different years. The Rasor Rd. site used in this research might have been characterized as low to medium *B. tournefortii* density overall during the time it was measured, compared to the potential cover and density observed elsewhere (personal observation). Certainly higher density and cover would be more likely to have strong impacts on native flora and fauna alike, and such strong impacts would be most likely to occur during years of high precipitation and productivity. Unfortunately, these years also represent important opportunities for native annual reproduction (Bowers 2005; Hereford, Webb et al. 2006). Although drier years may allow some native annuals to reproduce with less *B. tournefortii* interference (Barrows, Allen et al. 2009), or even facilitation (Chapter 2), these benefits are likely to be outweighed by the large reduction in native fecundity during wet years caused by *B. tournefortii* (Barrows, Allen et al. 2009).

Invasive plant management may be most critical during high-precipitation years, both to enable natives to reproduce and to prohibit *B. tournefortii* from dispersing further and increasing its seedbank (Steers 2008; Barrows, Allen et al. 2009). Since other exotic annuals also experience “boom” years with high precipitation, these events present an excellent opportunity to manage a suite of invasive plants (Salo 2004). Land managers need new techniques beyond hand-weeding to remove invasive species in the desert, and this dissertation provides an alternative in applying broad-spectrum herbicide immediately after *B. tournefortii* emergence. Although this method comes with major tradeoffs in native plant mortality and wasted herbicide, it gains a great deal over hand-weeding in time, effort, cost and efficiency (Chapter 2). Further research is needed to determine when and where herbicide application will produce the intended, selective results. First, ecologists must revisit the interaction of precipitation amount, timing, and temperature on seed germination in the desert, comparing invasive annuals with natives to determine if there is a time lag between exotics and natives and under what conditions the greatest window for weed control occurs. Ideally, such a test would involve several species over several conditions, with *a priori* knowledge of seedbank composition. Data could then be applied to various predictive models, as has been proposed by Kurt Anderson, Helen Regan, and Cameron Barrows (personal communication). Second, effects of treatment should be followed over the subsequent growing seasons. This research is already underway using the same plots measured in this dissertation. Finally, rapid emergence is often a feature of non-native species across ecosystems (Bartolome 1979; DiTomaso 2007), and emergence-stage herbicide application may be as successful, or possibly more so, if applied elsewhere.

Desert annuals worldwide have been shown to have density-dependent germination, but high densities may facilitate germination, as in the Negev desert (Lortie and Turkington 2002; Lortie and Turkington 2008) or inhibit germination, as in North America (Inouye 1980; Tielborger and Valleriani 2005). In the case of inhibition, density-dependent germination has not been studied in the context of plant invasions, and it is probable that increased densities of exotic annuals may inhibit germination in native annuals even under favorable climatic conditions. Inhibition may also differ between monocots and dicots (Turkington, Goldberg et al. 2005). Density-depending inhibition of native forbs by invasive annuals should be researched, especially for exotic grasses such as *Bromus* spp. and *Schismus* spp. compared with exotic forbs, including *E. cicutarium* and *B. tournefortii.*

Germination of all the above species differs dramatically from native annuals in North America's deserts in that invasive annuals have few of the germination requirements that are a hallmark of native desert forbs. These requirements have been long explained as bet-hedging strategies that enable a wide diversity of forbs to inhabit a dangerously variable ecosystem, ensuring success far into the future even through long droughts and extreme temperatures (Went 1979; Gutterman 1994; Pake and Venable 1996; Smith, Monson et al. 1997). Invasive annuals, as a group, lack similar bet-hedging strategies, yet have been extremely successful in short periods of time (Went 1979; Blackshaw 1992; Salo 2004; Bangle, Walker et al. 2008). However, invasives also appear vulnerable to population crashes, and indeed *Bromus rubens* has experienced large-scale crashes in the last few decades (R. Minnich, personal communication). Will desert invasions be intense, but brief? Perhaps not; population crashes are a strong force of natural selection, and with the rapid generation time of desert invasives, rapid adaptation seems likely. Rather than invade and vanish, desert invaders may develop seed bet-hedging strategies more similar to those of desert natives. *E. cicutarium* may provide the example to test this hypothesis, since it has been in southern California for hundreds of years (e.g. Kudoh, Nakayama et al. 2007). Future research should examine the seed germination requirements of *E. cicutarium* from different environments, and compare dormancy strategies among populations of native and invasive *E. cicutarium.*

In conclusion, the invasion of *B. tournefortii* in southern California's deserts is a case study for ecological principles, challenging long-held assumptions about life history patterns and interactions of plants in desert environments. *B. tournefortii*, and the handful of other successful exotics in desert ecosystems, proves that even the most demanding of earth's ecosystems are vulnerable to invasion. Ecologists can learn much from studying invasions at the extremes of earth's environments, but these stark, unproductive ecosystems are perhaps the most at risk. As invasive species encourage fires and transform the landscape, ecologists must work equally to inform management and prevent further invasions.

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