Invasive Plant Science and Management

# Models of Invasion and Establishment for African Mustard (*Brassica tournefortii*)

Kristin H. Berry, Timothy A. Gowan, David M. Miller, and Matthew L. Brooks*

*Invasive Plant Science and Management* 2014 7:599–616

# Models of Invasion and Establishment for African Mustard (*Brassica tournefortii*)

Kristin H. Berry, Timothy A. Gowan, David M. Miller, and Matthew L. Brooks*

Introduced exotic plants can drive ecosystem change. We studied invasion and establishment of *Brassica tournefortii* (African mustard), a noxious weed, in the Chemehuevi Valley, western Sonoran Desert, California. We used long-term data sets of photographs, transects for biomass of annual plants, and densities of African mustard collected at irregular intervals between 1979 and 2009. We suggest that African mustard may have been present in low numbers along the main route of travel, a highway, in the late 1970s; invaded the valley along a major axial valley ephemeral stream channel and the highway; and by 2009, colonized 22 km into the eastern part of the valley. We developed predictive models for invasibility and establishment of African mustard. Both during the initial invasion and after establishment, significant predictor variables of African mustard densities were surficial geology, proximity to the highway and axial valley ephemeral stream channel, and number of small ephemeral stream channels. The axial valley ephemeral stream channel was the most vulnerable of the variables to invasions. Overall, African mustard rapidly colonized and quickly became established in naturally disturbed areas, such as stream channels, where geological surfaces were young and soils were weakly developed. Older geological surfaces (e.g., desert pavements with soils 140,000 to 300,000 years old) were less vulnerable. Microhabitats also influenced densities of African mustard, with densities higher under shrubs than in the interspaces. As African mustard became established, the proportional biomass of native winter annual plants declined. Early control is important because African mustard can colonize and become well established across a valley in 20 yr.

**Nomenclature:** *Brassica tournefortii* Gouan BRSTO.

**Key words:** Dry washes, invasion, models, roads, African mustard, Sonoran Desert, stream channels.

The African mustard, also known as African or Sahara mustard (*Brassica tournefortii* Gouan), is a native of North Africa, the Middle East, and Mediterranean area of southern Europe (Minnich and Sanders 2000). It first appeared in California herbarium collections in 1927 and subsequently became abundant in the Sonoran Desert and parts of the Mojave Desert (Minnich and Sanders 2000). The distribution now extends into southern Nevada and Utah in the north, Texas in the east, and Mexico in the south (Bangle et al. 2008; Bowers et al. 2006; Minnich and Sanders 2000; Van Devender et al. 1997). *Brassica tournefortii* is considered to be a late 20th century annual invasive in the American Southwest (Minnich 2008) and is a noxious weed in California (California Invasive Plant Council 2006), Nevada (USDA 2005), and Australia (Chauhan et al. 2006a).

In the American Southwest, *B. tournefortii* is common at elevations below 1,000 m (3,281 ft) in dunes, sandy flats, and sandy-gravelly dry washes (Bangle et al. 2008; Minnich and Sanders 2000; Van Devender et al. 1997). It invades from road edges into deserts, abandoned fields, exotic grasslands, coastal sage scrub, beaches, and cities (Bangle et al. 2008; Barrows et al. 2009; Brooks 2009; Minnich and Sanders 2000), and thrives in disturbed soil in deserts (Suazo et al. 2012). The species has been reported to be scarce on alluvial fans and rocky hillsides (Minnich and Sanders 2000).

*Brassica tournefortii* is of particular concern to ecologists and land managers because of the high potential for impacts to wildlands, threatened and endangered species, and fragile and limited ecosystems. *Brassica tournefortii* successfully competes with native annuals and grasses for soil moisture, nutrients, and mesic microsites (Barrows et al. 2009; Minnich 2008; Van Devender et al. 1997) and can alter composition and abundance of native species, including threatened plant and animal species (Barrows

DOI: 10.1614/IPSM-D-14-00023.1

* First and second authors: Wildlife Biologist (Research) and Ecologist, U.S. Geological Survey, Western Ecological Research Center, 21803 Cactus Avenue, Suite F, Riverside, CA 92518; third author: Research Geologist, U.S. Geological Survey, 345 Middlefield Road, MS-973, Menlo Park, CA 94025; fourth author: Research Botanist, U.S. Geological Survey, Western Ecological Research Center, 40298 Junction Drive, Suite A, Oakhurst, CA 93644. Corresponding author's E-mail: kristin_berry@usgs.gov

## Management Implications

Our models of African mustard invasion and establishment in the western Sonoran Desert have broad application for designing surveillance and monitoring systems in other arid and semiarid lands in the American West. With this study we now know that topography (major and small ephemeral streams or "washes" in valleys) and ages of geological deposits and soils are important predictors of sites for African mustard invasion. In addition to roads, African mustard is most likely to invade and colonize areas through active major and minor ephemeral stream channels, especially where these features are numerous on the landscape or intersect highways and roads. These features are highly vulnerable because they are naturally disturbed and composed of young geological deposits (1 to 7 yr old). Less vulnerable are older deposits associated with desert pavements (20,000 to 300,000 yr old), and least vulnerable are the oldest geological deposits (140,000 to 300,000 yr) with well-developed desert pavements. Weed control specialists and land managers can use existing regional maps of topography, surficial geology, and landforms, coupled with aerial imagery, to design surveillance systems that emphasize ephemeral stream channels and young geological surfaces. Aerial views of desert ephemeral stream channels suitable for mapping can be obtained from sources such as the National Agricultural Imagery Program. Monitoring for evidence of arrival and early invasion can be achieved by walking transects several kilometers in length, both up and down stream channels, and where such channels cross or parallel roads or other disturbed areas. When the mustard is located, weed control specialists can take action to eradicate or limit spread with herbicides, which can be more effective and less costly than physical methods. Timing of herbicide application, i.e., at an early phenological stage, may determine effectiveness in controlling not only the mustard but also other exotic plant species. Herbicides that do not negatively affect native annuals (based on limited success reported by Marushia et al. 2010) are recommended.

et al. 2009). It may also contribute to fires by increasing fuel loads (Brooks and Minnich 2006; Brooks and Pyke 2001; Minnich and Sanders 2000).

Recent research on the biology of *B. tournefortii* indicates that seeds can germinate under a broad spectrum of moisture levels, salinity, and soil depths in late fall, early winter, and spring (Abella et al. 2011b; Bangle et al. 2008; Chauhan et al. 2006b; Van Devender et al. 1997). Plants grow rapidly, can reach heights of almost 2 m, have high reproductive rates, produce thousands of seeds, and can continue to produce viable seeds after physical treatments (Abella et al. 2013; Marushia et al. 2012; Trader et al. 2006).

Removal of *B. tournefortii* presents challenges for restoration projects because of high seed production (Trader et al. 2006), rapid phenology, and increased rates of germination in response to physically killing plants (Abella et al. 2013; Brooks 2009; Marushia et al. 2012). Physical methods are most effective if applied prior to seed development (Abella et al. 2013). Herbicides are also important tools and can be less costly than physical methods. Glyphosate and some other herbicides can reduce or eliminate germination (Abella et al. 2013), and glyphosate, if applied early, can be effective while at the same time avoiding negative impacts to natives (Marushia et al. 2010). The level of effectiveness was dependent on the presence and degree of invasion by other exotic annual species, as well as by local weather conditions. Another consideration is that some native perennial species facilitate certain species of exotics whereas others do not (Abella et al. 2011a; Abella and Smith 2013; Craig et al. 2010). Therefore when planning to restore severely damaged areas or burned areas where *B. tournefortii* occurs, selection of perennial shrubs and grass species to be planted should be taken into account.

Our objective was to develop a model of invasion and establishment for *B. tournefortii* in the western Sonoran Desert using long-term data from the Chemehuevi Valley. Specifically, we (1) conducted a retrospective analysis of available data on arrival and invasion of *B. tournefortii* in the Chemehuevi Valley; (2) determined differences in density and distribution of *B. tournefortii* in two sample years, 1999 and 2009; (3) determined correlates and contributors to invasion; (4) identified factors at a landscape scale that correlate with density and distribution (e.g., surficial geology, soil age, and topography); (5) identified variables at the microhabitat level that were associated with successful establishment and invasion of *B. tournefortii*; and (6) evaluated changes in biomass of native and exotic winter annual plants over multiple years. Based on available data in the literature, we predicted that *B. tournefortii* would be more abundant next to roads and in anthropogenically disturbed areas than in undisturbed areas (Brooks 2009; Frenkel 1970; Minnich and Sanders 2000). We also predicted that the abundance and distribution of *B. tournefortii* would be influenced by surficial geology type and soil age, vegetation type, and shrub cover.

## Materials and Methods

**Description of Study Area.** The study area was in the Chemehuevi Valley, eastern San Bernardino County, California, in the western Sonoran, or Colorado, Desert (Rowlands et al. 1982). Most field work was undertaken on a 4.66-$km^2$ (1.8 $mi^2$) plot adjacent to and east of State Highway 95, elevation 340 to 350 m (Figure 1), a long-term study area for vertebrates. Because *B. tournefortii* occurs in disturbed areas, we include a summary of historical and recent disturbances from human activities. In the late 1800s, settlers established dirt roads across the Chemehuevi Valley, connecting springs, wells, and settlements (Ruegers 1903; San Bernardino County 1925; Thurston 1915). In 1936, the current alignment of State Highway 95 was established, the road was paved, and a 5-m levee was constructed along the east edge of the highway,

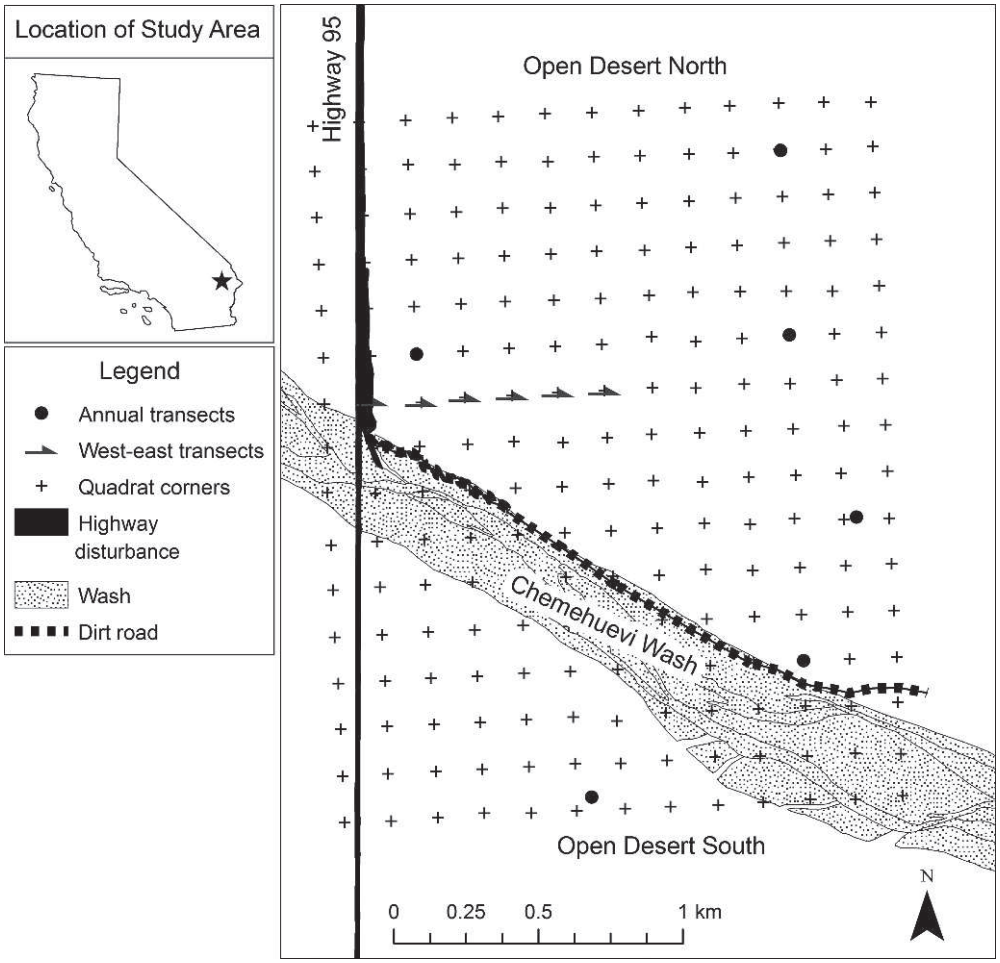


Figure 1. Location and overview of the study area in the Chemehuevi Valley, western Sonoran Desert. Locations, transects, and quadrat corners for transects, as well as the three habitat types—Open Desert North, Chemehuevi Wash, and Open Desert South—are shown. The jeep trail within the Chemehuevi Wash is not shown.

deflecting water to an ephemeral stream channel running parallel to the levee (R. Hatheway, personal communication; files of the California Department of Transportation, San Bernardino County; Figure 1). Two dirt roads cross the study area: one closely parallels and is north of the Chemehuevi Wash, and the other is a jeep trail in the Chemehuevi Wash itself, following the wash from State Highway 95 east to the Colorado River. The latter trail, poorly defined because of frequent flooding, is not shown on Figure 1. Recreationists have used the road and trail for off-highway vehicle travel. In 1942, General Patton trained troops for North Africa throughout the region (Prose 1985), and tracks from military vehicles are still evident on desert pavements. The study area and adjacent lands were also part of a cattle grazing allotment, which was terminated in 2002 (U.S. Department of the Interior, Bureau of Land Management [USDI BLM] 1980, 2002; USDI BLM and California Department of Fish and Game 2002). In all years on-site, we observed scat and hoof prints of feral burros (*Equus asinus* Linneaus 1758), primarily within the wash.

**Data Collection.** We collected data from photographs, transects, and biomass samples from different years to quantify the presence, density, and distribution of *B. tournefortii* over time. We also collected data on potential correlates of *B. tournefortii* density, including surficial geology, proximity to disturbances, and microhabitat.

*Precipitation.* We estimated mean annual precipitation for the hydrologic year (Manning 1992: October 1 to September 30) from the nearest weather stations, Lake Havasu (1985 to 1990) and Lake Havasu City (1991 to 2009) (National Oceanic and Atmospheric Administration 1985–2009). The stations are 5.6 km (3.5 mi) apart, at 142 and 147 m elevations , and approximately 25 km east of the study area. At the older station, Lake Havasu, the long-term means (1967 to 1990) were 116.3 mm (4.6 in) and

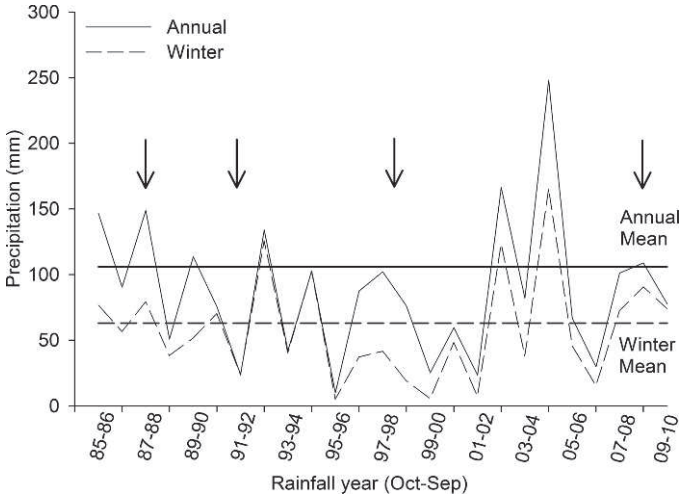


Figure 2. Annual (October 1 to September 30) and winter (October 1 to March 31) precipitation at the Lake Havasu (1985 to 1990) and Lake Havasu City (1991 to 2009) weather stations located 25 km from the study area in the western Sonoran Desert. Annual and winter means are from the Lake Havasu Weather Station, 1967 to 1990. Arrows indicate years when data for this study were collected.

69.6 mm (2.7 in) for annual and winter precipitation (October 1 to March 31) respectively (Figure 2). For the purposes of this study, we assumed that precipitation was generally spatially consistent across the desert for calendar years for cool and warm seasons (after Hereford et al. 2006) and that precipitation would be higher at the study area than at the weather stations because of higher elevations and a more westerly location (Rowlands 1995). However, we did not have rain gauges at our study area, and this assumption may be incorrect.

*Surficial Geology.* Surficial geology was included in the analysis because water is widely considered to be the primary driver of ecosystem processes in arid lands (Whitford 2002), and soil surface characteristics, texture, and horizonation can all modulate the effects of precipitation by influencing infiltration and soil water storage (Miller et al. 2009). These surficial geologic controls are seen as spatial patterning in perennial plant cover and composition (Bedford et al. 2009; Hamerlynck et al. 2002; Schenk et al. 2003). We first identified patterns of surface characteristics such geomorphic features, desert pavement and varnish, height above active stream channels, and smoothness of terrain. We then developed a classification of surface characteristics and studied each class further by examining natural cut banks and digging pits by hand to describe soil development. We avoided roads, disturbance from altered streams due to water bars along roads, tank tracks, and similar disturbed areas. We also collected locations of representative deposits at 102 way-stations with a handheld global positioning system and projected the data using geographic information system (GIS) software to black-and-white aerial photographs (nominal scale of 1 : 80,000, taken in 1998) from the National High Altitude Program (U.S. Geological Survey). The photographs were ortho-rectified at a 1-m resolution and mosaicked as quarter-quadrangles of 1 : 24,000-scale topographic maps. The aerial photographs provided a control to ground observations. Using the photographs, we converted our observations to maps displaying different ages of deposits (e.g., Figure 3).

We identified five stages of soil development, based on Miller et al. (2009), which correspond with five ages of alluvial fan and stream terrace deposits. The ages of these surficial geologic deposits span approximately 300,000 yr, from late Holocene (present) to middle Pleistocene. The stages of soil development were defined in standard geologic mapping units as Qya1, Qya2, Qya3, Qia, and Qia3 (complete definition in Table 1; Figure 3). This classification uses a unit symbol that codes for age and mode of deposition: Q represents the overall age (Quaternary), y or i represents relative age (young or intermediate), and the next letter represents source of deposition (a, alluvial fan deposit, or w, wash deposit). Numbers reflect relative age breakdowns within categories, with small numbers being younger. The deposits associated with the soils ranged from active ephemeral stream channels with no soil development (Qyw1, Qya1) to uplands characterized by strongly developed desert pavements with darkly varnished clasts and under which were well-developed soil horizons reflecting weathering and accumulation of aeolian dust (Qia3).

*Surficial Geology and Vegetation Associations.* To develop the model, we combined data on perennial vegetation, surficial geology, and soil development into three landscape-level habitat types (Figures 1 and 3): Open Desert North, Chemehuevi Wash, and Open Desert South. For convenience and to simplify descriptions of model variables, we refer to these three as surficial geology types.

Open Desert North is the largest and primarily a creosote bush [*Larrea tridentata* (D.C.) Coville] and white bur-sage [*Ambrosia dumosa* (A. Gray) W.W. Payne] association (Sawyer et al. 2009) with widely scattered ocotillo (*Fouqueria splendens* Engelm. subsp. *splendens*) on alluvial-fan deposited soils of granitic origin and Holocene and Pleistocene age. The relief is low and is cut by ephemeral stream channels draining from the Chemehuevi Mountains in the north to Chemehuevi Wash in the south. The stream channels are narrow in width (0.2 to 1 m, average 0.61 m) and shallow in depth (average 0.1 to 0.5 m), and thus do not appear on Figure 3. They support a higher density and diversity of perennial plants. Other species occurring throughout Open Desert North in stream

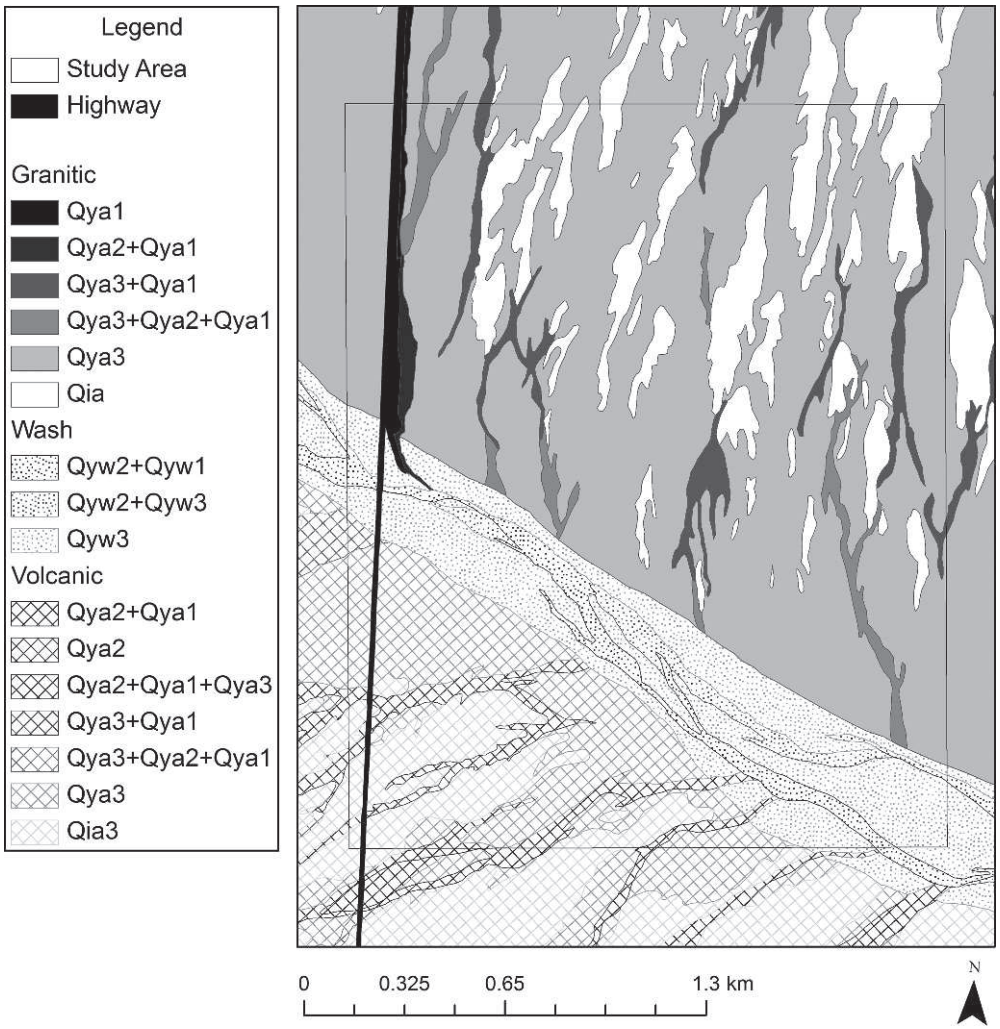


Figure 3. Surficial geology at the Chemehuevi Valley study area, western Sonoran Desert. Using a combination of perennial vegetation, surficial geology, and soils, we identified three habitat types (abbreviated as surficial geology): Open Desert North, of granitic origin; deposits in Chemehuevi Wash; and Open Desert South, of volcanic origin. For a description of geologic deposits described in map units see Table 1.

channels, but less common outside channels, include the following: white rhatany (*Krameria bicolor* S. Watson), Pima rhatany (*Krameria erecta* Schult), pencil cactus [*Cylindropuntia ramosissima* (Engelm.) F.M. Knuth], buckhorn cholla [*Cylindropuntia acanthocarpa* (Engelm. and J.M. Bigelow) F.M. Knuth var. *coloradensis* (L.D. Benson) Pinkava], beavertail cactus [*Opuntia basilaris* (Engelm. and J.M. Bigelow) var. *basilaris*], and wire-lettuce [*Stepanomeria pauciflora* (Torr.) A. Nelson)].

Chemehuevi Wash, the second surficial geology type, is a major axial-valley ephemeral stream channel composed of deposits ranging from modern to middle Holocene in age (Table 1; Figure 3). During rainfall events, axial-valley stream channels integrate flow from many smaller stream channels and flow when any part of the landscape floods, thus flowing more frequently and with greater volume than smaller stream channels. Vegetation in the wash is microphyll woodland, a mix of two vegetation associations, dominated by blue palo verde [*Parkinsonia florida* (A. Gray) S. Watson], smoke tree [*Psorothamnus spinosus* (A. Gray) Barneby], catclaw [*Senegalia greggii* (A. Gray) Britton and Rose], cheesebush [*Ambrosia salsola* (Torr. and A. Gray) Strother and B.G. Baldwin], and other shrubs (Sawyer et al. 2009).

The third surficial geology type is Open Desert South (Table 1; Figure 3). Although vegetation is similar to that described for Open Desert North, the surficial geology is composed of Holocene and Pleistocene–aged alluvial deposits from volcanic rocks and thus has more rocks than Open Desert North. The small, ephemeral stream channels associated with the southern fans are deeper (1 to 3 m) than in Open Desert North, have fine aeolian sands on the

Table 1. A summary of characteristics of the surficial geological deposits and mapping units (e.g., Qya1) occurring in the Chemehuevi Valley study area, western Sonoran Desert (adapted to local characteristics from Bedford 2003, 2009; McFadden et al. 1989; Miller et al. 2009; ages partly from Miller et al. 2010). The classification system includes surface topography, presence or absence of pavement or varnish, soil horizons, calcic morphology, and perennial plant species.

| Map unit label | Estimated age (yr) | Description of Quaternary surficial geological deposits |
|---|---|---|
| Qya1 | 1 to 7 (Holocene) | Deposits from adjacent alluvial fans occur in an active ephemeral stream channel or wash or on an active alluvial fan with no pavement and no varnish; no A or B soil horizons or calcic morphology is present. Perennial vegetation is typically microphyll woodland. |
| Qya2 | 20 to 200 (Holocene) | Alluvial fan deposits have strong bar and swale topography; no pavement and no to very weak varnish; Av[a] and B soil horizons are generally absent. Perennial vegetation (shrubs) is usually a creosote bush and white bur-sage association. |
| Qya3 | 3,000 to 6,000 (Holocene) | Alluvial fan with remnants of bar and swale topography with incipient desert pavement and weak desert varnish; Av soil horizon weak, sandy silt; Bw horizon is weak, reddish; and calcic morphology is at Stage 1. Perennial vegetation is similar to Qya2. |
| Qia | Uncertain, ≅20,000 to 300,000 (mid- to late Pleistocene) | Alluvial fan or piedmont with flat, faint bar and swale topography and with weak to moderate pavement and moderate varnish. Av soil horizon is structured silt, 2–6 cm thick; B horizon is strong, red, of weak clay; and calcic morphology is Stage II. Perennial vegetation is similar to Qya2 but shrubs are sparse. |
| Qia3 | 140,000 to 300,000 (middle Pleistocene) | Alluvial fan topography is crowned, desert pavement is strong and degraded with exposed Av horizon; desert varnish is strong with purplish casts. Av soil horizon is structured silt, 4 to 15 cm thick; Bt horizon is strong clay; and calcic morphology is Stage II to IV. Perennial vegetation similar to Qia but is sparse. |
| Qyw1, Qyw2, Qyw3 | | Deposits occurring in the active axial wash or ephemeral stream channels. Ages and soils approximately correspond with Qya mapping units (alluvial fan, Qya1, Qya2, Qya3) |

[a] Abbreviations: Av horizon, vesicular A horizon consisting of an accretionary silt cap that lies on the alluvial deposit; typically paired with an overlying desert pavement.

banks, and drain from southwest to northeast into the Chemehuevi Wash from mountains in the southwest, cutting through expansive areas of desert pavement (Figure 3). In general, stream flow in Open Desert South is confined to the deeply cut channels within the fan, whereas stream flow in Open Desert North may overtop the rounded, relatively low ridges between broad channels. Plant names follow Baldwin et al. (2014).

*Review of Color Photographs from 1979 to 1999.* We reviewed 132 color photographic images (35-mm slides) available from studies of Agassiz's desert tortoise [*Gopherus agassizii* Cooper 1861; K.H. Berry, unpublished data] for presence or absence of live or dead *B. tournefortii* at the study area. The images, taken during spring of 1979, 1982, 1988, 1992, and 1999, documented plant transects and landscapes.

*Sampling and Phenology of B. tournefortii.* We collected data on *B. tournefortii* and annual plants at the time of peak flowering in April of each survey year, with the exception of 1999, when we completed the *B. tournefortii* transects by May 9. In 1999, *B. tournefortii* plants were dry, and most seed pods had dehisced and separated from the pedicels. In 2009, most plants were still green and in fruit. By the time we completed transects in early May, the pods were dehiscing and seeds were scattering.

*Brassica tournefortii Transects.* We used three sources of data to evaluate distribution and densities of *B. tournefortii* and use of microhabitat. Hereafter we refer to these three sources of data as primary transects, microhabitat transects, and biomass transects. To determine densities and distribution at a landscape scale, the 4.66-km$^2$ study area was subdivided into 180 quadrats, each 161 m by 161 m, with rebar serving as permanent markers in quadrat corners (Figure 1). In 1999, we walked belt transects (the primary transects), 9.1 m wide by 227.6 m long (2,071.2 m$^2$), on each quadrat from the northwest to southeast corners or vice versa (total = 180) and counted the number of rooted *B. tournefortii* and the number of stream channels on each transect. *Brassica tournefortii* that were unrooted and in the intershrub space or tangled within a shrub were not counted. Each transect was assigned to one of three surficial geology types (Open Desert North, Chemehuevi Wash, or Open Desert South).We repeated the 180 transects again in 2009, with the exception that width of transects was reduced from 9.1 m to 0.91 m (207.1 m$^2$) because of high densities of *B. tournefortii*. Consequently, *B. tournefortii* counts in 2009 were multiplied by 10 to account for the reduced transect width.

To determine how far *B. tournefortii* had invaded the valley by 2009, we made observations along the east–west

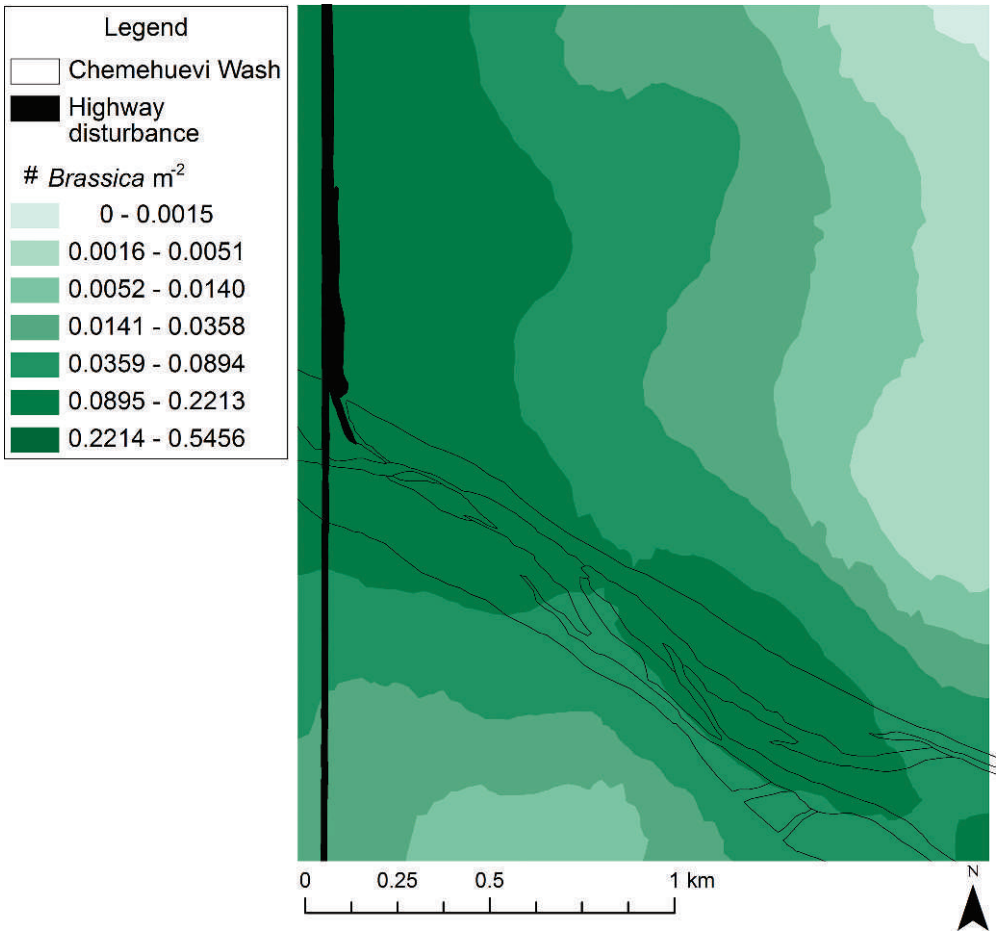


Figure 4. Estimated densities of *Brassica tournefortii* in 1999 in the Chemehuevi Valley, western Sonoran Desert. Densities were interpolated from 180 data points using an ordinary kriging method. Note the different scales for numbers of *Brassica* $m^{-2}$ between Figures 4 and 5.

dirt and paved roads eastward to within a few kilometers of the Colorado River. We then established a second group of primary transects: three sets of seven transects each, at 3,219, 4,828, and 6,437 m from the highway in Open Desert North. The transect size and methods were the same as for the primary transects.

*Microhabitat Transects and Sampling Variables.* We used a set of six transects to determine the association of *B. tournefortii* with microhabitat variables: stream channels, shrubs, and the space in between shrubs (intershrub space) both within and between stream channels. We walked transects along the northern boundary of six quadrats (Figure 1) from west to east in 1999 and again in 2009 and recorded numbers of rooted *B. tournefortii* (1) in the intershrub spaces between stream channels, (2) within canopies of shrubs between stream channels, (3) in intershrub spaces within stream channels, and (4) within canopies of shrubs within stream channels. Transects were 9.1 m wide by 161 m long in 1999 and 0.91 by 161 m long in 2009.

*Biomass Transects for Annual Plants, Collected in 1988, 1992, and 2009.* We established six randomly placed transects to estimate aboveground annual plant biomass: two in 1988, followed by an additional four in 1992. Transects 1 and 2 were 1,386 and 1,719 m from Highway 95, respectively. Transects 3, 4, 5, and 6 were located 1,455, 1,537, 804, and 196 m from Highway 95, respectively (Figure 1). All but transect 5 were in Open Desert North. Each transect was 2 by 100 m in length and subdivided into 2-m by 2-m quadrats. On each transect, annual plants were sampled on 25 subquadrats, each 20 cm by 50 cm (7.9 in by 19.7 in) and placed in alternating corners of every other quadrat, or about 4 m apart (total area sampled per transect = 2.5 $m^2$). The location of the subquadrats was alternated from year to year. Biomass of each species was estimated by clipping the aboveground portion of each annual plant in a subquadrat, air-drying, and then weighing the material. Biomass was expressed as g $m^{-2}$ (ounce $yard^{-2}$) and relative biomass for different species or groups of annual species as percent.

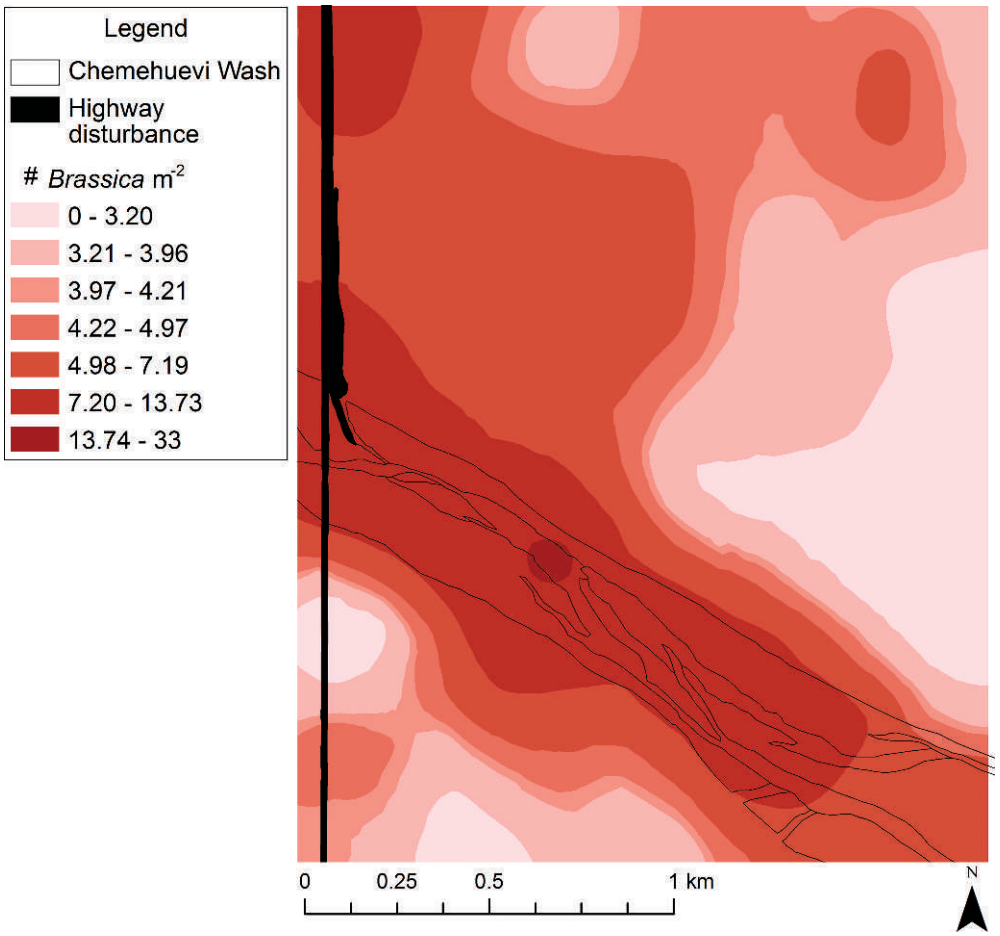


Figure 5. Estimated densities of *Brassica tournefortii* in 2009 in the Chemehuevi Valley, western Sonoran Desert. Densities were interpolated from 180 data points using an ordinary kriging method. Note the different scales for numbers of *Brassica* $m^{-2}$ between Figures 4 and 5.

**Data Analysis.** *Brassica tournefortii—Primary Transects.* To prepare contour maps of density, we constructed GIS layers containing the locations of Highway 95, Chemehuevi Wash, and corners of each 161-m by 161-m quadrat (Figure 1). We used the GIS layers to calculate the distances of each transect to the highway, to the Chemehuevi Wash, and to the dirt road lying north of the Chemehuevi Wash. For display purposes, *B. tournefortii* densities throughout the study area were interpolated from *B. tournefortii* counts on each transect and used to create contour maps representing *B. tournefortii* densities in 1999 and 2009 (Figures 4 and 5). Densities were interpolated with ordinary kriging, using spherical models based on the five nearest neighbors with ArcGIS version 9.2 (ESRI, Redlands, CA).

All *B. tournefortii* counts were divided by the transect area (2,071.2 $m^2$ in 1999, 207.1 $m^2$ in 2009) to calculate *B. tournefortii* density (plants $m^{-2}$) on each of the 180 belt transects. *Brassica tournefortii* densities were log-transformed to achieve normal distributions (Kolmogorov-Smirnov test, $P \geq 0.05$). We used a paired *t* test to compare *B. tournefortii* densities on each transect in 1999 to those in 2009, and we used Pearson's product-moment correlation to determine if quadrats with relatively high *B. tournefortii* densities in 1999 also had relatively high *B. tournefortii* densities in 2009.

To evaluate which variables influence *B. tournefortii* density, we analyzed densities from the 180 transects in 1999 and 2009 separately using generalized linear models (GLMs). Because data from all transects on the study area were used for analysis and these data were potentially spatially autocorrelated, five GLMs were conducted and compared: one model without a spatial term and four models (spherical, exponential, power, and Gaussian) with a spatial covariance term based on transect locations (Littell et al. 1996). Each model was evaluated by comparing Akaike information criterion values (AIC, a metric that balances goodness of fit with model complexity); the most parsimonious model was retained and is presented in the results.

To evaluate the effects of surficial geology and distance to a paved road, we first analyzed *B. tournefortii* densities

using a GLM with surficial geology types (Open Desert North, Chemehuevi Wash, or Open Desert South), distance to Highway 95, and the interaction between these two variables as predictor variables. To evaluate the effects of the wash and small stream channels (surficial geology), we performed a second GLM with *B. tournefortii* densities as the response variable and distance to highway, distance to wash, and number of stream channels as predictor variables. Transects located in or traversing Chemehuevi Wash were excluded from this analysis, because these transects did not contain small stream channels. We considered, but did not include the dirt road north and adjacent to the wash and the road in the wash as variables because of close proximity to or location within the wash. We also considered but did not use cattle and feral burro sign counts as disturbance variables, because data were insufficient and use levels were low.

*Brassica tournefortii Abundance in Microhabitats.* To analyze the set of six microhabitat transects for *B. tournefortii* density (plants $m^{-2}$), we estimated the area occurring in the intershrub space outside of stream channels, the area within canopies of shrubs between stream channels, intershrub space within stream channels, and the area within canopies of shrubs within stream channels. The area occurring in stream channels was estimated by multiplying the average stream channel width (0.61 m) by the transect width (9.1 m for 1999, 0.91 m for 2009), then multiplying the product by the number of stream channels in the transect. The area outside of stream channels was calculated as the remaining transect area. The stream channels and areas outside of stream channels were further subdivided into area under shrubs (number of shrubs multiplied by average shrub size [0.25 $m^2$]) and area of intershrub space (remaining area). The effect of microhabitat on *B. tournefortii* density, with transect identity as a random effect, was analyzed separately for 1999 and 2009 data using ANOVA and Tukey's honestly significant difference (HSD) tests. GLMs were developed with SAS version 9.1.3 (SAS Institute Inc., Cary, NC). All other statistical analyses were conducted using SYSTAT version 12.0 (SYSTAT., San Jose, CA).

*Biomass Transects: Samples of Annual Plants Collected in 1988, 1992, and 2009.* The percentage of aboveground biomass of native annuals and exotic annuals calculated from biomass transects was arcsine–square root transformed. These data were then analyzed using a linear mixed model (SYSTAT) with transect identity as a random effect and year as a fixed effect to determine if the relative proportion of native to exotic annual biomass changed over time.

## Results and Discussion

**Precipitation.** Annual and winter precipitation was variable among years (Figure 2). Between the winters of 1987 to 1988 and 2008 to 2009, winter precipitation was above the mean in eight of the 22 yr. In the years when annual plant biomass was measured and *B. tournefortii* was counted on transects, winter precipitation was above the long-term mean (69.6 mm) for the winters of 1987 to 1988 (79.2 mm) and 2008 to 2009 (90.7 mm), but below the long-term mean in 1991 to 1992 (23.6 mm) and 1998 to 1999 (19.1 mm). We observed germination, growth, and flowering of *B. tournefortii* in 1992, 1999, and 2009.

**Using Photographs and Densities of *B. tournefortii* to Estimate Invasion History.** Of the 132 photographic slides taken between 1979 and 1999, the precise locations of only a few photographs were known on the study area. Most were taken in Open Desert North or Open Desert South. In 1979, three images were taken on the east edge of the levee adjacent to Highway 95. *Brassica tournefortii* was rare or potentially not present; two images may have had one *B. tournefortii* in each view, but the plants in question were in the distance and identification could not be confirmed. In 1992, one *B. tournefortii* was present in the foreground of a photograph of plant transect 6. In 1999, dried *B. tournefortii* were present in 10 of 22 images.

In 1999, *B. tournefortii* densities ranged from 0 to 0.55 plants $m^{-2}$ but by 2009 had increased to range from 0.98 to 33 plants $m^{-2}$ (Figures 4 and 5). *Brassica tournefortii* was significantly more abundant in 2009 than in 1999 ($t_{179} = 41.1$, $P < 0.001$). Densities of *B. tournefortii* increased 84-fold in those 10 yr (mean *B. tournefortii* density 1999 = 0.066 plants $m^{-2}$; mean *B. tournefortii* density 2009 = 5.53 plants $m^{-2}$). There was a significant, positive correlation between *B. tournefortii* densities in 1999 and those in 2009 (Pearson $r = 0.449$; $P < 0.001$), indicating that transects that had relatively high *B. tournefortii* densities in 1999 also had relatively high densities in 2009. In 2009, we saw densely packed, fallen dried stems and branches of *B. tournefortii* that formed dense masses a meter in width by several meters in length in stream channels of Open Desert North and the Chemehuevi Wash. These mats were accumulations from previous years.

The pattern of invasion differed between Open Desert North and Chemehuevi Wash. In 1999 in Open Desert North, the invasion of *B. tournefortii* from Highway 95 into the eastern part of the valley appeared to diminish to near zero at a distance of approximately 1,700 m from the highway (Figure 6). Few *B. tournefortii* (= 5.2 per transect) were found on each of the easternmost transects, and none could be seen in the distance when scanning the landscape to the east. However, by 2009, mean counts were 5,406.1 per transect, > 1,000-fold higher approximately 1,700 m from the highway, and high counts continued in the newly established transects at 3.2, 4.8, and 6.4 km from Highway 95 (Figure 6). During a visual reconnaissance of the eastern Chemehuevi Valley, *B. tournefortii* was occasional in small

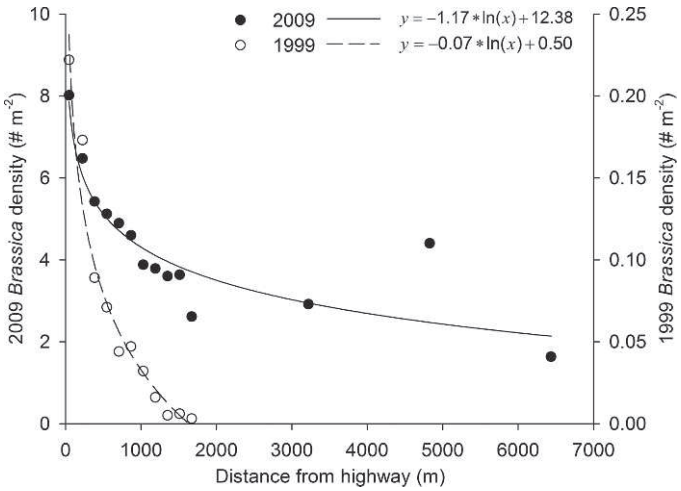


Figure 6. *Brassica tournefortii* densities as a function of distance to Highway 95 in the Chemehuevi Valley, western Sonoran Desert, in 1999 and 2009. Logarithmic trend lines are fitted through the means at each distance for each year. Data are from transects in the Open Desert North surficial geology type only and show the additional data from transects walked in the eastern part of the Chemehuevi Valley in 2009.

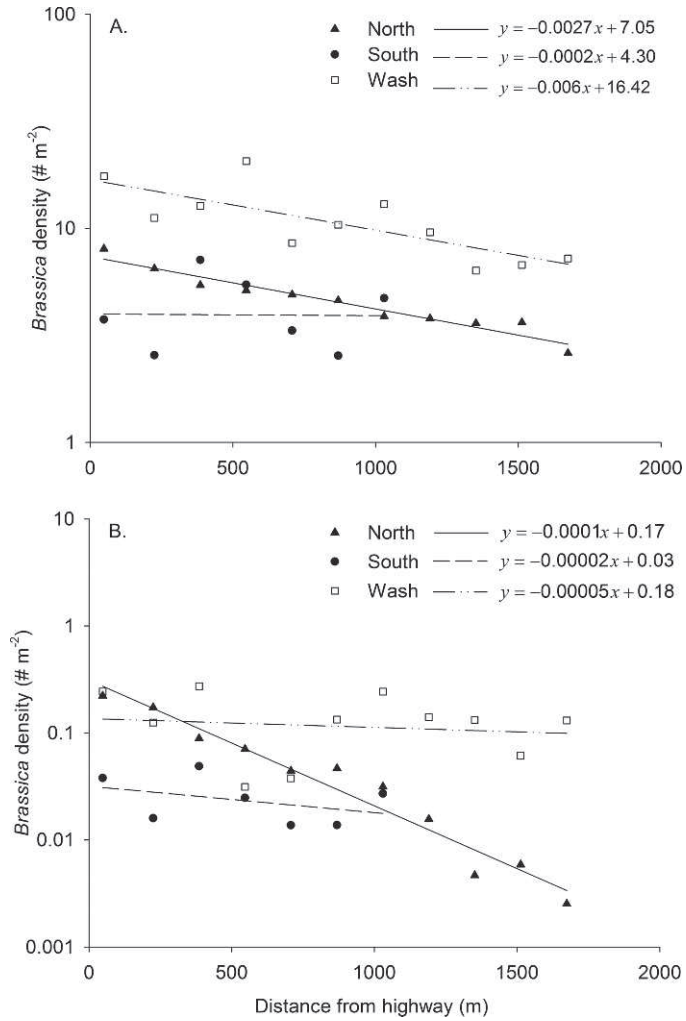


Figure 7. Log-scale *Brassica tournefortii* density as a function of distance to Highway 95 in the Chemehuevi Valley, western Sonoran Desert, in 1999 and 2009. Linear regression lines are fitted through the means at each distance for three surficial geology types: Open Desert North (North), Chemehuevi Wash (Wash), and Open Desert South (South). (A) 2009; (B) 1999.

stream channels 15 to 22 km from Highway 95. Thus, between 1999 and 2009, *B. tournefortii* colonized and became established approximately 20 km to the east in Open Desert North, arriving at the eastern end of the valley near the Colorado River.

Although counts of *B. tournefortii* north of the wash in Open Desert North in 1999 were nearly zero at 1,700 m from the highway (Figure 7), counts within and adjacent to Chemehuevi Wash remained high (Figure 4), indicating that *B. tournefortii* was becoming established more quickly and moving to the east much faster in the wash than in Open Desert North. The wash appeared to be the invasion front. The increase in *B. tournefortii* observed between 1999 and 2009 was dramatic, with higher numbers in Chemehuevi Wash than in Open Desert North.

Our evidence suggests that *B. tournefortii* probably first appeared along Highway 95 or Chemehuevi Wash at the study area in the late 1970s or early 1980s, but we really don't know the arrival date. Minnich and Sanders (2000) noted that *B. tournefortii* "seemed to have experienced a population explosion from 1977 to 1983, successive years of above-normal precipitation, becoming well established in all counties of southern California." It may have been during this time that *B. tournefortii* moved north and east from Imperial and Riverside counties into the Chemehuevi Valley. By 1992, when *B. tournefortii* was first evident on a plant transect 196 m east of the Highway 95, it was probably well established in Chemehuevi Wash and along the highway. Seven years later, in 1999, *B. tournefortii* had colonized the entire study area between the highway and 1,700 m into the desert, the eastern boundary of the study area. Thus, if an estimated arrival date at the edge of Highway 95 and the wash was 1980, *B. tournefortii* colonized the first 1.7 km of Open Desert in 20 yr (1980 to 1999) followed by an additional approximately 20 km 10 yr later. During this last 10 yr, winter rainfall exceeded the long-term mean in four of the years, possibly contributing to the speed of the invasion. Bowers et al. (2006) also reported that *B. tournefortii* spread quickly from the perimeter of the Desert Laboratory in Tucson, AZ, into the interior, more than doubling in frequency in the 22 yr between 1983 and 2005.

Together, the photographs and transects provide a potential timeline of arrival and invasion. Photographs, when included with other data sources, can be valuable

Table 2. Generalized linear model selection results comparing nonspatial to spatial covariance models for invasion and establishment of *Brassica tournefortii* in the Chemehuevi Valley, western Sonoran Desert, California. Models with the lowest Akaike's information criterion (AIC) were retained.[a]

| Predictor variables | Response variable | Spatial covariance model | AIC | ΔAIC | Null model likelihood ratio test P-value |
|---|---|---|---|---|---|
| *s*, *hd*, *s* × *hd* | log *bt* 1999 | None (null model) | 416.2 | 0.0 | |
| | | Spherical | 416.2 | 0.0 | 1.00 |
| | | Exponential | 418.2 | 2.0 | 1.00 |
| | | Power | 418.2 | 2.0 | 1.00 |
| | | Gaussian | 418.2 | 2.0 | 1.00 |
| *s*, *hd*, *s* × *hd* | log *bt* 2009 | None (null model) | −36.0 | 7.2 | |
| | | Spherical | −24.2 | 19.0 | 1.00 |
| | | Exponential | −34.0 | 9.5 | 1.00 |
| | | Power | −43.2 | 0.0 | < 0.01 |
| | | Gaussian | −34.0 | 9.2 | 1.00 |
| *hd*, *wd*, *w* | log *bt* 1999 | None (null model) | 341.3 | 0.0 | |
| | | Spherical | 343.3 | 2.0 | 0.99 |
| | | Exponential | 343.3 | 2.0 | 1.00 |
| | | Power | 341.5 | 0.2 | 0.18 |
| | | Gaussian | 343.3 | 2.0 | 1.00 |
| *hd*, *wd*, *w* | log *bt* 2009 | None (null model) | −68.3 | 21.0 | |
| | | Spherical | −80.4 | 8.9 | < 0.01 |
| | | Exponential | −66.3 | 23.0 | 1.00 |
| | | Power | −89.3 | 0.0 | < 0.001 |
| | | Gaussian | −66.3 | 23.0 | 1.00 |

[a] Abbreviations: *s*, surficial geology type; *hd*, distance to highway; *s* × *hd*, interaction between *s* and *hd*; *wd*, distance to wash; *w*, number of stream channels; *bt*, *B. tournefortii* density.

tools for providing information on exotic species. Photographs are often taken for purposes unrelated to exotic species and can be found in research collections and historical libraries maintained by universities and the government. If sufficient topographic features are available in an image, the exact site of the original photograph may be located and rephotographed. The transect data indicate that *B. tournefortii* moved more rapidly east from the highway via Chemehuevi Wash than in Open Desert North or South, suggesting that early establishment may have occurred where the wash crosses the highway rather than along the highway itself and the invasion front was in the axial valley wash (Figures 4–7).

**Modeling Factors that Affect *B. tournefortii* Density.** For the first GLM using 1999 data, the nonspatial model had the best fit (Table 2), indicating the data were not spatially auto-correlated. There were significant effects of surficial geology type ($F_{2,174} = 5.2$, $P = 0.006$), distance to the highway ($F_{1,174} = 10.4$, $P = 0.002$), and an interaction between these variables ($F_{2,174} = 4.6$, $P = 0.011$) on *B. tournefortii* density. In general, *B. tournefortii* densities were highest in the Chemehuevi Wash, followed by Open Desert North, and lowest in Open Desert South (Figures 4 and 7); however, for distances < 300 m from the highway, densities were greatest in the Open Desert North. For the 2009 data, the power covariance model had the best fit (AIC = −43.2; Table 2), indicating the data were spatially auto-correlated ($\rho = 0.9897$). There were significant effects of surficial geology type ($F_{2,32.8} = 14.9$, $P < 0.001$) and an interaction between surficial geology type and distance to the highway ($F_{2,43.7} = 4.7$, $P = 0.014$) on *B. tournefortii* density, but distance to the highway alone was not significant ($F_{1,27.8} = 1.0$, $P = 0.321$). *Brassica tournefortii* densities were also highest in Chemehuevi Wash in 2009, but no appreciable differences existed between Open Desert North and Open Desert South (Figures 5 and 7). In both years, distance to the highway appeared to have more influence on *B. tournefortii* density in Open Desert North compared to other surficial geology types (Figures 4, 5, and 7), resulting in significant interactions between surficial geology type and distance to the highway.

For the second GLM that incorporated distance to Chemehuevi Wash and number of stream channels as predictor variables, the significant variables differed between years. In 1999, the nonspatial model again had the best fit (AIC = 341.3; Table 2) indicating the data

were not spatially auto-correlated. *Brassica tournefortii* density increased with increasing proximity to the highway ($P < 0.001$) and to the Chemehuevi Wash ($P < 0.05$) as well as with increasing number of stream channels on transects ($P < 0.001$). For 2009 data, the power covariance model had the best fit (AIC = −89.3; Table 2), indicating the data were spatially auto-correlated ($\rho = 0.9936$). In 2009, *B. tournefortii* density increased with proximity to the highway ($P = 0.002$) and with increasing number of stream channels ($P < 0.001$), but was not related to proximity to the Chemehuevi Wash ($P = 0.42$).

**The Model for Invasion and Establishment of *B. tournefortii*.** Our 1999 and 2009 data sets, both showing *B. tournefortii* more abundant near the highway and in Chemehuevi Wash, point to the importance of highways and axial-valley ephemeral stream channels such as Chemehuevi Wash as being predictor variables for modeling invasions of this species. The GLM for 1999 data also indicates *B. tournefortii* first invaded from the highway and Chemehuevi Wash. Historically, highways and dirt roads have been typical routes for invasion of exotic plant species in California (Brooks 2009; Brooks and Lair 2009; Frenkel 1970) and elsewhere in the world (Forman et al. 2003); however, this is not always the case (Craig et al. 2010). The added disturbance of the levee and old road beds paralleling the east edge of the road north of the wash may have altered resource availability for *B. tournefortii*, enhancing the process in Open Desert North compared with Open Desert South (Figures 4 and 5; Brooks 2009). Jeep trails in and adjacent to the north edge of the wash also may have enhanced the rapid expansion of *B. tournefortii* in the wash, because seeds can be transported via vehicles (Brooks and Lair 2009; Forman et al. 2003). We were unable to separate effects of the dirt road that was north of and adjacent to the wash from the wash itself because of their close proximity. Unpaved roads and dirt trails may be important, however (Sánchez-Flores 2007). Cattle and feral burro use also may have contributed to colonization and spread, but data were insufficient to include livestock as variables in the model.

The numbers of ephemeral stream channels were critical predictors of *B. tournefortii* success and an important predictor variable for the model. These small channels carry less runoff than the axial-valley stream channel (Chemehuevi Wash) and support higher densities of shrubs, cacti, and perennial bunch grasses—microhabitats where tumbling dried mustards become entangled and drop their seeds—than adjacent desert. Although we did not evaluate invasion enhanced by geomorphic processes, such as wind, Aeolian, and stream transport, these factors may have played a role in the rapid eastward spread of *B. tournefortii*. Seeds can spread via water flow in stream channels and the Chemehuevi Wash and plants blowing as tumble mustards in the wind.

The surficial piedmont deposits and soils are significant predictors of colonization and establishment of *B. tournefortii*. The piedmont deposits most vulnerable to *B. tournefortii* contribute to Chemehuevi Wash and the stream channels (Qya1, Qyw1). These deposits have the youngest soils and surfaces, are essentially modern, and naturally disturbance-prone. The axial valley wash formed the invasion front, limited only in dispersal by water and potentially by vehicles. The smaller stream channels also provided means for dispersal, whether by water or wind (blowing tumble mustards). Next in vulnerability are deposits of Open Desert North, a landscape with expansive areas of incipient desert pavement and weak desert varnish estimated at 3,000 to 9,000 yr old (Qya3) and more limited areas with weak to moderate pavement 20,000 to 35,000 yr old (Qia; Figures 3 and 5). These deposits are granitic in origin. The least vulnerable and most resistant piedmont deposits are the oldest, represented by desert pavements with volcanic clasts, and with estimated ages of 140,000 to 300,000 yr (Qia3; Figures 3 and 5) in Open Desert South. Brooks (2009) reported that *B. tournefortii* seemed to colonize away from dirt roadsides more readily on sandy deep young soils typical of washes than on silty, rocky, and shallow older soils typical of uplands in the eastern Mojave Desert.

The landform mosaics of valleys, alluvial fans, axial-valley ephemeral stream channels, and stream channels of various sizes are typical of the Sonoran, Mojave, Chihuahuan, and (to a lesser extent) Great Basin deserts of North America. Piedmont deposits vary in age from valley to valley and by mountain range, and numerous local and regional maps of surficial geology depict distribution of the surficial geological deposits (e.g., Bedford et al. 2010; Miller 2012). Major highways, roads, axial-valley ephemeral stream channels, and smaller stream channels are ubiquitous in these deserts (e.g., McAuliffe 1994; Miller et al. 2009) and provide ample areas for *B. tournefortii* to rapidly colonize and establish. The open landscape and desert winds contribute to ease of dispersal of drying plants.

**The Effects of Microhabitats.** Microhabitat had a significant effect on *B. tournefortii* density in 1999 ($F_{3,15} = 14.0$, $P < 0.001$) and 2009 ($F_{3,15} = 608.3$, $P < 0.001$). *Brassica tournefortii* density was higher under shrubs than in intershrub spaces, regardless of whether the shrubs were within or outside of stream channels. A Tukey's HSD test revealed that *B. tournefortii* was more concentrated under shrubs both within and outside of stream channels than in the intershrub space in stream channels and least concentrated outside of stream channels in the intershrub spaces (Figure 8). In 2009, we also observed that although *B. tournefortii* was concentrated under the canopies and drip lines of *Larrea tridentata* and *Ambrosia dumosa* shrubs in stream channels, it also occurred under less common shrubs (e.g., *Krameria* spp.), the perennial grass, big galleta

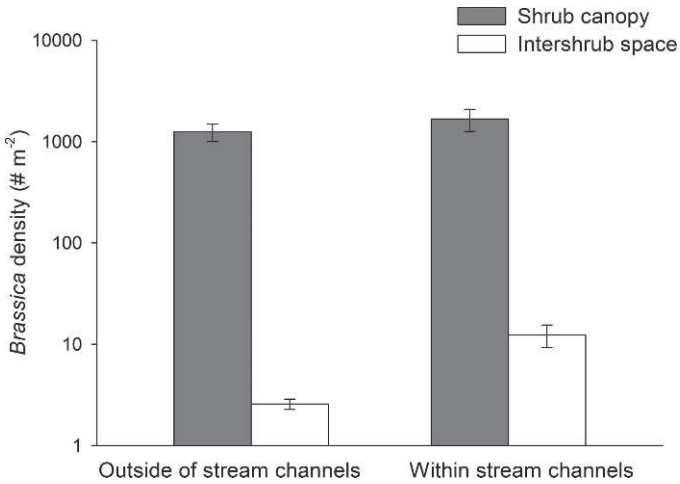


Figure 8. *Brassica tournefortii* density in 2009 was highest under the canopy of perennial shrubs and higher within than outside of stream channels for intershrub spaces at the Chemehuevi study area, western Sonoran Desert. Log-scale data are shown as the mean ± SE.

[*Hilaria rigida* (Thurb.) Scribn.], and cacti (*Cylindropuntia ramosissima, C. acanthocarpa* var. *coloradensis*). These latter species occurred primarily in stream channels in the northwestern part of the study area and contributed to a hot spot of higher densities of *B. tournefortii* on Figure 5.

The canopies, drip lines, and coppice mounds of shrubs, cacti, and grasses are nutrient-rich resource islands (Garcia-Moya and McKell 1970; Halvorson et al. 1994; Muller 1953; Schlesinger et al. 1996). They also provide more mesic environments than intershrub spaces on broad expanses of desert pavement on older geomorphic surfaces. The microhabitat preference of *B. tournefortii* for soils beneath shrub canopies is similar to the preferences of other exotics, the forb redstem filaree [*Erodium cicutarium* (L.) Aiton] and annual grasses red brome [*Bromus madritensis* subsp. *rubens* (L.) Husn] and Chilean chess (*Bromus trinii* Desv., now *Bromus berteroanus* Colla) (Abella and Smith 2013; Brooks 1999; Craig et al. 2010).

The high densities and concentrations of *B. tournefortii* beneath and within the canopies of perennial species may, in the long term, negatively affect the well-being and survival of shrubs, cacti, and grasses. *Brassica tournefortii* and other exotic annual species are facilitated by the microhabitats under native shrubs such as *L. tridentata* and *A. dumosa*. The exotic annual grass, Mediterranean grass [*Schismus arabicus* Nees, *S. barbatus* (L.) Thell.], has deleterious effects on *A. dumosa* seedlings, reducing growth, and at high densities, negatively affecting recruitment of *A. dumosa* (Rodríguez-Buriticá and Miriti 2009). *Brassica tournefortii* may have a similar effect on native shrubs.

**Data on Biomass of Annual Plants.** Plant transects with data on biomass of annuals were available for 1988, 1992, and 2009 (Table 3). We recorded 46 species of annuals, of which 93.5% were native (Appendix 1). The total biomass of annual plants on transects ranged from 13.8 to 66.8 g $m^{-2}$ for all years but differed little from transects walked in years when winter precipitation was above and below the long-term mean. For years when winter precipitation was above the long-term mean (1987 to 1988, 2008 to 2009), the mean for total biomass of annuals was 33.02 g $m^{-2}$ (range, 23.3 to 41.1 g $m^{-2}$). In comparison, when rainfall was below the long-term mean (1991 to 1992), total biomass was 39.03 g $m^{-2}$ (range, 13.8 to 66.8 g $m^{-2}$). For the five transects in Open Desert North, the total annual biomass of native species declined between the time the first transects were walked (1988, 1992) and 2009. Overall, the proportional biomass of natives on all six transects also declined during the same period ($F_{1,7}$ = 9.98, P = 0.016), and the proportional biomass of exotics increased ($F_{1,7}$ = 9.97, P = 0.016). Between 1988 and 2009, *B. tournefortii* became an increasingly important part of the biomass of annual exotics. In 1988, *B. tournefortii* was not observed on the two transects. In 1992, *B. tournefortii* was present only as a trace (one plant) on transect 6, the transect closest to Highway 95. Seventeen years later, in 2009, *B. tournefortii* was present on all six transects and composed from 31 to 76% of the annual biomass. *Schismus arabicus* was present in low amounts (≤ 1%) in 1988, higher (1.2 to 81.9%) in 1992, and again low (1.5 to 3.6%) in 2009, the year when *B. tournefortii* formed a substantial portion of the annual biomass. The exotic forb *Erodium cicutarium* was absent from all transects in all years, and the exotic grass *Bromus madritensis* subsp. *rubens* was noted (0.38% of annual biomass) on one transect in 1992.

Our finding of a significant change in the proportional biomass of native and exotic species, specifically *B. tournefortii*, in the winter annual flora of this *L. tridentata–A. dumosa* association is important. Between 1988 and 2009, the proportional biomass of native annuals declined while biomass of exotic annuals increased. This trend, if continued, is likely to bring long-term changes to the valley and, potentially, similarly situated areas. Other scientists have reported that *B. tournefortii* negatively affects the native annual flora in the Sonoran Desert (Barrows et al. 2009; Minnich 2008; Minnich and Sanders 2000; Van Devender et al. 1997). In experiments conducted in sand dunes in the Coachella Valley, Barrows et al. (2009) described shifts in composition of the annual flora increasingly toward *B. tournefortii* while decreasing the fraction of native species. Brooks (2000) reported similar results regarding the negative effects of the exotics *Schismus* spp. and *Bromus madritensis* subsp. *rubens* on native annual plants in the Mojave Desert.

Our findings indicate that landscape-scale monitoring programs for *B. tournefortii*, such as the Weed Sentry

Table 3. A summary of biomass data for native and exotic annual plants, including *Brassica tournefortii*, from six randomly placed vegetation transects established between 1988 and 1992 in the Chemehuevi Valley, western Sonoran Desert.

| Transect number | Year | No. ofannual native species | Total annual biomass g $m^{-2}$ | Total native annual biomass g $m^{-2}$ | % Native forbs in annual biomass | % Exotic grass in annual biomass | % BRSTO in annual biomass |
|---|---|---|---|---|---|---|---|
| 1 | 1988 | 11 | 23.3 | 23.1 | 99.0 | 1.0 | 0 |
| 2 | 1988 | 8 | 41.1 | 41.1 | 100 | trace | 0 |
| 1 | 1992 | 15 | 13.8 | 13.6 | 98.84 | 1.16 | 0 |
| 2 | 1992 | 12 | 16.8 | 15.9 | 94.77 | 5.23 | 0 |
| 3 | 1992 | 21 | 42.4 | 33.2 | 78.39 | 21.61 | 0 |
| 4 | 1992 | 11 | 62.4 | 59.3 | 95.07 | 4.93 | 0 |
| 5 | 1992 | 16 | 66.8 | 12.0 | 18.03 | 81.97 | 0 |
| 6 | 1992 | 9 | 32.0 | 23.2 | 72.46 | 27.54 | trace |
| 1 | 2009 | 17 | 22.8 | 14.4 | 63.33 | 1.49 | 35.18 |
| 2 | 2009 | 19 | 27.64 | 18.2 | 65.84 | 3.39 | 30.77 |
| 3 | 2009 | 21 | 38.22 | 8.6 | 22.6 | 1.54 | 75.86 |
| 4 | 2009 | 14 | 36.64 | 20.1 | 54.83 | 2.92 | 42.25 |
| 5 | 2009 | 18 | 34.82 | 18.8 | 53.97 | 3.11 | 42.92 |
| 6 | 2009 | 14 | 39.70 | 21.7 | 54.74 | 3.62 | 41.64 |

program initiated in the eastern Mojave Desert (Abella et al. 2009, 2013), would benefit by including axial-valley ephemeral stream channels and smaller ephemeral stream channels in the interior of valleys and alluvial fans in addition to roads. Small stream channels also are likely foci for establishing new populations of *B. tournefortii* (e.g., see hot spot in the northwest part of the study site, as shown on Figure 5). The naturally disturbed soils may also produce taller plants with more siliques, as reported in experimental studies with *B. tournefortii* (Suazo et al. 2012). In addition to ephemeral stream channels, other areas should be included in monitoring plans, e.g., a range of older geological surfaces and sites more distant from human disturbances.

We suggest that *B. tournefortii* qualifies as an invasive "transformer" of ecosystems, because, like other transformer species, it has the potential to "change the character, condition, form or nature of ecosystems over a substantial area" (Richardson et al. 2000). To address this topic in the future, we need to know more about (1) the role of *B. tournefortii* in changing composition of local and regional floras, and ultimately, the effects on animal communities; (2) the geomorphic agents of plant and seed transport; (3) the role of precipitation; and (4) effective control measures.

## Acknowledgments

We thank J. Yee, C. Barrows, R. Marushia, K. Phillips, S. Jones, and two anonymous reviewers for helping to improve the manuscript and J. Mack for assistance with figures. M. Waggoner, D. LaBerteaux, P. Seamount, C. Knowles, P. Knowles, S. Olson-Edge, P. Wood, and P. Woodman assisted with field work. Roger Hatheway provided historical information on roads and Highway 95. Funding was provided by the USDI BLM, Geological Survey, and California Department of Fish and Game, and Off-Highway Motor Vehicle Recreation Division of the California Department of Parks and Recreation to the BLM and U.S. Geological Survey. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. government.

## Literature Cited

Abella SR, Craig DJ, Chiquoine LP, Prengaman KA, Schmid SM, Embrey TM (2011a) Relationships of native desert plants with red brome (*Bromus rubens*): toward identifying invasion-reducing species. Invasive Plant Sci Manag 4:115–124

Abella SR, Lee AC, Suazo AA (2011b) Effects of burial depth and substrate on the emergence of *Bromus rubens* and *Brassica tournefortii*. Bull South Calif Acad Sci 110:17–24

Abella SR, Smith SD (2013) Annual–perennial plant relationships and species selection for desert restoration. J Arid Land 5:298–309

Abella SR, Spencer JE, Hoines J, Nazarchyk C (2009) Assessing an exotic plant surveying program in the Mojave Desert, Clark County, Nevada, USA. Environ Monit Assess 151:221–230

Abella SR, Suazo AA, Norman CM, Newton AC (2013) Treatment alternatives and timing affect seeds of African mustard (*Brassica tournefortii*), an invasive forb in American Southwest arid lands. Invasive Plant Sci Manag 6:559–567

Baldwin BG, Keil DJ, Markos S, Mishler BD, Patterson R, Rosatti TJ, Wilken DH, eds. (2014) Jepson Flora Project. Jepson eFlora. http:/ucjeps.berkeley.edu/IJM.html. Accessed June 5, 2014

Bangle DN, Walker LR, Powell EA (2008) Seed germination of the invasive plant *Brassica tournefortii* (Sahara mustard) in the Mojave Desert. West N Am Nat 68:334–342

Barrows CW, Allen EB, Brooks ML, Allen MF (2009) Effects of an invasive plant on a desert sand dune landscape. Biol Invasions 11: 673–686

Bedford DR (2003) Surficial and bedrock geologic map database of the Kelso 7.5 minute quadrangle, San Bernardino County, California. U.S. Geological Survey Open-File Report 03–501. 34 p

Bedford DR, Miller DM, Phelps GA (2010) Surficial geologic map of the Amboy 30′ × 60′ quadrangle, San Bernardino County, California. U.S. Geological Survey Scientific Investigations Map 1309, scale 1 : 100,000

Bedford DR, Miller DM, Schmidt KM, Phelps GA (2009) Landscape-scale relationships between surficial geology, soil texture, topography, and creosote bush size and density in the eastern Mojave Desert of California. Pages 252–277 *in* Webb RH, Fenstermaker LF, Heaton JF, Hughson DL, McDonald EV, Miller DM, eds. The Mojave Desert: Ecosystem Processes and Sustainability. Reno: University of Nevada Press

Bowers JE, Bean TM, Turner RM (2006) Two decades of change in distribution of exotic plants at the Desert Laboratory, Tucson, Arizona. Madroño 53:252–263

Brooks ML (1999) Habitat invasibility and dominance by alien annual plants in the western Mojave Desert. Biol Invasions 1:325–337

Brooks ML (2000) Competition between alien annual grasses and native annual plants in the Mojave Desert. Am Midl Nat 144:92–108

Brooks ML (2009) Spatial and temporal distribution of nonnative plants in upland areas of the Mojave Desert. Pages 101–124 *in* Webb RH, Fenstermaker LF, Heaton JF, Hughson DL, McDonald EV, Miller DM, eds. The Mojave Desert: Ecosystem Processes and Sustainability. Reno: University of Nevada Press

Brooks ML, Lair BM (2009) Ecological effects of vehicular routes in a desert ecosystem. Pages 168–195 *in* Webb RH, Fenstermaker LF, Heaton JF, Hughson DL, McDonald EV, Miller DM, eds. The Mojave Desert: Ecosystem Processes and Sustainability. Reno: University of Nevada Press

Brooks ML, Minnich RA (2006) Southeastern Deserts Bioregion. Pages 391–414 *in* Sugihara NG, van Wagtendonk JW, Shaffer KE, Fites-Kaufman J, Thode AE, eds. Fire in California's Ecosystems. Berkeley: University of California Press

Brooks ML, Pyke DA (2001) Invasive plants and fire in the deserts of North America. Pages 1–14 *in* Galley KEM, Wilson TP, eds. Proceedings of the Invasive Species Workshop: The Role of Fire in the Control and Spread of Invasive Species. Fire Conference 2000: The First National Congress on Fire Ecology, Prevention, and Management. Tallahassee, FL: Tall Timbers Research Station, Misc Publ No 11

California Invasive Plant Council (2006) California Invasive Plant Inventory, Cal-IPC Publication 2006–02. Berkeley: California Invasive Plant Council., http://www.cal-ipc.org/ Accessed June 6, 2013

Chauhan BS, Gill G, Preston C (2006a) African mustard (*B. tournefortii*) germination in southern Australia. Weed Sci 54:891–897

Chauhan BS, Gill G, Preston C (2006b) Seedling recruitment pattern and depth of recruitment of 10 weed species in minimum tillage and no-till seeding systems. Weed Sci 54:658–668

Craig DJ, Craig JE, Abella SR, Vanier CH (2010) Factors affecting exotic annual plant cover and richness along roadsides in the eastern Mojave Desert, USA. J Arid Environ 74:702–707

Forman RT, Sperling D, Bissonette JA, Clevenger AP, Cutshall CD, Dale VH, Fahrig L, France R, Goldman CR, Heanue K, Jones JA, Swanson FJ, Turrentine T, Winter TC (2003) Road Ecology: Science and Solutions. Washington, DC: Island Press. 481 p

Frenkel RE (1970) Ruderal Vegetation Along Some California Roadsides. University of California Publications in Geography Vol. 29. Berkeley: University of California Press. 173 p

Garcia-Moya E, McKell CM (1970) Contribution of shrubs to the nitrogen economy of a desert-wash plant community. Ecology 51: 81–88

Halvorson WL, Bolton Jr. J, Smith JL, Rossi RE (1994) Geostatistical analysis of resource islands under *Artemisia tridentata* in the shrub-steppe. Great Basin Nat 54:313–328

Hamerlynck EP, McAuliffe JR, McDonald EV, Smith SD (2002) Ecological responses of two Mojave Desert shrubs to soil horizon development and soil water dynamics. Ecology 83:768–779

Hereford R, Webb RH, Longpré CI (2006) Precipitation history and ecosystem response to multidecadal precipitation variability in the Mojave Desert region, 1893–2001. J Arid Environ 67(Suppl):13–34

Littell RC, Milliken GA, Stroup WW, Wolfinger RD (1996) SAS System for Mixed Models. Cary, NC: SAS Institute Inc. 633 p

Manning JC (1992) Applied Principles of Hydrology. 2nd edn. New York: Macmillan. 294 p

Marushia RG, Brooks ML, Holt JS (2012) Phenology, growth, and fecundity as determinants of distribution in closely related nonnative taxa. Invasive Plant Sci Manag 5:217–229

Marushia RG, Cadotte MW, Holt JS (2010) Phenology as a basis for management of exotic annual plants in desert invasions. J Appl Ecol 47:1290–1299

McAuliffe JR (1994) Landscape evolution, soil formation, and ecological patterns and processes in Sonoran Desert bajadas. Ecol Monogr 64:111–148

McFadden LD, Ritter JB, Wells SG (1989) Use of multiparameter relative-age methods for age estimation and correlation of alluvial fan surfaces on a desert piedmont, eastern Mojave Desert, California. Quat Res 32:276–290

Miller DM (2012) Surficial geologic map of the Ivanpah 30′ × 60′ quadrangle, San Bernardino County, California, and Clark County, Nevada. U.S. Geological Survey Scientific Investigations Map 3206, scale 1 : 100,000, 14 p

Miller DM, Bedford DR, Hughson DL, McDonald EV, Robinson SE, Schmidt KM (2009) Mapping Mojave Desert ecosystem properties with surficial geology. Pages 225–251 *in* Webb RH, Fenstermaker LF, Heaton JS, Hughson DL, McDonald EV, Miller DM, eds. The Mojave Desert: Ecosystem Processes and Sustainability. Reno: University of Nevada Press

Miller DM, Schmidt KM, Mahan SA, McGeehin JP, Owen LA, Barron JA, Lehmkuhl F, Löhrer R (2010) Holocene landscape response to seasonality of storms in the Mojave Desert. Quat Int 215:45–61

Minnich RA (2008) California's Fading Wildflowers: Lost Legacy and Biological Invasions. Berkeley and Los Angeles: University of California Press. 344 p

Minnich RA, Sanders AC (2000) *Brassica tournefortii* Gouan. Pages 68–72 in Bossard CC, Randall JM, Hoshovsky MC, eds. Invasive Plants of California's Wildlands. Berkeley: University of California Press

Muller CH (1953) The association of desert annuals with shrubs. Am J Bot 40:52–60

National Oceanic and Atmospheric Administration (1985–2009). Climatological Data for California and Arizona. National Climatic Data Center, Asheville, NC http://www.ncdc.noaa.gov/oa/ncdc.html. Accessed August 1, 2010

Prose DV (1985) Persisting effects of armored military maneuvers on some soils of the Mojave Desert, California. Environ Geol Water Sci 7:163–170

Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. Divers Distrib 6:93–107

Rodríguez-Buriticá S, Miriti MN (2009) Biting the hand that feeds: the invasive grass *Schismus barbatus* (Poaceae) is facilitated by, but reduces establishment of, the native shrub *Ambrosia dumosa* (Asteraceae). J Veg Sci 20:241–250

Rowlands PG (1995) Regional bioclimatology of the California Desert. Pages 95–134 *in* Latting J, Rowlands PG, eds. The California Desert:

An Introduction to Natural Resources and Man's Impact. Riverside, California: June Latting Books
Rowlands P, Johnson H, Ritter E, Endo A (1982) The Mojave Desert. Pages 103–162 *in* Bender GL, ed. Reference Handbook on the Deserts of North America. Westport, Connecticut: Greenwood Press
Ruegers H (1903) Rueger's automobile and miners' road map of Southern California. Los Angeles: Henry Ruegers
San Bernardino County, California (1925). Map of San Bernardino County, California, Showing roads, railroads, springs and mining districts of the desert portion. JP Kemmerer, County Surveyor
Sánchez-Flores E (2007) GARP modeling of natural and human factors affecting the potential distribution of the invasives *Schismus arabicus* and *Brassica tournefortii* in 'El Pinacate y Gran Desierto de Altar' Biosphere Reserve. Ecol Model 204:457–474
Sawyer JO, Keeler-Wolf T, Evens JM (2009) A Manual of California Vegetation. 2nd edn. Sacramento: California Native Plant Society Press
Schenk HJ, Holzapfel C, Hamilton JG, Mahall BE (2003) Spatial ecology of a small desert shrub on adjacent geological substrates. J Ecol 91:383–395
Schlesinger WH, Raikes JA, Hartley AE, Cross AF (1996) On the spatial pattern of soil nutrients in desert ecosystems. Ecology 77:364–374
Suazo AA, Spencer JE, Engel EC, Abella SR (2012) Responses of native and non-native Mojave Desert winter annuals to soil disturbance and water additions. Biol Invasions 14:215–227
Thurston AG (1915) Thurston's auto-highway, mountain and desert map. Pasadena, California: Western Map and Publishing Co
Trader MR, Brooks ML, Draper JV (2006) Seed production by the non-native *Brassica tournefortiii* (Sahara mustard) along desert roadsides. Madroño 53:313–320
[USDA] U.S. Department of Agriculture (2005) Noxious Weed List. Berkeley: University of California Press
[USDI BLM] U.S. Department of the Interior, Bureau of Land Management (1980) California Desert Conservation Area Plan, 1980. Riverside, CA: U.S. Department of the Interior, Bureau of Land Management, California Desert Program
[USDI BLM] U.S. Department of the Interior, Bureau of Land Management (2002) Northern and Eastern Colorado Desert Coordinated Management Plan. Record of Decision. Riverside, CA: U.S. Department of the Interior, Bureau of Land Management, D1–D11
[USDI BLM and California Department of Fish and Game] U.S. Department of the Interior, Bureau of Land Management, and California Department of Fish and Game (2002) Northern and Eastern Colorado Desert Coordinated Management Plan, an Amendment to the California Desert Conservation Area Plan 1980 and Sikes Act Plan with the California Dept. of Fish and Game, and Final Environmental Impact Statement. Vol. 1. Riverside, CA: U.S. Department of the Interior, Bureau of Land Management
Van Devender TR, Felger RS, Búrquez MA (1997) Exotic plants in the Sonoran Desert region, Arizona and Sonora. Pages 10–15 *in* Kelly M, Wagner E, Warner P, eds. Proceedings: California Exotic Pest Plant Council Symposium, Vol 3. U.S.: California Exotic Pest Plant Council
Whitford WG (2002) Ecology of Desert Systems. London, UK: Academic Press. 343 p

*Received March 24, 2014, and approved August 4, 2014.*

Appendix 1. The biomass of annual plants recorded on vegetation transects in 1988, 1992, and 2009 at the Chemehuevi Valley study area, San Bernardino County, California. Nomenclature from the University of California's Jepson Herbarium online eflora (Baldwin et al. 2014).

| | Biomass g $m^{-2}$ and year of transect | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1988 | | 1992 | | | | | | 2009 | | | | | |
| | Transect number | | | | | | | | | | | | | |
| Plant species | 1 | 2 | 1 | 2 | 3 | 4 | 5 | 6 | 1 | 2 | 3 | 4 | 5 | 6 |
| *Acmispon strigosus* | | | | | | | | | | | 0.02 | | | 0.14 |
| *Amsinckia tessellata* var. *t.* | | | | | | | | | | | | 0.15 | | 0.06 |
| *Brassica tournefortii*[a] | | | | | | | | Tr[b] | 8.03 | 8.50 | 28.99 | 15.48 | 14.95 | 16.53 |
| *Bromus madritensis* subsp. *rubens*[a] | | | | | 0.2 | | | | | | | | | |
| *Caulanthus lasiophyllus* | | | | | | | | | | | | | 0.06 | |
| *Chaenactis carphoclinia* var. *c.* | 2.8 | 0.2 | 0.05 | | 0.9 | | 0.3 | 0.9 | 5.98 | 3.79 | 1.03 | 0.60 | | 0.03 |
| *Chaenactis stevioides* | | | | | | | | | | 0.06 | 0.03 | 0.07 | 1.38 | 0.30 |
| *Chorizanthe brevicornu* var. *b.* | Tr | 18.8 | 0.4 | 0.3 | 0.2 | 0.05 | 1.6 | 0.1 | 0.05 | 0.49 | | 0.09 | 0.30 | 0.13 |
| *Chorizanthe corrugata* | | | 0.2 | | | | | | Tr | | | | 0.05 | |
| *Chorizanthe rigida* | Tr | | 0.3 | 0.3 | 0.1 | | Tr | 0.2 | 0.19 | 1.21 | | 0.05 | | |
| *Chylismia claviformis* subsp. *aurantiaca* | | | | | | | Tr | | | | | | 0.11 | |
| *Cryptantha angustifolia* | 2.0 | | 0.1 | 0.02 | 0.6 | 0.1 | 6.5 | 0.4 | 0.01 | 0.06 | 0.04 | 0.38 | 8.29 | 1.87 |
| *Cryptantha barbigera* | | | | | | | | | | 0.09 | | | | |
| *Cryptantha dumetorum* | | | | | 0.6 | | | | | | | | | |
| *Cryptantha maritima* | | | | | | | | | 0.38 | 0.07 | 0.40 | 0.07 | 0.04 | |
| *Cryptantha micrantha* | | | | | Tr | | | | | | | | | |
| *Cryptantha nevadensis* | | | | | 0.2 | | | | | 0.30 | 0.01 | | | |
| *Cryptantha pterocarya* | | | | | 0.2 | | | | | | 0.01 | | 0.02 | |
| *Cryptantha utahensis* | | | | | 0.3 | 0.05 | 0.1 | | | | | | | |
| *Eremothera boothii* subsp. *desertorum* | | | 0.05 | | 0.1 | 0.1 | 0.1 | | | 0.05 | 0.05 | | 0.01 | 0.27 |
| *Eriogonum pusillum* | | | | | 1.5 | 0.2 | 0.7 | | | | | | | |
| *Eriogonum reniforme* | | | | | Tr | Tr | Tr | | | | | | | |
| *Eriogonum thomasii* | | | | | | | | | 0.01 | 0.01 | | 0.03 | | |
| *Eriogonum trichopes* | | Tr | | 1.4 | | | | | | 0.28 | 0.01 | 1.58 | 0.11 | |
| *Eriophyllum lanosum* | | | | | | | | | | Tr | 0.03 | Tr | | 0.02 |
| *Erodium texanum* | | | 0.6 | | | 0.1 | | | 0.16 | 0.16 | | | | |
| *Eschscholzia minutiflora* | | | | | 0.2 | | | | | | | | | |
| *Euphorbia micromera* | | | | | | | | | | | 2.02 | | | 0.27 |
| *Geraea canescens* | | | | | | | | | | | | | 0.03 | |
| *Langloisia setosissima* subsp. *punctata* | Tr | | | | | | | | 0.01 | | | | | |
| *Lepidium flavum* | 3.8 | 8.3 | | | | | | | | | | | | |
| *Lepidium lasiocarpum* var. *l.* | | | | | | | | | 0.90 | 1.04 | 0.46 | 7.70 | 0.07 | 8.53 |
| *Lepidium nitidum* | | | 0.05 | 1.6 | 1.4 | 2.2 | 0.2 | 1.8 | | | | | | |
| *Linanthus jonesii* | | | | | | | | | | | 0.01 | | | 0.03 |

Appendix 1. Continued.

| | Biomass g $m^{-2}$ and year of transect | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1988 | | 1992 | | | | | | 2009 | | | | | |
| | Transect number | | | | | | | | | | | | | |
| Plant species | 1 | 2 | 1 | 2 | 3 | 4 | 5 | 6 | 1 | 2 | 3 | 4 | 5 | 6 |
| *Loeseliastrum schottii* | | | 0.1 | 0.03 | | | Tr | | | | | | | |
| *Malacothrix glabrata* | | | | | 0.1 | | | | | | | | | |
| *Monoptilon bellioides* | Tr | Tr | 0.05 | | 0.1 | | | | 0.04 | 0.04 | 0.01 | | | |
| *Nemacladus rubescens* | | | 0.1 | 0.05 | | | | | | | | | | |
| *Oligomeris linifolia* | 0.8 | Tr | | 0.1 | | | | | | | Tr | | | |
| *Pectocarya heterocarpa* | | | 0.2 | 0.8 | 0.2 | 0.6 | 1.7 | 0.6 | 0.37 | 0.62 | 0.11 | 0.66 | 1.53 | 2.74 |
| *Pectocarya platycarpa* | 1.5 | Tr | 0.5 | 3.4 | 3.8 | 2.0 | 0.8 | 1.3 | 0.38 | 0.74 | 0.51 | 0.71 | 0.98 | 2.14 |
| *Pectocarya recurvata* | | | | 0.1 | 0.2 | | | | 0.04 | | 0.05 | | 0.04 | |
| *Phacelia crenulata* var. *minutiflora* | | | | | | | | | 0.07 | | Tr | | | |
| *Physaria tenella* | 0.1 | | 0.1 | | 0.1 | | | 0.1 | 0.12 | 0.11 | 0.20 | | | |
| *Plantago ovata* | 11.3 | 13.8 | 10.8 | 7.8 | 22.4 | 53.9 | 0.1 | 17.8 | 5.74 | 9.08 | 3.64 | 8.00 | 5.50 | 5.20 |
| *Rafinesquia neomexicana* | | | | | | | | | | | | | 0.26 | |
| *Schismus arabicus*[a] | 1.0 | Tr | 0.2 | 0.9 | 9.0 | 3.1 | 54.7 | 8.8 | 0.34 | 0.94 | 0.59 | 1.07 | 1.08 | 1.44 |
| *Stylocline intertexta* | | | | | | | | 0.1 | | | | | 0.01 | |

[a] Exotic annual species.

[b] Abbreviation: Tr, trace.