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Responses of native and non-native Mojave Desert winter annuals to soil disturbance and water additions

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Abstract Habitat modification (i.e., disturbance) and resource availability have been identified as possible mechanisms that may influence the invasibility of plant communities. In the Mojave Desert, habitat disturbance has increased dramatically over the last 50 years due to increased human activities. Additionally, water availability is considered to be a main limiting resource for plant production. To elucidate the effects of soil disturbance and water availability on plant invasions, we created experimental patches where we varied the levels of soil disturbance and water availability in a fully crossed factorial experiment at five replicated field sites, and documented responses of native and non-native winter annuals. The treatments did not significantly affect the density (seedlings m^{-2}) of the non-native forb, *Brassica tournefortii*. However, the relationship between silique production and plant height differed among treatments, with greater silique production in disturbed plots. In contrast to *Brassica*, density of the non-native *Schismus* spp. increased in soil disturbed and watered plots, and was greatest in disturbed plots during 2009 (the second year of the study). Species composition of the native annual community was not affected by treatments in 2008 but was influenced by treatments in 2009. The native forb *Eriophyllum* sp. was most dense on water-addition plots, while density of *Chaenactis freemontii* was highest in disturbed plots. Results illustrate that habitat invasibility in arid systems can be influenced by dynamics in disturbance regimes and water availability, and suggest that invasiveness can differ between non-native annual species and among native annuals in habitats undergoing changing disturbance and precipitation regimes. Understanding the mechanistic relationships between water availability and non-native plant responses will be important for understanding the effects of shifting precipitation and vegetation patterns under predicted climate change in arid ecosystems.

Keywords *Brassica tournefortii* · Invasibility · Invasiveness · Nitrogen · Precipitation · Resource pulse · *Schismus*

Introduction

Worldwide, non-native plant species pose a major threat to biological conservation (Vitousek et al. 1996; Mack et al. 2000) and to the integrity of

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ecosystem functions and processes (D'Antonio and Vitousek 1992). Because biological communities are complex and dynamic, generalizations about their susceptibility to invasion have been elusive. However, increases in nutrient availability (Davis et al. 2000) and soil disturbance (Burke and Grime 1996; Huston 2004) have been hypothesized to increase susceptibility of an environment to invasion. Davis et al. (2000) proposed a fluctuating resource availability hypothesis of invasibility which suggests that a mechanistic relationship exists between invasibility and resource availability: a plant community becomes more invasible whenever the amount of unused water, soil nutrients, and light increases. Others have pointed to particular attributes of non-native plants in determining their ability to invade, including dispersal abilities of seeds (DiVittorio et al. 2007) and capability to produce copious amount of seeds (Rejmánek 2000) for increasing propagule pressure (Von Holle and Simberloff 2005).

In arid and semi-arid systems, water is the main limiting resource for annual plant seedling emergence and survival. Thus, plant abundance (native and non-native) should be positively related to water availability (Sala et al. 1992; Schwinning et al. 2005). Evaluating the influence of limiting resources on community invasibility in natural systems is critical for understanding factors, which may differ among ecosystems, governing non-native plant invasions. An important characteristic of arid and semi-arid systems is the beneficial role of water availability on germination, growth, and reproduction of resident native plants (Beatley 1974). A 25 mm or greater precipitation event, properly timed during the winter rainy season (October–April, most importantly October–January), is required to stimulate the germination of native winter annual species in the Mojave Desert of the southwestern USA (Beatley 1974). For many species, the germination of seeds is restricted to periods of abundant moisture and coincides with favorable soil and air temperatures (Ooi et al. 2009). Many native annuals have long-lived seed banks that delay germination until the onset of suitable environmental conditions but do not germinate all at once (Baskin and Baskin 1998; Adondakis and Venable 2004).

Species-specific patterns of germination for desert native and non-native winter annuals have been demonstrated in field conditions in response to water manipulations (Gutierrez and Whitford 1987; Pake and Venable 1995; James et al. 2006), suggesting that changes in the amount and timing of precipitation pulses could have major effects on population dynamics and plant community composition. For example, Adondakis and Venable (2004) found heterogeneous germination responses to environmental conditions in a guild of Sonoran Desert winter annuals. As groups, native and non-native species differed in their tendency to germinate. Non-native species showed an early germination pattern in response to precipitation timing and temperature. The tendency to germinate early should be important in determining competitive success of non-native species. Post-germination patterns of non-native species in the Mojave Desert suggest that invasive species compete with natives for water and soil nutrients (Brooks 2000). Furthermore, field and greenhouse experiments have linked the competitive superiority of non-native annuals to their ability to quickly utilize available resources for biomass and seed production (DeFalco et al. 2003; Pake and Venable 1995; Huxman et al. 2008). Because plant population dynamics in arid lands is highly dependent on water availability, under future climate change these systems are expected to be drastically affected by changes in precipitation and temperature. For instance, changing precipitation regimes (such as increases in large rainfall events) may enhance the susceptibility of habitats to invasion by non-native plant species (Weltzin et al. 2003; Bradley 2009). However, accurate prediction of precipitation changes in arid lands of the southwestern USA is difficult because of the region's complex topography and the challenges of modelling El Niño events (Randall et al. 2007). This highlights a pressing need for experimental work at the local scale to better address the role of water availability on a community's vulnerability to invasions by non-native plant species (Weltzin et al. 2003; Bradley et al. 2009).

Although resource availability may influence community invasibility, anthropogenic and natural disturbances can also play a key role in enhancing habitat susceptibility to invasion by non-native plant species. Disturbances can alter resource availability (Burke and Grime 1996) and habitat structure (Hobbs and Huenneke 1992) at multiple scales, creating empty niches that invaders can occupy. In arid lands of the southwestern USA, for example, large disturbances caused by wildfires facilitate invasions by non-native grasses (Brooks and Matchett 2006). Total production of non-native annual grasses increases in response to elevated soil N in a post-fire environment (Esque et al. 2010). Non-native species invasions are also facilitated by fine-scale disturbances that alter the physical characteristics of soil surfaces and create microhabitats conducive to seed entrapment that can lead to seedling survival and plant establishment (Chambers 2000). The physical activity of animals also alters soil nutrients, with patches of high soil N and P occurring near animal dwellings (Wagner et al. 2004; Eldridge et al. 2009). These areas provide microsites with increased available resources that non-native species may exploit.

Also, human activity can aid in the expansion of non-native plant species into unoccupied areas. Promoting recreational use of natural areas has resulted in the construction of linear features such as roads and trails (e.g., foot and bicycle) that act as corridors for seed dispersal of non-native plant species (Parker et al. 1993; Cutway and Ehrenfeld 2010). Road construction and maintenance operations provide safe sites for seed germination and establishment where water runoff keeps soil moisture relatively high so that non-native species can invade new habitat from road edges (Parker et al. 1993; Gelbard and Belnap 2002). In addition, ground-disturbing activities from the development of solar energy in the desert could result in the removal of dominant native vegetation (Abella 2010). Based on a fluctuating resources mechanism for invasions, non-native species are expected to proliferate, persist, and become dominant after the disturbance (Chambers et al. 2007; Prevey et al. 2010). Therefore, understanding the causal relationships between ground disturbance and non-native plant invasions is essential for identifying appropriate management strategies, especially under future scenarios of increased human activity.

During the last 50 years, the Mojave Desert has experienced an exponential increase in human habitation, typically associated with increased proliferation of non-native plant species linked to increased human activities (Hunter et al. 2003). This setting, coupled with its limited water availability, makes the Mojave Desert a model system for testing hypotheses on plant invasions. However, the roles of water and disturbance in community invasibility have not been well studied in this system. In a sampling study, Brooks (1999) found that soil disturbance was not significantly associated with habitat invasibility by non-native plants in the western Mojave Desert, but soil nutrients were correlated with invasibility. Here, we experimentally isolated the influences of water, disturbance, and their interaction in influencing non-native and native species establishment.

Two of the most invasive non-native annuals at the lower elevations in the Mojave Desert include the forb, *Brassica tournefortii* (Sahara mustard), and the grasses *Schismus* spp. (Mediterranean grass). *Brassica tournefortii* is a winter annual native to the southern and eastern parts of the Mediterranean rim, where it establishes viable populations on sandy soils (Thanos et al. 1991). In the Mojave Desert in southern Nevada, *B. tournefortii* has spread into a variety of habitats, including gypsum-derived soils (which are inhabited by numerous rare endemic plant species) (Abella et al. 2009). As a winter annual, *B. tournefortii* seeds germinate after winter rainfall (October through April) and before many of the native annuals. The population densities of this species are influenced by among-year rainfall patterns (Barrows et al. 2009), and during years of high rainfall, dense stands can establish. The non-native annuals *Schismus* spp. (Mediterranean grass), comprised of the closely related *S. arabicus* and *S. barbatus*, are invasive grasses native to southern Europe, northern Africa, and the near East (Jackson 1985). *Schismus* is now common in the Mojave and Sonoran Deserts, especially in disturbed areas, and has been shown to favor interspaces between shrubs (Brooks 1995). As a winter annual, seed germination is stimulated by winter rains, and its rapid growth, seed dispersal, and germination capabilities make it a superior competitor for resources over native annuals (Gutterman 2000). In addition, *Schismus* has the potential to promote wildfires by increasing fuel load and connectivity between perennial shrubs (Brooks and Matchett 2006).

We assessed the effects of water manipulations and ground-surface disturbance in five independent sites in the eastern Mojave Desert during 2 years by quantifying the density of non-native and native annuals and reproductive characteristics of the non-native *B. tournefortii*. Based on the resource availability hypothesis of plant invasion (Davis et al. 2000), and germination patterns of Mojave Desert winter annuals in response to precipitation, we hypothesized that a high density of native and non-native invasive species would become established in patches where resource availability was experimentally manipulated through water additions. We further hypothesized that soil disturbance would promote the establishment of non-native species, and would decrease the density of native species.

Materials and methods

Study area

We conducted this study in Lake Mead National Recreation Area (LMNRA) in Clark and Mohave Counties located in Nevada and Arizona, USA. The dominant plant community within LMNRA is creosote-scrub (*Larrea tridentata*) (Rundel and Gibson 1996). Soils of the study sites are sandy with a small percent of clay and silt (Table 1). Most precipitation in the eastern Mojave Desert falls during the winter season (October to April) (Beatley 1974; Hereford et al. 2006). Long-term (1937–2006) average annual precipitation for the nearby city of Las Vegas, Nevada is 110 mm, and average monthly temperatures range from a low of 1.3°C in January to a high of 40°C in July (Western Regional Climate Center, Reno, NV). The total amount of winter precipitation recorded in October-January during the first year of the study (2007–2008) was 33 mm (83% of the long-term average of 39 mm) and 42 mm (108% of average) during the second year (2008–2009) (Western Regional Climate Center, Reno, NV).

Experimental treatments

We selected five sites based on land management records of non-native species occurrences (Abella et al. 2009) to evaluate our experimental treatments. Field surveys of non-native species indicated that the populations we selected were in the early stages of establishment. At each site, we established 12, 1 m × 1 m plots in a four column × three row matrix. Plots were established in open areas (i.e., interspaces between shrubs) and separated from each other by 3 m. Plots were placed more than 150 m from paved and unpaved roads. Treatment combinations were assigned using a random block design and consisted of water additions, soil disturbance, water additions + soil disturbance, and a control. We applied water (7.57 L plot^{-1}) at approximately 2-week intervals during October through January (7 applications) using a watering can with a broad, multiple-perforated spout that applied a gentle stream of water. The entire amount of water for a given watering was applied within a day. We applied a total of 106 L m^{-2} of water in 14 applications over 2 years (2007/2008 and 2008/2009). Our water applications added 53 mm of water each year, increasing October-January precipitation by 1.6-fold over natural precipitation in 2007/2008, 1.2-fold in 2008/2009, and 1.3-fold over the long-term, October-January average. The soil disturbance treatment was implemented in October 2007 and 2008 before plant emergence, using a rake to disturb the upper soil surface. Raking loosened up the soil and created small depressions where water accumulated during water applications. All treatments were

Table 1 Soil characteristics of study sites for the habitat invasibility study conducted in the eastern Mojave Desert, USA

Site	Location[a]	Clay[b] (%)	Silt (%)	Sand (%)	C (%)	N (%)	Mean ± SE		Elevation (m)
							Air temp (°C)[c]	Soil temp (°C)	
Box car	NV	5	13	82	0.13	0.014	10.7 ± 3.0	11.0 ± 2.0	374
Govt. wash	NV	4	9	87	0.27	0.017	11.0 ± 2.5	10.9 ± 2.5	382
Jumbo wash	AZ	6	8	86	0.25	0.016	11.2 ± 2.5	11.0 ± 2.0	360
Willow beach	AZ	4	25	71	0.41	0.034	11.6 ± 2.5	11.2 ± 2.0	287
Six mile	NV	5	6	89	0.17	0.017	14.2 ± 2.8	11.6 ± 2.8	450

[a] *NV* Nevada, *AZ* Arizona

[b] Analyses are from soil samples collected from open spaces at a 5 cm depth. Soil texture was analyzed using the hydrometer method and a C/N analyzer was used to obtain percent soil N

[c] HOBO temperature data loggers were used to collect ambient and soil temperatures and averaged over winter months

implemented in two consecutive years; therefore, the experiment provided an opportunity to detect temporal variation in seedling emergence patterns.

To evaluate treatment effects, we counted all plants on each plot to obtain density estimates for both native and non-native annual species. *Brassica tournefortii* seedlings were counted as they first emerged in December, and height (cm) and silique production (number of seed pods per plant) were measured after the plants had stopped flowering in late March as an indirect way to measure resource availability (Whitford and Gutierrez 1989). Individuals of native and *Schismus* species were counted in March when plant production peaked for accurate species identification. Species nomenclature follows Baldwin et al. (2002).

Statistical methods

A non-parametric ranks approach was used to estimate relative treatment effects on *B. tournefortii* and *Schismus* density separately (Brunner et al. 2002). Within the analysis, plots were used as the subject effect, nested within site and water and disturbance treatments, and year was the within-subject effect. Fixed effects included water, disturbance, year, and two- and three-way interactions. Random effects included site and interactions with the fixed effects. We followed Brunner et al. (2002) and Shah and Madden (2004) to estimate relative effects and confidence intervals using the 'LD_CI' SAS macro developed by Brunner et al. (2002).

To evaluate treatment effects on *B. tournefortii* silique production, plant height was included as a covariate and analysis of covariance (ANCOVA) was used on $\log_{10}$ transformed data in order to meet parametric assumptions. Because *B. tournefortii* emergence was sporadic during the study, site was used as the subject effect to obtain a reasonable estimate of treatment response and to deal with the missing year (2008) by plot combinations resulting simply from absences of *B. tournefortii* occurrences on some plots. The model treated year, water, disturbance, plant height, and all interactions as fixed effects. Akaike Information Criterion (AIC) was used to obtain parameter estimates and to determine the final model. Reduced major axis (RMA) regression was used to compare slopes post-hoc (Sokal and Rohlf 1995) and was implemented using RMA software (Bohonak 2004).

Treatment effects on the species composition (using density) of native winter annuals were compared using a permutational multivariate analysis of variance (Anderson 2001; McArdle and Anderson 2001) implemented in 'distlm' (Anderson 2004). Data were standardized by observation, and dissimilarity was estimated by the Hellinger distance (Legendre and Legendre 1998). We analyzed each year separately, and treated water, disturbance, and their interactions as fixed effects tested over a random site effect. Results are based on Monte Carlo simulations for *P* values due to the modest number of permutations possible in the data set. All analyses, other than those using RMA and 'distlm', were performed in SAS v9.1 (SAS Institute 2002–2003). Treatment effects were considered significant at alpha = 0.05 for all analyses.

Results

Water addition and soil disturbance did not have a statistically significant effect ($P > 0.05$) on the density of *B. tournefortii* plants in either year of the study. In 2008 during the first year of the study, *B. tournefortii* density m^{-2} ranged from 25 ± 17 (mean ± SE, $n = 5$ sites) in watered + disturbed plots, to 42 ± 34 in the control. In 2009, density ranged from 7 ± 4 in watered plots, to 27 ± 22 in disturbed plots.

Brassica tournefortii silique production also was not influenced by the experimental treatments (Table 2). However, including plant height as a covariate significantly predicted silique production. Additionally, there was a significant interaction

Table 2 Analysis of covariance (ANCOVA) models explaining treatment and *Brassica tournefortii* height (cm) relationships with silique production (number of siliques/plant) in a habitat invasibility study in the eastern Mojave Desert, USA

Effect	*df*	*F*	*P* value
Water	1, 4	0.13	0.733
Disturbance	1, 4	1.14	0.346
Water + disturbance	1, 4	2.56	0.184
Height	1, 149	174.95	0.000
Height × water	1, 149	0.00	0.952
Height × disturbance	1, 149	2.50	0.116
Height × water × disturbance	1, 149	4.35	0.038

Plant height was used as a covariate. Degrees of freedom (*df*) are reported as numerator, denominator between plant height and experimental treatments associated with silique production, demonstrating heterogeneity of slopes among water and disturbance treatment combinations. Plants in watered and soil disturbed plots produced more siliques for their size (Fig. 1); however, RMA regressions indicated that soil disturbance alone led to the production of more siliques per unit height (Table 3; Fig. 2).

In contrast to *B. tournefortii*, *Schismus* showed a significant pattern in its ability to invade habitats among treatments. Relative treatment effects on *Schismus* density were greater when compared to control plots (Fig. 3). *Schismus* density was not influenced by time, as the year effect and the interaction between water additions and year were not statistically significant (Table 4). In soil disturbed plots, *Schismus* density was significantly influenced by time, as soil disturbance and year interacted. Density was greater with water addition in 2008 and also increased with disturbance in non-watered plots in 2009 (Table 4; Fig. 4).

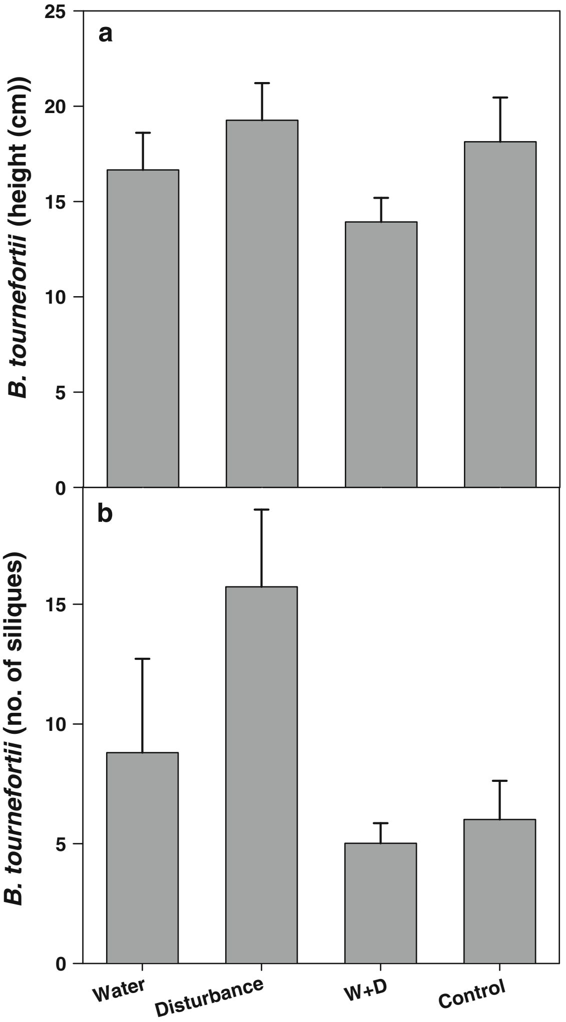

Fig. 1 Mean (+1 SE) *Brassica tournefortii* **a** height (cm) and **b** number of siliques. Plants in watered and disturbed plots produced a significantly greater number of siliques for their size

Table 3 Slopes obtained from reduced major axis (RMA) regression between height ($\log_{10}$ transformed) and water and soil manipulations for *Brassica tournefortii* silique production ($\log_{10}$ transformed)

Treatment	Slope	SE	95% CI	Pattern[a]	R^2
Control	1.055	0.151	0.740 ± 1.370	a	0.567
Water	1.738	0.264	1.194 ± 2.282	ab	0.422
Disturbance	1.714	0.147	1.417 ± 2.010	b	0.678
W + *D*	1.294	0.095	1.104 ± 1.485	ab	0.653

[a] Pattern denotes significant differences based on *t* statistics for linear approximations in RMA

Over the duration of the study, 30 species of native winter annuals were recorded, and we observed variable density patterns among species across treatments (Table 5). The density of *Chaenactis fremontii* was highest in soil disturbed plots while *Eriophyllum* sp. was most dense in watered plots. Native annual species composition was not influenced by water and disturbance manipulations in 2008, but treatment effects were statistically significant in 2009 based on permutational multivariate analysis of variance (Table 6).

Discussion

The spread and establishment of non-native plant species can be facilitated by the physical condition and resource availability of the invaded habitat (Davis et al. 2000; Burke and Grime 1996). In our study, the two non-native species (*B. tournefortii* and *Schismus*) responded differently to specific conditions of water availability and soil disturbance. Invasive ability appears to be controlled by a resource-based mechanistic process in which invasion success increases with availability of unused water, at least for *Schismus*. *Schismus* seems to have the greatest invasive potential at these sites, as it positively responded to water availability and soil disturbance. Water pulses at approximately 2-week

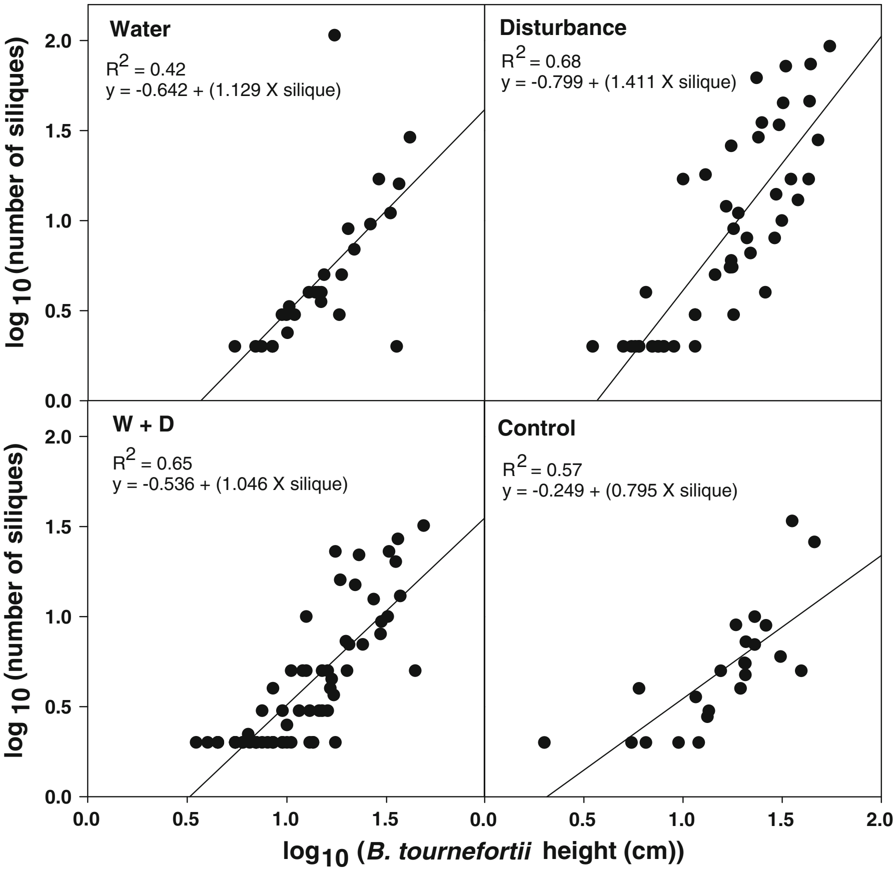

Fig. 2 Log–log plots of silique production (numbers per plant) as a function of *Brassica tournefortii* height (cm) in experimental plots. Water and disturbance treatments stimulated silique production. See Table 2 for results of ANCOVA, and Table 3 for RMA regression

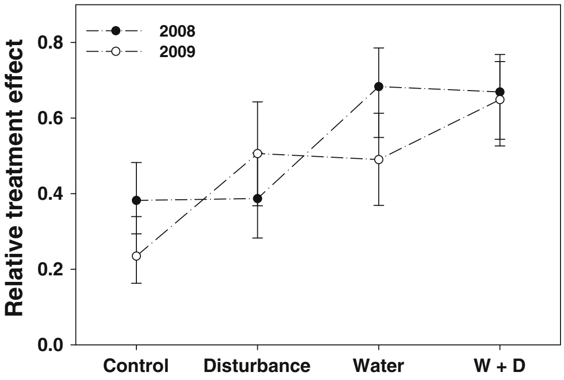

Fig. 3 Mean relative treatment effects on *Schismus* spp. density by year interaction. *Error bars* represent 95% CI

Table 4 Non-parametric ANOVA for the habitat invasibility experiment testing effects of water addition and soil disturbance on *Schismus* spp. density (seedlings m^{-2})

Treatment	*df* (num, den)	*F*	*P* value
Water	1, 112	11.0	0.001
Disturbance	1, 1.5	1.5	0.375
Water + disturbance	1, 112	0.3	0.610
Year	1, inf	0.4	0.535
Water × year	1, inf	1.7	0.186
Disturbance × year	1, inf	8.4	0.003
Water × disturbance × year	1, inf	0.3	0.588

inf infinity, see Brunner et al. (2002) and Shah and Madden (2004) for further details on the technique

intervals stimulated high densities of *Schismus* seedlings over two field seasons. Others have observed similar responses by *Schismus* to increased levels of water availability (James et al. 2006; Gutierrez and Whitford 1987; Pake and Venable 1995). The observed plant density patterns are likely due to lack of competition for available resources in open areas. For example, the presence or absence of dominant native shrubs has been documented to influence invasion success (Chambers et al. 2007; Prevey et al. 2010). In the presence of neighbor shrubs, available resources are captured by shallow and deep roots,

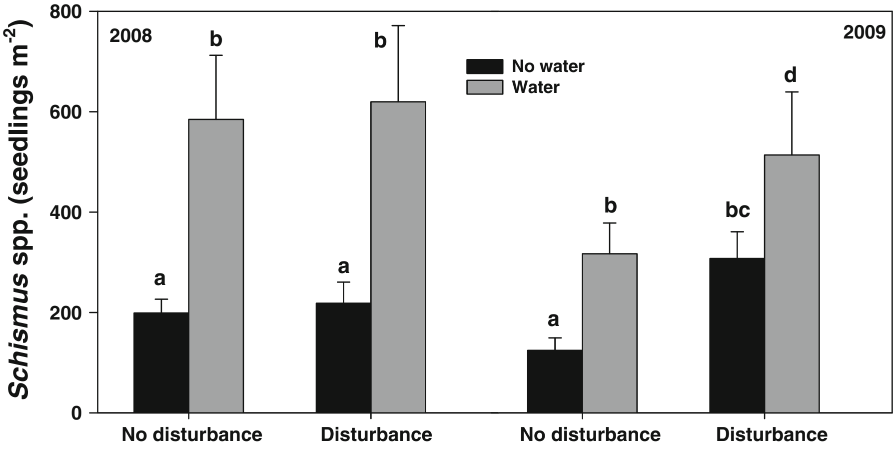

Fig. 4 Mean (+1 SE) density of *Schismus* spp. seedlings in plots where resource availability was manipulated through water additions and soil disturbance. *Different letters* denote significant differences

resulting in lower amounts of unused resources following water additions, anticipated to reduce *Schismus* density (Ogle et al. 2004). However, these effects would need to be balanced with the potentially positive influences (e.g., shading) of the shrubs on *Schismus*, suggesting that competition studies would be necessary to achieve an accurate mechanistic understanding of species interactions and their roles in plant community invasibility.

Although we did not experimentally manipulate N levels, soil N has been suggested to be a co-limiting factor for non-native plant establishment in the Mojave Desert (Brooks 2003; Rao and Allen 2010; James et al. 2006). Nitrogen is typically more available following pulses of precipitation, which increase mineralization and nutrient supply to roots (Fisher et al. 1987). As a result, it is possible that available N may have influenced the density of *Schismus* in this study. At our study sites, soil N was lower in the interspaces between shrubs (total soil N = 0.01%) when compared to underneath shrub canopies (0.39%), typical of arid ecosystems such as the Mojave Desert (Titus et al. 2002). However, significantly higher biomass of *Schismus* in the interspaces between shrubs can be experimentally achieved through N additions during years of above-average precipitation (Brooks 2003; James et al. 2006). Hence, the additive effects of increased water and N availability may exacerbate the susceptibility of a habitat to invasions by *Schismus* and other non-native grasses (e.g., *Bromus rubens* [red brome]) (Rao and Allen 2010). However, a full analysis of the effects of water and N availability on non-native plant establishment, growth, and reproduction should be the focus of additional research.

In accordance with the fluctuating resource invasibility hypothesis, an increase in water availability led to an increase in community invasibility (measured by quantifying non-native species plant density; Davis et al. 2000). A resource addition of 53 mm of water supplied over a 4-month time period during winter, a critical time for seed germination, was intended to increase resource availability, likely due to soil moisture augmentation at different soil depths during the time of water applications (Muldavin et al. 2008). The observed responses by *Schismus* to water manipulations suggest that increased water availability due to changes in precipitation patterns may enhance the susceptibility of this system to invasions by non-native plant species. Climate change scenarios predict significant alterations in the timing and magnitude of precipitation in arid and semiarid ecosystems, which may result in the expansion and establishment of non-native invasive plants (Bradley et al. 2009). Therefore, in understanding patterns of invasions under future climate conditions, it would be important to combine experimental and modeling approaches to create more accurate models and to validate existing ones (Bradley 2009).

In arid systems, soil disturbance has been implicated in facilitating invasions (e.g., Burke and Grime 1996) because disturbance alters the distribution of water, the primary limiting resource for plant production, and soil nutrients and surface characteristics

Table 5 Response of native winter annuals to water addition, soil disturbance, and their combination during the second year of a habitat invasibility study

Species	Water (*W*)	Disturbance (*D*)	*W* + *D*	Control
Amsinckia tessellata	0	1 ± 0	0	1 ± 0
Astragalus sp.	3 ± 1	5 ± 0	1 ± 0	0
Calochortus flexuosus	0	1 ± 0	0	1 ± 0
Camissonia sp.	1 ± 0	4 ± 1	4 ± 1	1 ± 0
Chaenactis carphoclinia	1 ± 0	0	1 ± 0	0
Chaenactis fremontii	75 ± 36	143 ± 82	116 ± 62	68 ± 36
Chamaesyce albomarginata	0	0	1 ± 0	0
Chorizanthe brevicornu	3 ± 1	4 ± 1	3 ± 0	4 ± 1
Cryptantha sp.	29 ± 8	23 ± 9	22 ± 10	40 ± 28
Draba cuneifolia	2 ± 1	0	5 ± 4	2 ± 0
Eriogonum sp.	2 ± 1	0	0	1 ± 0
Eriophyllum sp.	236 ± 129	153 ± 96	163 ± 83	80 ± 53
Eschscholzia sp.	2 ± 1	3 ± 0	12 ± 3	3 ± 1
Gilia sp.	0	8 ± 6	4 ± 1	0
Guillenia lasiophylla	0	1 ± 0	2 ± 0	0
Langloisia setosissima	1 ± 0	0	1 ± 0	2 ± 0
Lepidium sp.	4 ± 1	1 ± 0	3 ± 1	5 ± 2
Linanthus sp.	15 ± 6	4 ± 1	5 ± 1	8 ± 3
Lupinus sp.	3 ± 1	3 ± 1	4 ± 1	3 ± 1
Malacothrix sp.	1 ± 0	3 ± 2	3 ± 2	1 ± 0
Mentzelia sp.	3 ± 1	1 ± 0	3 ± 1	6 ± 5
Nama demissum	2 ± 1	0	0	9 ± 0
Pectocarya sp.	21 ± 6	30 ± 10	11 ± 4	22 ± 6
Phacelia sp.	1 ± 0	1 ± 0	1 ± 0	0
Plantago ovata	63 ± 37	67 ± 31	65 ± 49	112 ± 47
Rafinesquia sp.	1 ± 0	1 ± 0	0	0
Salvia columbariae	0	3 ± 2	0	1 ± 0
Stephanomeria exigua	0	1 ± 0	1 ± 0	0
Streptanthella sp.	0	5 ± 0	2 ± 0	0
Vulpia octoflora	4 ± 2	9 ± 3	10 ± 3	1 ± 0

Data are mean ± SE for the density (m^{-2}) for each treatment combination averaged across five experimental sites

Table 6 Treatment effects on winter native annual composition in 2009

Treatment	*df*	SS	MS	*P* (perm)
Water	1	0.590	0.590	0.005
Disturbance	1	0.648	0.648	0.017
Water × disturbance	1	0.107	0.107	0.720
Site	4	10.363	2.591	
Total	59	24.416		

Results are from permutational MANOVA and *P* values were generated from 999 permutations constrained within site

(Yair and Shachak 1982). Thus activities, natural or anthropogenic, that disturb top soil layers can create areas conducive to invasions. The density of *Schismus* increased in soil disturbed plots, suggesting that the disturbance treatment created conditions suitable for germination and establishment, possibly by introducing resources into habitat patches. Our soil disturbance treatment may have increased water availability by increasing water retention and infiltration in soil disturbed plots because water accumulated in depressions created by raking the top soil surface during water applications. Moreover, soil depressions may have increased the availability of sites for successful seed arrival (Chambers 2000; James et al. 2010) or enhanced microhabitat conditions suitable for seed germination (James et al. 2010).

Successful invasions require the arrival, establishment, growth, and reproduction of non-native plant species and the subsequent spread into un-invaded habitat (Rejmánek 2000; DiVittorio et al. 2007). *Schismus* seeds are adapted for long distance wind dispersal (Gutterman 2000), and could utilize disturbed habitat patches as stepping stones to spread and colonize new habitats. At the patch scale, invasion by *Schismus* could be facilitated by soil disturbance associated with small fossorial mammals (Schiffman 1994) and soil turnover created by harvester ants (Wagner et al. 2004). The activities of rodents and ants in desert ecosystems are important in the creation of spatiotemporal resource patches (Wagner et al. 2004; Eldridge et al. 2009). At the landscape scale, invasion by *Schismus* could be facilitated by increased human activity. For example, hundreds of square kilometers of native vegetation are being considered for removal to construct solar structures and support facilities in the Mojave Desert (US Bureau of Land Management 2010). Such activities could create habitat conditions suitable for invasions through the removal of vegetation and soil disturbance. Land managers will be challenged to manage vulnerable areas following disturbance in ways that reduce habitat invasibility.

In contrast to our expectations, *B. tournefortii* density was not influenced by experimental manipulations: water additions and soil disturbance did not increase plant density over time. This finding is surprising because mass germination of *B. tournefortii* has been correlated with precipitation patterns, increasing during years of above average rainfall, and decreasing during years of below average rainfall (Barrows et al. 2009). Our water manipulations simulated a 53-mm precipitation addition each year, and the amount of experimental water was anticipated to be sufficient for stimulating germination of *B. tournefortii*, as the germination of winter annuals is stimulated by 25 mm of precipitation in the Mojave Desert (Beatley 1974). A plausible explanation for the lack of response to watering may be the duration of the applied resource pulse, and whether it was long enough for water to have infiltrated to some soil depth where soil conditions would be favorable for *B. tournefortii* seed germination. The deeper water infiltrates, the longer it usually takes to deplete, and soil water remains at levels conducive for seed germination for longer times (Chesson et al. 2004). On the other hand, sufficient natural precipitation may have existed for *B. tournefortii* emergence, making *B. tournefortii* non-responsive to further water additions. This species' lack of response to water addition was similar to some native annual species but not others (Table 5). The Westoby-Bridges' pulse-reserve model (Noy-Meir 1973) has been instrumental in explaining responses of native desert vegetation to pulses of precipitation, and in light of future climate change, future studies should evaluate the effects of pulsed resource duration and intensity on community invasibility.

Another possibility for the lack of treatment response in *B. tournefortii* density is seed dispersal limitations, and as a result, seed densities may have been low in our study plots. However, potential seed sources were located within a few meters from our study plots. Dispersal mechanisms for *B. tournefortii* have not been empirically shown, and wind dispersal is not likely due to the heavy mass (1.17 mg) and lack of dispersal features of the seeds. The ability of seeds to disperse into new habitats has been shown to be an important determinant of colonization and invasion success (DiVittorio et al. 2007). Lastly, the lack of response to watering treatments may also be explained by granivory pressure by harvester ants (*Pogonomyrmex* sp.) and rodents (Heteromyidae) being high in the interspaces between shrubs, reducing soil seed banks. Seed-eating ants and rodents can have profound effects on plant distributions in desert systems (Brown et al. 1979). In our study area, *B. tournefortii* seed removal by harvester ants is higher in spaces between shrubs than under shrubs (Suazo et al., unpublished data), and post-dispersal seed predation has been suggested as a potential mechanism controlling invasions and spread of non-native plant species (Maron and Vilá 2001). However, interactions between *B. tournefortii* seeds and native seed granivores are yet to be determined in the Mojave Desert. Consequently, it is unknown whether native granivores will facilitate or suppress invasions by non-native plant species. In other systems, rodent seed predation can be a barrier to invasions by non-native plant species (Nunez et al. 2008). Due to the important role that native granivores (i.e., rodents and ants) play in structuring plant populations and soil seed banks in North American deserts, in future studies it would be beneficial to assess granivore influence on non-native plant species population dynamics.

Plants growing in environments where water availability and soil nutrients are high are likely to become larger and produce more seeds than plants growing in resource-limited environments (Greipsson and Davy 1997). *Brassica tournefortii* silique production was significantly associated with soil disturbed plots. Plants produced more siliques for their height relative to plants in control plots, indicating that *B. tournefortii* utilized available resources for silique production. Therefore, an increased number of siliques can be equated to an increase in the number of seeds produced per plant. Greater seed production would translate into a high probability for persistence and possibly expansion of populations. Although we did not directly measure seed production, others have found a strong relationship between plant size and seed count, and have reported that individual plants can produce more than 16,000 seeds (Trader et al. 2006). Clearly, *B. tournefortii* is capable of copious seed production, and our results have demonstrated that individuals on average can be more fecund in disturbed habitats. At these sites, disturbance of the soil layers also could bring seeds to the surface where they would be exposed to optimal germination conditions. Disturbed patches could therefore become seed sources from which *B. tournefortii* could potentially move into un-invaded habitats.

Combinations of temperature and quantity and timing of precipitation are known to affect germination of native desert plants (Noy-Meir 1973; Beatley 1974), and our results support this tenet. Water additions as well as disturbance significantly influenced native annual community composition during the second year of the study in 2009 (Table 6). Under potential changing precipitation scenarios due to climate change, an increase in large-pulse water events (Knapp et al. 2008) could have variable effects on both native and non-native winter annuals. However, non-native species are more efficient than natives at capturing available water and soil nutrients, and utilize these resources for seed production (Monaco et al. 2003; Huxman et al. 2008; DeFalco et al. 2003). Therefore, a shift in precipitation patterns could have profound impacts on the structure and function of Mojave Desert ecosystems.

Conclusion

Understanding the factors that facilitate the establishment of non-native species can help develop strategies to identify potentially invasive species, as well provide information on designing and implementing control techniques. Our study supports a resource-based community invasibility process in which greater water availability and soil disturbance enhanced the overall establishment of non-native species at low-elevation experimental sites in the eastern Mojave Desert. However, responses of the two non-native species differed, with *Schismus* responding more strongly than *B. tournefortii* to water additions and disturbance. Native annual community composition also was significantly altered by water addition and disturbance. Based on future climate change models, it is difficult to predict patterns of invasibility, but an increase in water availability and disturbance is likely to enhance invasibility in this ecosystem (Weltzin et al. 2003; Bradley et al. 2009; Bradley 2009; Bradley 2010). Further experimental studies are needed to identify potential response patterns among native and non-native species under an array of changing water availability and disturbance scenarios to support the development of comprehensive management plans.

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