

2010

# Distribution and Ecotypic Variation of the Invasive Annual Barb Goatgrass (*Aegiolops triuncialis*) on Serpentine Soil

Kelly G. Lyons  
*Trinity University*, [klyons@trinity.edu](mailto:klyons@trinity.edu)

A.M. Shapiro

Mark W. Schwartz

Follow this and additional works at: [http://digitalcommons.trinity.edu/bio\\_faculty](http://digitalcommons.trinity.edu/bio_faculty)



Part of the [Biology Commons](#)

---

## Repository Citation

Lyons, Kelly G.; Shapiro, A.M.; and Schwartz, Mark W., "Distribution and Ecotypic Variation of the Invasive Annual Barb Goatgrass (*Aegiolops triuncialis*) on Serpentine Soil" (2010). *Biology Faculty Research*. 19.  
[http://digitalcommons.trinity.edu/bio\\_faculty/19](http://digitalcommons.trinity.edu/bio_faculty/19)

This Article is brought to you for free and open access by the Biology Department at Digital Commons @ Trinity. It has been accepted for inclusion in Biology Faculty Research by an authorized administrator of Digital Commons @ Trinity. For more information, please contact [jcostanz@trinity.edu](mailto:jcostanz@trinity.edu).

## **Distribution and Ecotypic Variation of the Invasive Annual Barb Goatgrass (*Aegilops triuncialis*) on Serpentine Soil**

Author(s) :Kelly G. Lyons, A. M. Shapiro, and Mark W. Schwartz

Source: Invasive Plant Science and Management, 3(4):376-389. 2010.

Published By: Weed Science Society of America

DOI: 10.1614/IPSM-09-036.1

URL: <http://www.bioone.org/doi/full/10.1614/IPSM-09-036.1>

---

BioOne ([www.bioone.org](http://www.bioone.org)) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/page/terms\\_of\\_use](http://www.bioone.org/page/terms_of_use).

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

# Distribution and Ecotypic Variation of the Invasive Annual Barb Goatgrass (*Aegilops triuncialis*) on Serpentine Soil

Kelly G. Lyons, A. M. Shapiro, and Mark W. Schwartz\*

Successful colonization of newly introduced species is driven by a multitude of factors and is highly dependent on the species. It has long been hypothesized that preadaptation and postestablishment natural selection of introduced species can facilitate their invasion; however, to date, limited research has been dedicated to these theories. In addition, although the correlation between establishment of invasive species and disturbance has been noted and widely studied, the susceptibility of undisturbed habitats to invasion remains unclear. In California, serpentine habitats are severe edaphic environments that have been relatively free of anthropogenic disturbance and nonindigenous species invasions. In this study, we documented the occurrence of the nonindigenous barb goatgrass on serpentine and nonserpentine grasslands in the California Northern Interior Coast Range and the western foothills of the Sierra Nevada Mountains and conducted greenhouse and field experiments to assess the species' degree of adaptation to serpentine soils. Reconnaissance of serpentine intrusions and yearly monitoring suggest that barb goatgrass may grow preferentially on serpentine soil, particularly disturbed serpentine sites. In the greenhouse, for most measures of performance, serpentine populations performed better than nonserpentine populations when grown on serpentine soil. Particularly noteworthy was that serpentine populations had higher root-mass ratios than nonserpentine populations when grown on serpentine soil. In contrast to the greenhouse study, field-grown populations from serpentine and nonserpentine sources performed equally well on nonserpentine; alluvial, disturbed serpentine; and shallow, undisturbed serpentine, although the overall species' performance was diminished on severe serpentine soils. Alarmingly, even in the absence of previous exposure to serpentine, barb goatgrass was capable of establishing and spreading into minimally disturbed sites with strong serpentinic characteristics.

**Nomenclature:** Barb goatgrass, *Aegilops triuncialis* L.

**Key words:** Serpentine, edaphic, invasive plant, nonindigenous, preadaptation.

Factors influencing successful introductions of new species include the characteristics of the species, the genetics of the founding individuals, and the biotic and abiotic features and the disturbance history of the new ecosystem (Crawley 1987; Mack 1996; Moyle and Light 1996; Orians 1986; Rejmanek 1989; Rejmanek and Richardson 1996). Response to natural selection or preadaptation of newly introduced species is suggested to facilitate their invasion (Baker 1965) and may be a more important attribute than physiological flexibility or

tolerance (Lee 2002). Nevertheless, to date, few studies have investigated adaptation, either preintroduction or postintroduction, as a factor in the invasion process (sensu Rice and Mack 1991; Frietas and Mooney 1996; Harrison et al. 2001). Furthermore, although studies on invasive species have traditionally focused on species in highly disturbed areas, intact habitats and communities are also at risk (Rejmánek 1989; Simberloff 1995).

Serpentine (more appropriately referred to as ultramafic [Proctor 1999]) formations occur as intrusions in the Earth's surface, mostly near tectonic collisions. Soils formed from serpentine are rocky, relatively thin, and characterized by low levels of calcium, nitrogen, and phosphorus and by high levels of magnesium and heavy metals, such as chromium, nickel, and iron (Brooks 1987; Gordon and Lipman 1926; Kruckeberg 1985; Proctor and Woodell 1975; Vlamis and Jenny 1948; Walker 1954). The serpentine edaphic environment selects for specially

DOI: 10.1614/IPSM-09-036.1

\* Associate Professor, Department of Biology, Trinity University, One Trinity Place, San Antonio, TX 78212; Professor, Center for Population Biology, University of California, Davis, CA 95616; Professor, Department of Environmental Science and Policy, University of California, Davis, CA 95616. Corresponding author's E-mail: klyons@trinity.edu

## Interpretive Summary

Barb goatgrass, a nonindigenous, invasive, annual plant, threatens serpentine grasslands throughout Northern California. The consistent observation that barb goatgrass is more often on disturbed serpentine sites with deeper, and presumably richer, soils suggests that intact, undisturbed serpentine sites with poor soil development are relatively safe from barb goatgrass invasion. Nevertheless, in this study, we found that, although barb goatgrass performed better on well-drained, nonserpentine soils and disturbed, alluvial serpentine soils, we also found that it was capable of colonizing and reproducing on more severe, undisturbed serpentine soils. Furthermore, we anticipate that intensified propagule pressure will increase the likelihood that an appropriate genotype will successfully establish on thin, intact serpentine soil, despite the harsh conditions. In light of these findings, among sites where barb goatgrass is firmly established, adjacent to intact serpentine sites, prudent management will involve the following: (1) careful surveying of intact serpentine soils for early detection of barb goatgrass, (2) monitoring and removal of the weed where established on the edges of sites not yet invaded, (3) conserving sites with little or no history of land use, and (4) educating the public on the effects of recreational activity on the spread of barb goatgrass to remote sites.

adapted species and ecotypes, including rare endemics (Kruckeberg 1985). Because of their unusual species composition, serpentine sites are of high conservation priority. Kruckeberg (1985) estimates that 217 vascular plant species or ecotypes are restricted to serpentine habitats in California and, among edaphic anomalies, serpentine ranks the highest in contributions to the California Native Plant Society rare plant inventory (Fiedler 1995).

Nonindigenous species introductions have resulted in enormous alteration of the once widespread, perennial dominated California grasslands (Barbour et al. 1993; Murphy and Ehrlich 1989; Shapiro 2002). In stark contrast to this trend, serpentine grasslands in California have remained relatively pristine (Kruckeberg et al. 1985). The limited occurrence of invasive species on serpentine soils is presumably a result of the severity of the substrate (Huenneke et al. 1990; Kruckeberg 1985) combined with relatively low levels of human impact and colonization. Nonetheless, serpentine sites in California are experiencing an ever-increasing amount of anthropogenic disturbance through mining, grazing, road cuts and off-road vehicle use.

In northern California, common nonindigenous annual grass species, such as medusahead [*Taeniatherum caput-medusae* (L.) Nevski], wild oat (*Avena fatua* L.), and soft brome (*Bromus hordeaceus* L.) are now well established on numerous serpentine outcrops (Harrison 1999; Harrison et al. 2001). Disturbed serpentine sites, as well as the disturbed margins of intact sites, are especially susceptible (K. Lyons, personal observation). Particularly alarming,

however, was the observation in the mid-1990s that the Mediterranean annual barb goatgrass (*Aegilops triuncialis* L.) grew vigorously, and perhaps preferentially, on serpentine soils in the foothills of the Sierra Nevada Mountains (A. Shapiro, personal observation). Shortly thereafter, we confirmed a similar trend among serpentine outcrops in the southern portion of the Northern Interior Coast Range of California. We also found that barb goatgrass was present, and in higher abundance, on naturally and anthropogenically disturbed serpentine sites. Since this time, the species' presence and spread on serpentine soil has been documented in the literature (Batten et al. 2006; Drenovsky and Batten 2007; Harrison et al. 2001).

The presence of barb goatgrass on serpentine soil is cause for concern for many reasons. Barb goatgrass is listed by the California Department of Food and Agriculture as a noxious weed that often establishes in dense, monotypic stands (K. Lyons, personal observation) and is capable of establishing on rocky, well-drained soils (Davis 1985). The species also alters soil microbial communities (Batten et al. 2006) and ecosystem processes, such as nutrient cycling (Drenovsky and Batten 2007). In addition, barb goatgrass is congeneric with the serpentinophile ovate goatgrass (*Aegilops geniculata* Roth syn. *A. ovata* L. of former publications) (Brooks 1987). Subspecies status has been recommended for two ecotypes of *A. geniculata* that grow on serpentine soils in the Tras-os-Montes of Portugal and the Upper Tiber Valley of Italy (Brooks 1987), although there is currently no formal designation for these subspecies (J.K. Williams, personal communication). In addition, barb goatgrass, as part of the taxonomic wheat group (including *Triticum* and *Aegilops*), belongs to a complex of polyploids known for their weedy and highly adaptive character (Barrett and Richardson 1986; Garcia et al. 1991; Zohary 1965). Unlike their diploid relatives, *Aegilops* polyploids show little ecological affinity and have large environmental flexibility (Zohary 1965).

In their native range, barb and ovate goatgrasses are distributed throughout the Mediterranean Basin (Zohary 1965) and northern Africa as well as southwest Asia (Davis 1985). The genus is also found in Turkey, Greece, Iraq, Iran, Afghanistan, Syria, and Israel, the center of its distribution (Rechinger 1970; Zohary 1965). Nonetheless, barb goatgrass has the most widespread distribution of all *Aegilops* species (Zohary 1965). Species of this wheat group are primarily self-pollinated, facultative outcrossers, a condition that may lend itself to rapid, local species selection (Zohary 1965). In addition, this high degree of selfing, combined with the polyploid condition, may facilitate the selection process by protecting coadapted gene complexes from segregation (Garcia et al. 1989).

It is widely hypothesized that, among indigenous species, early colonization of serpentine soil was successful because

of a preadapted condition (Brady et al. 2005; Kruckeberg 1954). Barb goatgrass' genetic status as a congener with *A. ovata* suggests that the species may be preadapted to serpentine substrates (sensu Baker 1986). Evidence of direct crosses between barb goatgrass and *A. ovata* has not been found; however, hybridization among all *Aegilops* polyploids is expected (Zohary 1965). It is therefore possible that barb goatgrass' genetic condition, combined with repeated exposure to a severe edaphic substrate, may facilitate the weed's current and future success on serpentine soils through postinvasion selection.

Stressful edaphic anomalies are selective forces that can operate over relatively short periods (Heywood 1986; Jain and Bradshaw 1966; Kruckeberg 1951, 1967; Lechowicz and Bell 1991; Li et al. 2000; Lin and Wu 1994; MacNair et al. 1989; McNeilly 1968; Rice and Mack 1991; Wu and Kruckeberg 1985). For example, MacNair et al. (1989) demonstrated that McNulty Mine monkeyflower (*Mimulus cupriphilus* M. Mcnair) in California speciated from seep monkeyflower (*Mimulus guttatus* DC.) on copper mine tailings in a period of only 50 yr. Serpentine soil acts as a strong selective force (Kruckeberg 1951, 1954; Proctor and Wooddell 1975; Sambatti and Rice 2006, 2007; Westerburg and Saura 1992; Wild and Bradshaw 1977). Indeed, Kruckeberg (1951) found that serpentine races consistently outperformed their nonserpentine counterparts when grown on serpentine soil. Recent investigations have demonstrated adaptation among serpentine populations of nonindigenous plant species, suggesting postintroduction genetic changes. For example, Freitas and Mooney (1996) found divergence among populations of soft brome in response to water stress. In addition, Harrison et al. (2001) found differences in edaphic adaptation among populations of the nonindigenous annual grasses wild oat and soft brome.

Through this study, we aimed to address conservation concerns regarding the occurrence and threat of barb goatgrass to serpentine communities in northern California as well as the phenomenon of local adaptation of a noxious weed to a novel edaphic environment. The following questions were asked: (1) is barb goatgrass found more frequently on serpentine or nonserpentine soils, and (2) are serpentine populations of barb goatgrass specially adapted to serpentine soils? To address the first question, a reconnaissance was conducted in the Central Valley and neighboring foothills of the Coast and Sierra Nevada ranges. The second question was addressed by assessing the performance measures of nonserpentine and serpentine populations grown on parent and novel soil types in the greenhouse and in field studies.

## Materials and Methods

**Initial Observations and Occurrence on Serpentine Soil.** To address observations that barb goatgrass grew preferen-

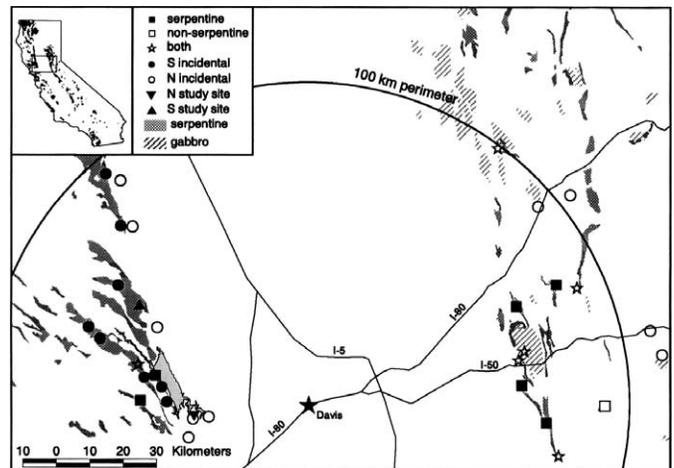


Figure 1. Localities for barb goatgrass found during the 1995 reconnaissance. Also included are the incidental sightings and locations of sites used for the field study. Areas of serpentine and gabbro substrates are shown. Abbreviations: S, serpentine population; N, nonserpentine population.

tially on serpentine soils, a reconnaissance was conducted of all major roads (visible on a 1 : 250,000 quadrangle) crossing ultramafic intrusions within a 100-km (62-mi) radius of the city of Davis, CA. The search was conducted over a 3-wk period at peak growing season, mid-May 1995. Presence and absence of barb goatgrass was recorded along stretches of roads crossing serpentine intrusions and the adjacent 3.22 km of nonserpentine stretches on either end of the intrusion. Only populations along the roadside were recorded. No attempt was made to detect interior populations at each site. Serpentine intrusions and roads crossing them were located using a combination of 1 : 750,000 and 1 : 250,000 geologic maps<sup>1</sup> developed by the California Department of Conservation, Division of Mines and Geology (CDMG), and a Northern California Gazetteer map book<sup>2</sup> (DeLorme 1998). Roads not indicated on these maps were ignored. In a number of cases, serpentinitic geologic formations were complexed with gabbroic formations (Figure 1). Gabbro and serpentine differ notably in color, texture, and dominant plant taxa that reflect differences in mineralogy of the soils types. Cases where the two substrates abut were noted.

**Greenhouse Study.** Caryopses used in this study were collected in late-summer 1996 from eight populations in Yolo, Napa, and El Dorado counties, CA; four of the populations were on serpentine soil, and the remaining four were on a variety of nonserpentine soils types (Table 1). In all cases, geologic type was assessed using the CDMG geologic maps, soil surveys, and in the case of serpentine soils, visual recognition.

Soil was collected from two sites in the southeastern portion of the northern, interior Coast Range. Weathered sandstone–shale (Layman–Los Gatos complex; Lambert

Table 1. Source of the eight populations from Yolo, Napa, and El Dorado counties, CA, collected late-summer 1996.

Site name (ID)	Geologic substrate <sup>a</sup> (sheet, date)	Soil series <sup>b</sup> (survey date)	Elevation m	General location <sup>c</sup>	Habitat	Latitude	Longitude
Iowa Hill (IH)	Mesozoic ultramafic (Chico, 1992)	Dubakella (1980)	400	SN FH	Disturbed interior	39°06'N	120°55'W
Meadowbrook Road (MB)	Mesozoic ultramafic (Sacramento, 1985)	Serpentine Rock Land (1974)	600	SN FH	Disturbed interior	38°52'N	120°49'W
Pope Valley Road (PV)	Mesozoic ultramafic (Santa Rosa, 1988)	Henneke (1978)	300	SE NICR	Disturbed roadside	38°33'N	122°22'W
Newtown Road (NT)	Mesozoic ultramafic (Chico, 1992)	Dubakella (1975)	700	SN FH	Disturbed roadside	39°15'N	121°05'W
Bass Lake (BL)	Mesozoic gabbroic (Sacramento, 1985)	Serpentine Rock Land (1974)	400	E CV	Disturbed roadside	38°04'N	121°01'W
Hwy 128—Lake Berryessa (LB)	Cretaceous—Jurassic/ Great Valley Sequence—marine sandstone, mudstone, and conglomerate (Santa Rosa, 1988)	Layman-Los Gatos complex (1978)	200	SE NICR	Disturbed roadside	38°34'N	122°14'W
Slow Dusty Road (SD)	Paleozoic—Mesozoic metamorphic rock (Sacramento, 1985)	Sites (1974)	600	SN FH	Disturbed roadside	38°51'N	120°49'W
Sly Park Road (SP)	Tertiary Andesitic— conglomerate, sandstone, and breccia (Sacramento, 1985)	McCarthy (1974)	900	SN FH	Disturbed roadside	38°45'N	120°33'W

<sup>a</sup> Map (1 : 250,000), Division of Mines and Geology, California Department of Conservation.

<sup>b</sup> Soil surveys, U.S. Department of Agriculture, Soil Conservation Service, Forest Service, and University of California Agricultural Experiment Station.

<sup>c</sup> Abbreviations: SN FH, Sierra Nevada foothills; SE NICR, southeast northern interior Coast Range; E CV, east Central Valley.

and Kashiwagi 1978) was chosen as representative nonserpentine (N) soil. Loose soil, produced by a natural landslide in the fall of 1996, was collected outside the gates to the University of California Natural Reserve System (UC NRS) Cold Canyon Reserve on Highway 128. Disturbed serpentine, gravelly loam (S)(Henneke series; Lambert and Kashiwagi 1978) was collected along Pope Canyon Road, adjacent to a gravel mine operation, 0.80 km from Lake Berryessa. A third soil type (M) was made by mixing in equal parts of these two soils. All soils were passed through a 2-cm (0.0044-in) filter to remove large rocks and loosely packed into 15.24 cm (ht) by 5.08 cm (width, at opening) Conetainers.<sup>3</sup> A 4 by 4-cm metal screen with 0.5-cm openings was placed in the bottom of each conetainer to slow drainage.

In December 1996, 12 replicates from the 8 source populations were sown on each of the three soil types ( $n_{total} = 288$ ) in a fully randomized design. Only the large

caryopsis from exclusively proximal spikelets was used. Before sowing, each caryopsis was separated from the glumes and weighed. To reduce edge effects, conetainers with soil but no seed occupied the perimeter of each tray. The experiment was misted from above with deionized water for 1 min, twice daily; placed on a long-day light regime of 15 h; and systematically rotated twice weekly.

Plants were harvested in early May 1997. The following aboveground performance parameters were measured: plant height, vegetative shoot biomass, inflorescence length and mass, and the number of fertile spikelets. To obtain belowground biomass, the roots were separated from the soil using a root washer<sup>4</sup> (located at the University of California, Davis, Land Air and Water Resources facility), dried for 24 h at 70 C, and weighed.

**Field Study.** Seeds used in this study were collected in late-summer 1999 from the same populations used in the

greenhouse study. Three soil types (sites) in the northern Coast Range of California were used: (1) nonserpentine (NS); (2) alluvial, mesic serpentine (AS); and (3) exposed, rocky, and severe serpentine (SS)(Figure 1). All sites were threatened by barb goatgrass colonization from nearby populations; however, to minimize the possible introduction of new populations of barb goatgrass into these sites, two replicate plots were established in just one site per soil type. Gopher (*Thomomys* spp.) disturbance was common on both soil types, and all sites were browsed by Columbian black-tailed deer (*Odocoileus hemionus* ssp. *columbianus* Richardson) and black-tailed jackrabbits (*Lepus californicus* Gray)(K. Lyons, personal observation).

Nonserpentine plots were established at the UC NRS Quail Ridge Reserve (Figure 1, Yolo County, 38°29'N, 122°14'W). Barb goatgrass began to invade the reserve in the early 1990s and today it is pervasive. The reserve is dominated by Mediterranean mixed oak (*Quercus* spp.) woodland and chaparral. In the area where the plots were established, there were small stands of relictual, perennial grasses, such as purple needlegrass [*Nassella pulchra* (Hitcb.) Barkworth] and California melicgrass (*Melica californica* Scribn.), and nonindigenous species, such as redstem filaree [*Erodium cicutarium* (L.) L'Hér. ex Ait.] and dovefoot geranium (*Geranium molle* L.), which are both Geraniaceae (nomenclature follows Hickman 1993). The experimental plots were established in flat, open grassland.

The two serpentine sites (SS and AS) were established at the UC NRS McLaughlin Reserve, along Hunting Creek (Figure 1; Lake County, 38°49'N, 122°23'W). The SS site was slightly sloped (+5°), north facing, rocky, and highly exposed, with little soil development. The experimental plots were established in open habitat between shrubs in an area occupied by diminutive, herbaceous species, such as Purdy's fritillary (*Fritillaria purdyi* Eastw.) and scytheleaf onion (*Allium falcifolium* Hook. & Arn.), which are both Liliaceae. No nonindigenous species were present in the plots.

The AS site at the McLaughlin Reserve was flat and was characterized by relatively deep alluvial soils with high rates of gopher disturbance and a long history of grazing. A number of nonindigenous annual grasses were identified in this field, such as medusahead [*Taeniatherum caput-medusae* (L.) Nevski] and wild oat (*Avena fatua* L.). Native perennial grasses, such as meadow barley (*Hordeum brachyantherum* Nevski.) and purple needlegrass, and forbs, such as coast range false bindweed [*Calystegia collina* (Greene) Brummitt], a Convolvulaceae; Tracy's clarkia [*Clarkia gracilis* (Piper) Nelson & J.F. Macbr. ssp. *tracyi* (Jeps) Abdel-Hamee & R. Snow], an Onagraceae; and California dwarf-flax [*Hesperolinon californicum* (Benth.) Small], a Linaceae, were abundant and widespread, despite historical disturbance at the site and the presence of nonindigenous species.

On each soil type (or site), two 1.6 by 2.0-m (5.25 by 6.56-ft) plots were established and divided into a 10 by 8 grid of 20 by 20-cm subplots. Each row of eight subplots constituted a block. On December 13 and 14, 1999, 10 spikelets per population ( $n = 8$ ; 4 serpentine and 4 nonserpentine) were sown in each replicate plot in a randomized complete-block design (20 total replicates per soil type per population). The location of each spikelet was marked using an 8-cm wooden skewer. As in the greenhouse study, only the largest, proximal spikelet of an inflorescence was used in this experiment. Preliminary work demonstrated that naked caryopses of barb goatgrass are highly susceptible to pathogens when removed from the glumes and sown on bare soil in the field. Thus, in the field, entire spikelets containing 1–2 caryopses were sown. The spikelets were cut from the inflorescence and weighed, numbered, and individually bagged. At the time of sowing, seedlings of other species were removed by hand in a 3-cm radius around each spikelet. To ensure that the spikelets were not moved or trampled, a hardware cloth (2 cm) cage was constructed over each plot. Along the perimeter of the plot, the hardware cloth was flattened to talus or vegetation. The edges were then secured with railroad nails. The cages did not interfere with plant growth and remained in place until the plants were approximately 5 cm in height.

On May 15, 2000, the maximum height of each plant at maturity was determined. The plants were then removed, along with the parental spikelet, which remained attached to the base of the plant at the soil surface. This was done to remove the species from the site, to ensure each plant developed from a single caryopsis, and to retrieve the sibling caryopsis for viability studies to validate work by Dyer (2004) demonstrating suppression of sibling caryopses in barb goatgrass. Upon completion of each harvest, live and dead biomass was collected from five 20 by 20-cm areas around the perimeter of each plot ( $n = 2$  per site). This was done to assess differences in plant productivity among the sites and experimental plots.

Within each plot, five soil samples were collected, from the center and each of the four corners, using a 5-cm (deep) by 15-cm (length) soil auger.<sup>5</sup> The five samples from a plot were combined in the field in a polypropylene bag and returned to the laboratory, where they were sifted through a 2-mm (0.079-in) sieve. Soil analyses were conducted on the six soil samples (2 per soil type) by A & L Western Agricultural Laboratories.<sup>6</sup> The following soil properties were analyzed: the percentage of organic matter (OM); the estimated nitrogen release (estimated from OM); the plant-available phosphorus, potassium, magnesium, calcium, and sodium in ppmw (using the Mehlich-3 extraction method; Mehlich 1984); the pH; and the cation-exchange capacity (A & L Laboratories 1997).

Performance measures on barb goatgrass included maximum height, total aboveground biomass, the number

of inflorescences, inflorescence length, number and mean mass of fertile inflorescences, the mean mass of the proximal spikelet, and the number and mean mass of caryopses therein. All nongerminated, sibling caryopses were removed from the parental spikelets and weighed. Viability of these caryopses was assessed by germination on University of California soil mix No. 1 using a heated misting bench.

**Statistics.** The effects of main, crossed, and nested factors on all response variables were analyzed using the PROC GLM procedure and multivariate analysis of variance (MANOVA) in SAS.<sup>7</sup> Reported significance levels are Pillai's trace probabilities. For the greenhouse experiment, we analyzed the effect of soil type and source population as well as the interaction between these two factors on plant measures. In the field experiment, soil type and source population were used as main factors. We also tested for the effect of the interactions among soil type by source population and the following nested factors: plot(soil type); block(plot[soil type]); source by (plot[soil type]). For both the greenhouse and field experiments, initial seed mass was standardized by the average mass of the parent population using the equation:  $W_{ij} = W_{ij}/W_{avg(j)}$ , where  $W_{avg(j)}$  is the mean seed mass of the seeds from population  $j$ . This was done to maintain systematic differences among a population's seed mass while accounting for large deviations within a population that might have significant effects on the final plant performance. In all cases, dependent variables were tested for univariate normality and, where necessary, transformed to comply with normality assumptions. Differences between standing biomass of the sites were analyzed by ANOVA and Tukey-Kramer comparisons among means. Percentage of survivorship among soil types and source populations was analyzed using Pearson's chi-square test. The two latter analyses were conducted using JMP4 software.<sup>8</sup>

## Results

### Initial Observations and Occurrence on Serpentine Soil.

Thirty-one roads crossing serpentine intrusions were surveyed during this study. Barb goatgrass was found on serpentine, nonserpentine, or both soil types in 45.2% of all crossings (14/31; Figure 1). In 22.6% (7/31) of the encounters, the species was found exclusively on serpentine soil, whereas it was found on adjacent serpentine and nonserpentine stretches in 16.1% (5/31) of the crossings. In contrast, barb goatgrass was found exclusively on nonserpentine sections of intrusions in just 6.5% (2/31) of those roads surveyed. Of the 14 barb goatgrass populations found (2 exclusively off serpentine, 7 exclusively on serpentine, and 5 on adjacent serpentine and nonserpentine sites), barb goatgrass was present on

Table 2. Multivariate analysis of variance on the overall performance of greenhouse-grown barb goatgrass (*Aegilops triuncialis* L.).<sup>a</sup>

Factor	df	F	P
Soil type <sup>b</sup>	12	17.110	< <b>0.0001</b>
Source population <sup>c</sup>	6	0.600	0.732
Soil type by source population	12	3.620	< <b>0.0001</b>
Initial seed weight	1	21.000	< <b>0.0001</b>
Contrasts			
N soil, N vs. S population	6	2.000	0.066
M soil, N vs. S population	6	1.180	0.319
S soil, N vs. S population	6	4.760	< <b>0.0001</b>

<sup>a</sup> Reported significance levels are Pillai's trace probabilities. Bolded values are significant at  $P < 0.05$ .

<sup>b</sup> N, nonserpentine; M, mixed; or S, serpentine soil.

<sup>c</sup> S, serpentine; or N, nonserpentine populations.

serpentine or nonserpentine soils in 85.7% (12/14) and 14.3% (2/14) cases, respectively. Figure 1 also includes incidental sightings on paved roads by car from 1995 to 2002. Of the 15 sites, 40.0% (6/15) were on serpentine substrate.

**Greenhouse study.** Barb goatgrass performance was significantly affected by soil type. In general, the species performed better on serpentine than on nonserpentine soil (Table 2; Figure 2). In contrasts among source populations, the overall effect of soil type on source population did not differ on N (nonserpentine) or M (mixed) soils; however, on S (serpentine) soil, serpentine populations had overall higher performances (Table 2). The MANOVA also demonstrated a significant interaction between the effects of soil type and source population. Adjusted initial seed mass significantly affected overall performance outcomes and was, therefore, maintained as a covariate in these analyses. A protected ANOVA was conducted to determine the main effects and interactions on species performance (Table 3). Soil type had a significant effect on the performance of barb goatgrass for all measures, with the exception of number of fertile spikelets. Significant differences among response variables for source by soil type interactions were found in total plant mass, root mass, root mass ratio (percentage of root dry mass to total plant dry mass, g/g), and average inflorescence mass (Table 3; Figure 2).

**Field study.** Standing biomass at the sites, measured at the termination of the experiment, demonstrated an overall significant difference among sites with means ( $\pm$  SE) of NS: 10.8 (1.126), AS: 9.07 (1.306), SS: 1.598 (0.431)(ANOVA:  $F = 22.713$ ;  $P < 0.0001$ ). Biomass differences between SS and both AS and NS were

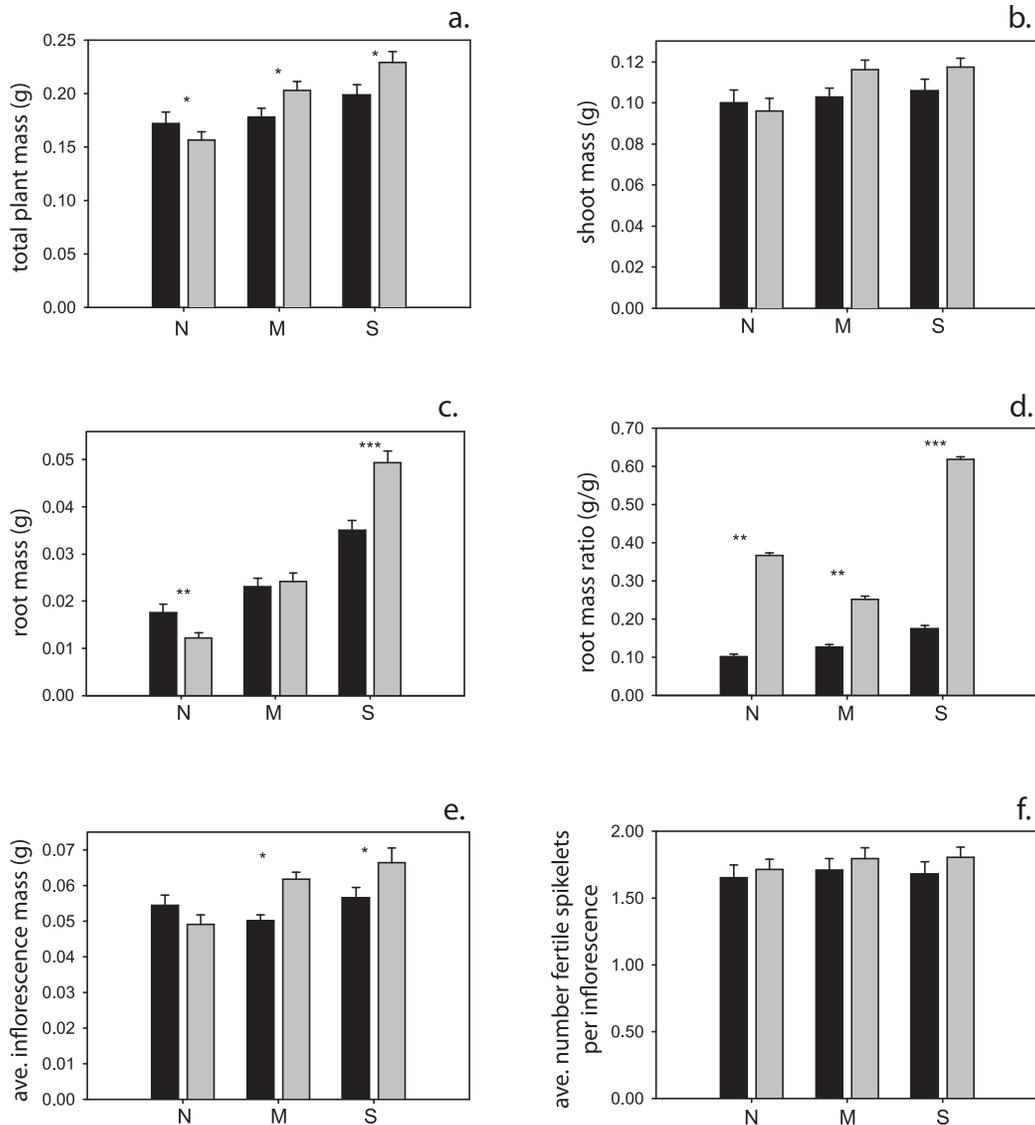


Figure 2. Performance measures (mean  $\pm$  1 SE) by soil type and population for greenhouse-grown barb goatgrass on serpentine (S), mixed (M), and nonserpentine (N) soil. Nonserpentine populations: black bars; serpentine populations: gray bars. Letters indicate (a) total plant mass (g); (b) shoot mass (g); (c) root mass (g); (d) root : mass ratio (g root : g total plant); (e) average inflorescence mass (g); and (f) average number fertile spikelets per inflorescence. Data were analyzed by multivariate analysis of variance using adjusted initial seed mass as a covariate. There was a significant overall soil effect and a soil by source interaction (Table 2). The overall effect of soil type on population did not differ on N soils; however, on S soils, serpentine populations had an overall higher performance (Table 2). \*  $P < 0.050$ , \*\*  $P < 0.010$ , \*\*\*  $P < 0.001$ .

significant (Tukey-Kramer:  $P < 0.05$ , +3.815 and +5.543, respectively), whereas differences between AS and NS were not significant ( $P > 0.05$ , -1.931). Soil analyses demonstrate differences in nutrient status among these soils and confirmed the determination of each site (Table 4). As expected, serpentine soils (AS and SS) had a lower overall nutrient status and lower OM content compared with NS soils, with slightly higher values in the AS compared with SS soils (Table 4). In addition, the Ca : Mg ratio was substantially lower on SS and AS than on NS, with the lowest ratio for SS soils.

Agents of mortality, as determined by visual cues, did not differ among source populations or sites, with the exception of higher herbivory on NS soils. Only successful individuals, those that germinated and flowered, were included for the following performance analyses. In the field experiment, adjusted initial seed mass was not a significant factor and was, therefore, removed from the model. Overall significant performance effects were found for source populations and soil type; however, there was no significant interaction between these factors (Table 5). Replicate plot nested within soil type did have an overall

significant effect on barb goatgrass performance. In light of this result, the data were reanalyzed to determine the source population by soil type effects for each replicate plot. Again, main effects were overall significant, whereas the interaction between source population and soil type were not significant (not shown).

Contrasts were conducted to explore the effect of soil type alone on the performance of all population types of barb goatgrass (Table 6; Figure 3). For three response variables (height, total mass, and inflorescence mass), barb goatgrass performance decreased, as predicted, from NS to AS, with the lowest performance on SS soil (Table 6; Figures 3a–c). Barb goatgrass performance, as determined by the average combined mass of the caryopses of the proximal spikelet, was equivalent on serpentine soil types and lower on both serpentine soils than on NS (Table 6; Figure 3g). For the remaining three variables (average number of fertile spikelets, average mass proximal spikelet, and average number of caryopses per proximal spikelet), performance of barb goatgrass was equivalent on NS and AS, whereas both differed significantly from SS (Table 6; Figures 3d–f).

Germination of the recovered second seed was high (91.3%,  $n = 208$ ) and was similar regardless of the soil from which the seeds were retrieved (Pearson's chi-square:  $\chi^2 = 3.238$ ;  $P = 0.1981$ ) or whether they originated from serpentine or nonserpentine populations (Pearson's chi-square, NS:  $\chi^2 = 0.982$ ,  $P = 0.3217$ ; AS:  $\chi^2 = 0.747$ ,  $P = 0.387$ ; SS:  $\chi^2 = 0.362$ ,  $P = 0.548$ ).

**Survivorship: Greenhouse and Field Studies.** Percentage of survival in the greenhouse among the N and S populations on parent, novel, and mixed soil types was similar, with the exception of particularly high survivorship for N populations on mixed soils and slightly higher survivorship across all N populations (Figure 4). In the field, differences in survivorship on N soil between N and S populations was similar, whereas S populations appeared to have slightly higher survival rates on both serpentine soil types (AS and SS) (Figure 4). Nevertheless, analysis with Pearson's chi-square test demonstrates no statistically significant differences among percentage of survival for either the greenhouse or field studies (greenhouse:  $\chi^2 = 7.188$ ,  $P = 0.2070$ ; field:  $\chi^2 = 3.719$ ,  $P = 0.5906$ ).

## Discussion

Our reconnaissance, combined with cumulative yearly observations, confirm our initial observations that barb goatgrass can grow on serpentine soils and may do so preferentially. Among all occurrences ( $n = 19$ , including locations where barb goatgrass was on both serpentine and nonserpentine substrate), the species was more often on serpentine areas than on surrounding nonserpentine areas

Table 3. Two-way protected ANOVA (generalized linear model) of the performance of greenhouse-grown barb goatgrass (*Aegilops triuncialis* L.).<sup>a</sup>

Factor	df	Total plant mass			Shoot mass			Root mass			Root : mass ratio			Average inflorescence mass			Average No. of fertile spikelets inflorescence <sup>-1</sup>			
		F	P		F	P		F	P		F	P		F	P		F	P		
Soil type <sup>b</sup>	2	35.72	< 0.0001		10.23	< 0.0001		159.16	< 0.0001		120.58	< 0.0001		13.61	< 0.0001		0.02	0.02		0.98
Source population <sup>c</sup>	1	0.40	0.53		0.06	0.81		0.76	0.38		0.05	0.83		1.02	0.31		0.72	0.72		0.40
Soil type by source population	2	4.22	<b>0.02</b>		1.52	0.22		14.11	< 0.0001		9.59	< 0.0001		4.81	<b>0.01</b>		0.22	0.22		0.80
Initial seed weight	1	101.60	< 0.0001		88.25	< 0.0001		78.34	< 0.0001		6.69	<b>0.01</b>		66.45	< 0.0001		20.81	20.81		< 0.0001

<sup>a</sup> Reported significance levels are Pillai's trace probabilities. Bolded values are significant at  $P < 0.05$ .

<sup>b</sup> N, nonserpentine; M, mixed; or S, serpentine soils.

<sup>c</sup> S, serpentine; or N, nonserpentine populations.

Table 4. Nutrient values for the soils at the sites in the northern interior Coast Range and western foothills of the Sierra Nevada Mountains in California, 1999–2000.<sup>a,b</sup>

Soil type	OM	ENR	P	K	Mg	Ca	Na	Ca : Mg ratio	pH	CEC	Soil texture
	%	kg ha <sup>-1</sup>	ppm							mEq 100 g <sup>-1</sup>	
NS											
Mean	5.25	151	30.0	218.5	241	2,080	16	9.037	6.20	14.80	Loam
SE	0.45	9	2.0	29.5	39	239	0	2.438	0.10	0.60	Loam
AS											
Mean	3.60	115	19.0	164.0	2,416	690	15	0.294	6.80	24.45	Clay loam
SE	0.20	4	15.0	8.0	392	5	3	0.050	0.10	2.95	Clay loam
SS											
Mean	3.10	103	3.5	42.0	1,782	329	15	0.184	6.90	15.45	Sandy loam
SE	0.50	10	1.5	3.0	160	32	1	0.001	0.10	0.05	Sandy loam

<sup>a</sup> Abbreviations: OM, organic matter; ENR, estimated nitrogen release; CEC, cation exchange capacity; NS, nonserpentine soil; AS, alluvial soil; SS, serpentine soil.

<sup>b</sup> Plant-available P, K, Mg, Ca, and Na values were determined by Mehlich-3 extractions.

(63% vs. 37%). These trends also suggest that colonization may occur first on serpentine areas and secondarily on nonserpentine roadsides; however, virtually all species are more easily sighted on less-congested serpentine soils.

Direct support for the hypothesis that populations of barb goatgrass are locally adapted (either before or after colonization) to serpentine soils comes from our greenhouse study (Figure 2). General trends shown in Figure 2 suggest that, under controlled conditions, serpentine genotypes generally performed better on their soils of origin. Statistically, serpentine populations performed significantly

better on serpentine soil than did nonserpentine populations in total root mass and in root : mass ratio (g root : g total plant). In contrast, on nonserpentine soil, nonserpentine populations outperformed serpentine populations in total aboveground biomass and root mass. These trends are reflected in a statistically significant interaction between source population and soil type (Table 2).

The higher root mass ratio for serpentine populations across all three soil types used in the greenhouse was highly significant and consistent. Adaptation for a high allocation to root biomass in serpentine populations might be expected because both soil chemical properties and water availability are critical factors driving the ecology and evolutionary history of serpentine soils (Gardner and McNair 2000; Harrison et al. 2000). In a common garden greenhouse experiment, using serpentine and riparian soils, Sambatti and Rice (2007) found a similar trend in the early stages of growth in serpentine sunflower (*Helianthus bolanderi* A. Gray), a species native to California that can grow both on and off serpentine substrates. Sambatti and Rice (2007) also found that serpentine populations of *H. exilis* had higher root allocation than riparian populations regardless of soil type. Barb goatgrass deviates from the trend found for *H. exilis*, however, in that nonserpentine populations of barb goatgrass do not appear to share the ability to allocate more resources to roots when grown on serpentine soil (Figure 2d).

Our greenhouse findings were not supported by the common garden field experiment. Barb goatgrass performance generally declined from NS to AS to SS, but the interaction between soil type and source population was

Table 5. Multivariate analysis of variance (generalized linear model) of the performance of field-grown barb goatgrass (*Aegilops triuncialis* L.).<sup>a</sup>

Factor	Overall model		
	df	F	P
Soil type <sup>b</sup>	12	12.090	< <b>0.0001</b>
Source population <sup>c</sup>	6	3.080	<b>0.007</b>
Soil type × source population	12	0.460	0.935
Plot (soil type)	18	3.680	< <b>0.0001</b>
Block(plot[plot site])	324	1.100	0.136
Source × plot(soil type)	18	1.100	0.352

<sup>a</sup> Reported significance levels are Pillai's trace probabilities. Bolded values are significant at P < 0.05.

<sup>b</sup> NS, nonserpentine; AS, alluvial; or SS, severe serpentine soils.

<sup>c</sup> S, serpentine; or N, nonserpentine populations.

Table 6. *F* statistics for contrasts between soil types by performance of field-grown barb goatgrass (*Aegilops triuncialis* L.).<sup>a</sup>

Contrasts between soil types	Height (cm)	Total plant mass (g)	Average inflorescence mass (g)	Average No. of fertile spikelets	Average mass of proximal spikelet (g)	Average No. of caryopses in proximal spikelet	Ave. Mass caryopses in proximal spikelet (g)
NS vs. AS	41.48***	20.57***	17.21***	0.53 <sup>ns</sup>	2.71 <sup>ns</sup>	3.04 <sup>ns</sup>	40.07***
NS vs. SS	137.42***	44.93***	84.84***	45.50***	20.01***	4.86*	28.64***
AS vs. SS	27.88***	4.60*	25.85***	37.26***	8.11**	17***	1.14 <sup>ns</sup>

<sup>a</sup> Abbreviations: NS, nonserpentine; AS, alluvial serpentine; SS, severe serpentine soils.

\*  $P < 0.050$ ; \*\*  $P < 0.010$ ; \*\*\*  $P < 0.0001$ ; <sup>ns</sup> not significant.

nonsignificant (Table 5). A number of reasons may account for the contrasting findings of the greenhouse and field study. Differences in performance between serpentine and nonserpentine populations in the greenhouse depended heavily on the effect of the root mass and the root : mass ratio (Table 3; Figures 2c and 2d), measurements that could not be made effectively in the field study. It is also possible that the lack of competition in the greenhouse study will have enhanced our ability to detect differences in our source populations. In similar fashion, in a common garden experiment, conducted in the field and greenhouse using serpentine and nonserpentine populations of *H. exilis*, Simbatti and Rice (2006, 2007) found that differences in some performance measures demonstrated among serpentine and nonserpentine populations in the greenhouse did not manifest in the field study. In addition, field-grown serpentine and riparian populations of *H. exilis* exhibited soil adaptation only in the absence of competition. In our field study, we removed vegetation from a small area (3-cm radius) when the seeds of barb goatgrass were sown. This removed competition for the early stages of growth; however, adult plants were grown in competition.

The effects of competition are expected to be more pronounced on the NS or AS soils than on SS soils, where resource availability and plant productivity is low and individual plants are widely spaced (*sensu* Grime 1977). As with all plant species growing on serpentine soils, we found consistently lower performance on SS than on NS or AS. Nevertheless, competition may, in fact, be more intense on SS than on NS or AS because of water and nutrient limitations. Unfortunately, microsite and micronutrient studies to determine the putative connection between resource availability and competitive dynamics on serpentine soils have yet to be conducted.

Differences in spatial allotment for roots and access to soil nutrients may also explain why we were able to detect differences among barb goatgrass populations in our greenhouse study. Overall lower performance of barb goatgrass in the greenhouse, relative to the field study, suggests that plants in the greenhouse were nutrient deprived. In addition, greenhouse soils became clayey and

compacted over time. Depletion of resources may have resulted in more pronounced manifestation of soil tolerances among species. It is also possible that variability in field conditions, such as soil–water infiltration, weather, competition, and herbivory may dampen variation in ecotypes or maternal factors associated with barb goatgrass populations.

It is well documented that habitats exposed to anthropogenic, as well as natural, disturbance tend to be more heavily invaded than more remote, undisturbed sites (Griffin et al. 1989; Harper 1965; Hobbs and Mooney 1985, 1991; Kowarik 1995; Mack 1989; Pysek et al. 1995). On serpentine substrates, nonindigenous species abundance is often positively correlated with human activities, such as road construction, ranching, mining, hunting, and horseback riding, as well as with natural disturbances from gopher and water movement (K. Lyons, personal observation). Clearly, establishment and spread of barb goatgrass is complicated and depends on the soil structure and type of disturbance as well as the anthropogenic and biotic elements. This has been shown to be the case for other species, such as soft brome on serpentine soils in northern California (Hobbs and Mooney 1985, 1991) and athel tamarisk [*Tamarix aphylla* (L.) Karsten] in Australia (Griffin et al. 1989), which were facilitated by gopher disturbance and periodic flooding, respectively.

Although most forms of disturbance appear to aid barb goatgrass (K. Lyons, personal observation), Eviner and Chapin (2003) showed that gophers, when given a choice, preferentially disturb barb goatgrass stands in deeper soil resulting in high mortality of the grass. In addition to the direct, physical disturbance of barb goatgrass, gophers may also disrupt the association between barb goatgrass and the fungus *Ulocladium atrum* (Preuss) Sacc., which putatively increases germination rates in the species by softening the glumes. Gopher mounds are common on disturbed, alluvial, serpentine soils and virtually absent on severely serpentine sites (K. Lyons, personal observation). Thus, where established on more severe sites, barb goatgrass will be free of gopher disturbance and may be more successful in the long term. In contrast, in this study, more disturbed, alluvial, serpentine substrates supported more standing

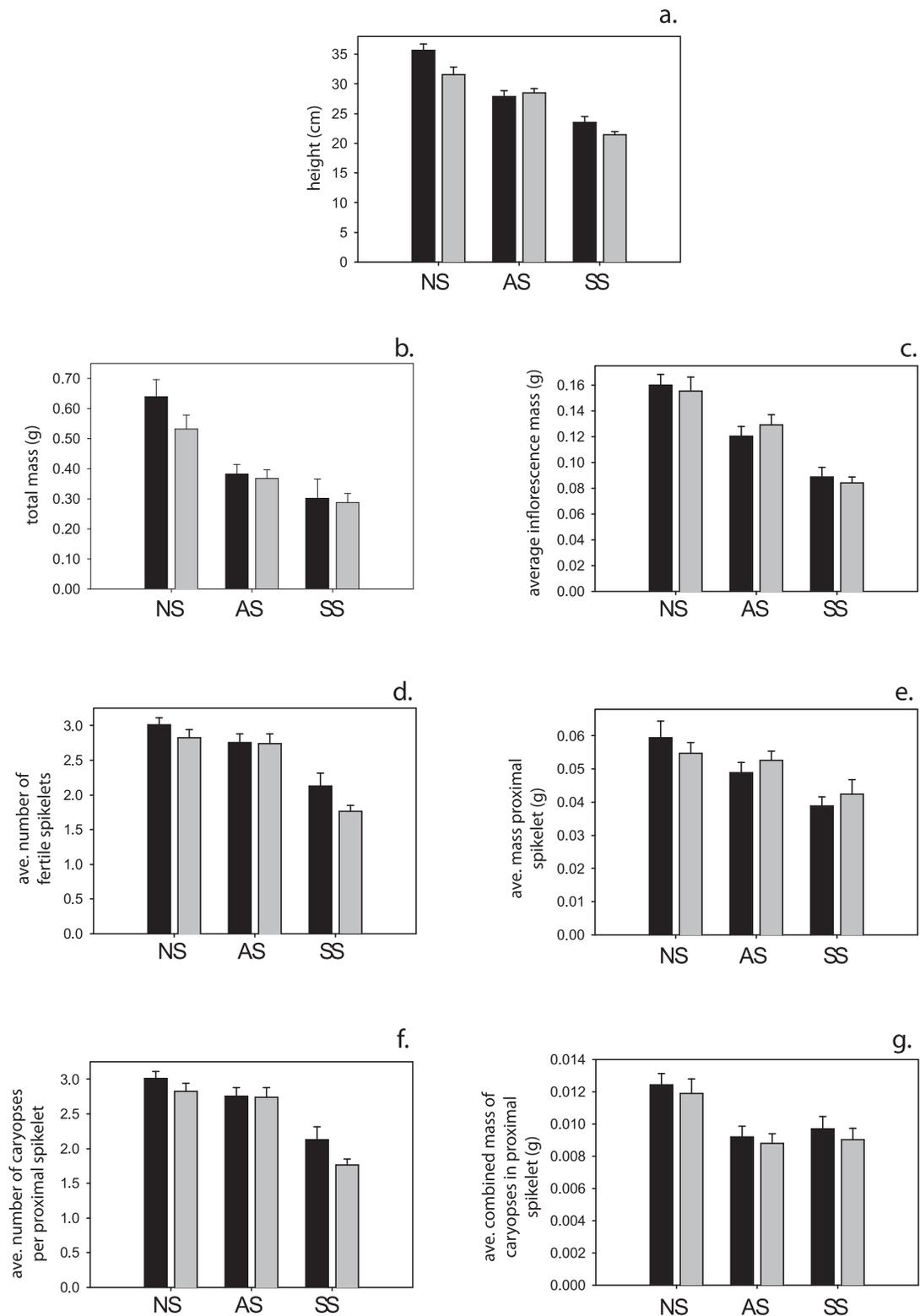


Figure 3. Performance measures by soil type and population for field grown barb goatgrass. NS, nonserpentine; AS, alluvial serpentine; SS, severe serpentine soils. Nonserpentine populations: black bars; serpentine populations: gray bars. Letters indicate (a) height (cm); (b) total mass (g); (c) average inflorescence mass (g); (d) average number of fertile spikelets; (e) average mass proximal spikelet (g); (f) average number caryopses per proximal spikelet; and (g) average combined mass of caryopses in proximal spikelet (g). Analyses were conducted using multivariate analysis of variance (generalized linear model) with initial seed mass as a covariate. No significant overall interaction was found between soil type and population source (Table 5); however, significant differences were found in performance of barb goatgrass between soils types (Table 6). \*  $P < 0.050$ , \*\*  $P < 0.010$ , \*\*\*  $P < 0.001$ .

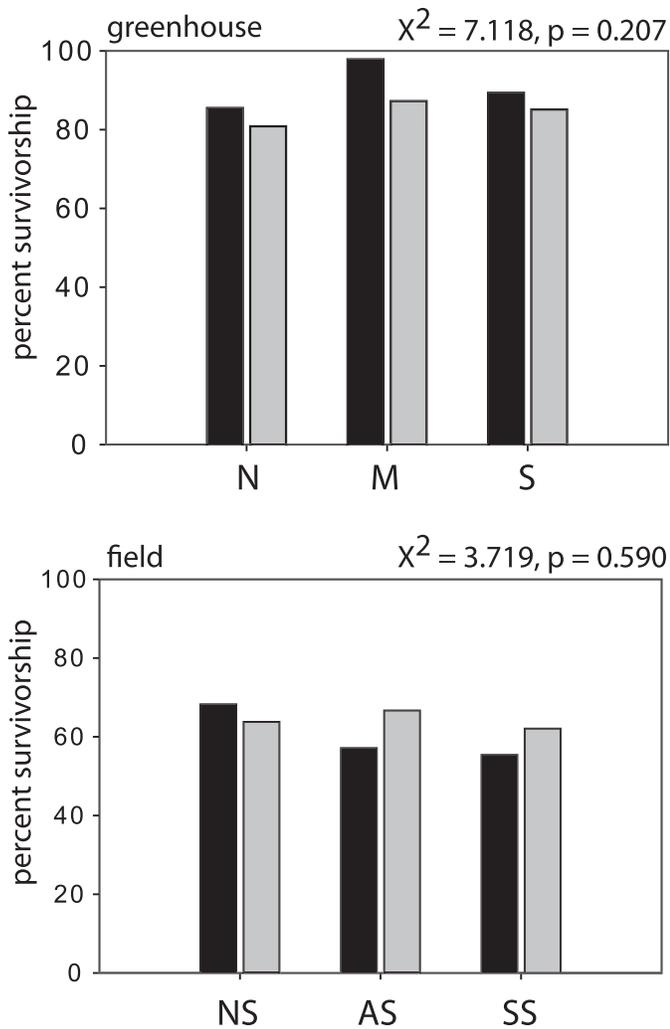


Figure 4. Percent survivorship of barb goatgrass in greenhouse and field experiments. Soil designations: N, nonserpentine; M, mixed; and S, serpentine. Sites soils: NS, nonserpentine; AS, alluvial serpentine; and SS, severe serpentine. Nonserpentine populations: black bars; serpentine populations, gray bars.

biomass and individuals with higher reproductive performance than did undisturbed, severely serpentine sites (Figure 3; Table 6). In fact, for three performance parameters (Figure 3), barb goatgrass performed equally well on alluvial, serpentine and nonserpentine sites, whereas its performance on severely serpentine sites consistently differed from either or both (Table 6).

Increase in soil nitrogen through deposition and disturbance is of major global concern and has come under close examination in California (Weiss 2006). In general, these increases (as  $\text{NO}_x$  and  $\text{NH}_3$ ) are positively correlated with increases in nonindigenous and indigenous, invasive species fitness, establishment, and spread (Abraham et al. 2009; Bell and Treshow 2002; Burke and Grime 1996; Hobbs et al. 1988; Metcalfe and Fowler 1998;

Scherer-Lorenzen et al. 2000; Wedin and Tilman 1996). It has been hypothesized that increases in these species may be due to their high soil nutrient requirements (e.g., Kowarik 1995; Pysek et al. 1995; Scherer-Lorenzen et al. 2000). In oligotrophic systems, such as serpentine sites, where native species are adapted to low nutrient availability, these findings are particularly alarming (Scherer-Lorenzen et al. 2000). As a result, nitrogen deposition on serpentine sites near urban areas has become a conservation concern (Weiss 1999, 2006). Serpentine soils are demonstrated to be highly nutrient retentive (Hooper and Vitousek 1998), and a direct correlation between nutrient addition and invasion on serpentine soils has been documented (Huenneke et al. 1990; Sommer and Jensen 1991). Our experimental study was not designed to make inferences regarding the effect of nitrogen on establishment, but nitrogen deposition may explain the rapid spread of barb goatgrass on serpentine soils.

Most alarming from our study is that all populations of barb goatgrass were able to germinate and reproduce on the serpentine substrate studied here. This trend was supported by the work of Thomson (2007), who showed, using a demographic model, that barb goatgrass is capable of establishing and spreading into more severe serpentine sites without sustained propagule pressure from other populations. It is, therefore, possible that founder effects or self-fertilization, which might decrease barb goatgrass genetic variability, will be inconsequential, at least during the colonization phase. Our studies substantiate the findings of Zohary (1965) that barb goatgrass, perhaps because it is a polyploid, demonstrates a high degree of plasticity, and has limited ecological constraints.

### Sources of Materials

<sup>1</sup> 1:750,000 and 1:250,000 geologic maps, California Department of Conservation, Division of Mines and Geology, 801 K Street, MS 24-01, Sacramento, CA 95814.

<sup>2</sup> Northern California Gazetteer maps, 6th ed. 127 p, DeLorme Publishing, 2 DeLorme Drive, Yarmouth, ME 04096.

<sup>3</sup> Conetainers, Stuewe & Sons Inc., 31933 Rolland Drive, Tangent, OR 97389.

<sup>4</sup> Root washer, Gillison's Variety Fabrication Inc., 3033 Benzie Highway, Benzonia, MI 49616-9747.

<sup>5</sup> Soil auger, Ben Meadows, P.O. Box 5277, Janesville, WI, 53547-5277.

<sup>6</sup> A & L Western Agricultural Laboratories, 1311 Woodland Avenue, Modesto, CA 95351-1221.

<sup>7</sup> SAS software, Version 8.2, SAS Institute Inc., 100 SAS Campus Dr., Cary, NC 27513.

<sup>8</sup> JMP4 statistical software, Version 4.0, SAS Institute Inc., 100 SAS Campus Dr., Cary, NC 27513.

### Acknowledgments

We owe many thanks to the efforts of Susan Harrison, Shorty Boucher, and Dan Tolson of the University of

California, Davis, Natural Reserve System, and Dean Enderlin of the Homestake Mining Company. These individuals encouraged early research at the McLaughlin Reserve and secured the transfer of the property to the UC NRS. Many thanks go, as well, to Ernesto Sandoval for his assistance in maintaining the greenhouse experiment, Jennifer Rudgers for help with statistics, and Justin Williams for guidance on taxonomic usage. Finally, we are indebted to the Spice and Rice laboratories for their support through the years. These studies were funded by Sigma Xi grants-in-aid of research, the California Native Plant Society, the University of California at Davis public service outreach/bioregional grant, and the University of California NRS Mathias grant.

### Literature Cited

- Abraham, J. K., J. D. Corbin, and C. M. D'Antonio. 2009. California native and exotic perennial grasses differ in their response to soil nitrogen, exotic annual grass density, and order of emergence. *Plant Ecol.* 201:445–456.
- Baker, H. G. 1965. Characters and modes of origin of weeds. Pages 147–168 in H. G. Baker and G. L. Stebbins, eds. *The Genetics of Colonizing Species*. New York: Academic.
- Baker, H. G. 1986. Patterns of plant invasion in North America. Pages 44–57 in H. A. Mooney and J. A. Drake, eds. *Ecology of Biological Invasions of North America and Hawaii*. Volume 58. New York: Springer-Verlag.
- Barbour, M., B. Pavlik, F. Drysdale, and S. Lindstrom. 1993. California's Changing Landscape: Diversity and Conservation of California Vegetation. Sacramento, CA: California Native Plant Society. 244 p.
- Barrett, S.C.H. and B. J. Richardson. 1986. Genetic attributes of invading species. Pages 21–23 in R. H. Groves and J. J. Burdon, eds. *Ecology of Biological Invasions: An Australian Perspective*. Canberra, Australia: Australian Academy of Science.
- Batten, K. M., K. M. Scow, K. F. Davies, and S. P. Harrison. 2006. Two invasive plants alter soil microbial community composition in serpentine grasslands. *Biol. Invasions* 8:217–230.
- Bell, J.N.B. and M. Treshow. 2002. *Air Pollution and Plant Life*. Chichester, UK: J. Wiley.
- Brady, K. U., A. R. Kruckeberg, and H. D. Bradshaw, Jr. 2005. Evolutionary ecology of plant adaptations to serpentine soil. *Annu. Rev. Ecol. Evol. Syst.* 36:243–266.
- Brooks, R. R. 1987. *Serpentine and its Vegetation: A Multidisciplinary Approach*. Portland, OR: Dioscorides. 462 p.
- Burke, M.J.W. and J. P. Grime. 1996. An experimental study of plant community invasibility. *Ecology* 77(3):776–790.
- Crawley, M. J. 1987. What makes a community more invisable? Pages 429–453 in A. J. Gray, M. J. Crawley, and P. J. Edwards, eds. *Colonization, Succession and Stability*. London: Blackwell.
- Davis, P. H., ed. 1985. *Flora of Turkey and the East Aegean Islands*. Volume 9. Edinburgh: Edinburgh University Press.
- DeLorme Publishing. 1998. *Northern California Atlas and Gazetteer*. 4th ed. Yarmouth, ME: DeLorme.
- Drenovsky, R. E. and K. M. Batten. 2007. Invasion by *Aegilops triuncialis* (barb goatgrass) slows carbon and nutrient cycling in a serpentine grassland. *Biol. Invasions* 9:107–116.
- Dyer, A. R. 2004. Maternal and sibling factors induce dormancy in dimorphic seed pairs of *Aegilops triuncialis*. *Plant Ecology* 172: 211–218.
- Eviner, V. T. and F. S. Chapin III. 2003. Gopher–plant–fungal interactions affect establishment of an invasive grass. *Ecology* 84(1):120–128.
- Fiedler, P. L. 1994. Rarity in vascular plants. Pages 2–3 in M. W. Skinner and B. M. Pavlik, eds. *Inventory of Rare and Endangered Vascular Plants of California*. 5th ed. Sacramento, CA: California Native Plant Society Special Publication I.
- Frietas, H. and H. Mooney. 1996. Effects of water stress and soil texture on the performance of two *Bromus hordeaceus* ecotypes from sandstone and serpentine soils. *Acta Oecol.* 17:307–317.
- Garcia, P., M. I. Morris, L. E. Saenz-De-miera, R. W. Allard, M. Perez de la Vega, and G. Ladizinsky. 1991. Genetic diversity and adaptedness in tetraploid *Avena barbata* and its diploid ancestors *Avena hirtula* and *Avena wiestii*. *Proc. Natl. Acad. Sci. U. S. A.* 88(4):1207–1211.
- Garcia, P., F. J. Vences, M. Perez de la Vega, and R. W. Allard. 1989. Allelic and genotypic composition of ancestral Spanish and colonial California gene pools of *Avena barbata*: evolutionary implications. *Genetics* 12(3):687–694.
- Gardner, M. and M. McNair. 2000. Factors affecting the co-existence of the serpentine endemics *Mimulus nudatus* Curran, and its presumed progenitor, *Mimulus guttatus* Fisher ex DC. *Biol. J. Linn. Soc.* 69: 443–459.
- Gordon, A. and C. B. Lipman. 1926. Why are serpentine and other magnesian soils infertile? *Soil Sci.* 22:291–302.
- Griffin, G. F., D. M. Stafford-Smith, S. R. Morton, G. E. Allan, K. A. Masters, and N. Preece. 1989. Status and implications of the invasion of tamarisk (*Tamarix aphylla*) on the Finke River, Northern Territory, Australia. *J. Environ. Manag.* 29(4):297–316.
- Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* 111:1169–1194.
- Harper, J. L. 1965. Establishment, aggression and cohabitation in weedy species. Pages 243–268 in H. G. Baker and G. L. Stebbins, eds. *The Genetics of Colonizing Species*. New York: Academic.
- Harrison, S. 1999. Local and regional diversity in a patchy landscape: native, alien and endemic herbs on serpentine soils. *Ecology* 80: 70–80.
- Harrison, S., K. Rice, and J. Maron. 2001. Habitat patchiness promotes invasion by alien grasses on serpentine soil. *Biol. Conserv.* 100:45–53.
- Harrison, S., J. H. Viers, and J. F. Quinn. 2000. Climatic and spatial patterns of diversity in the serpentine plants of California. *Divers. Distrib.* 6:153–161.
- Heywood, J. S. 1986. Edaphic races of *Gaillardia pulchella* in central Texas. *J. Hered.* 77:146–150.
- Hickman, J. C., ed. 1993. *The Jepson Manual: Higher Plants of California*. Berkeley: University of California Press.
- Hobbs, R. J., S. L. Gulmon, V. J. Hobbs, and H. A. Mooney. 1988. Effects of fertiliser addition and subsequent gopher disturbance on a serpentine annual grassland community. *Oecologia (Berl.)* 75: 291–295.
- Hobbs, R. J. and H. A. Mooney. 1985. Community and population dynamics of serpentine grassland annuals in relation to gopher disturbances. *Oecologia (Berl.)* 67:342–351.
- Hobbs, R. J. and H. A. Mooney. 1991. Effects of rainfall variability and gopher disturbance on serpentine annual grassland dynamics in N. California. *Ecology* 72:59–68.
- Hooper, D. U. and P. M. Vitousek. 1998. Effects of plant composition and diversity on nutrient cycling. *Ecol. Monogr.* 68:121–149.
- Huenneke, L. F., S. P. Hamburg, R. Koide, P. M. Mooney, and P. M. Vitousek. 1990. Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. *Ecology* 71: 478.
- Jain, S. K. and A. D. Bradshaw. 1966. Evolutionary divergence among adjacent plant populations. *Heredity* 21:407–441.
- Kowarik, I. 1995. On the role of alien species in urban flora and vegetation. Pages 85–103 in P. Pysek, K. Prach, M. Rejmanek, and

- M. Wade, eds. Plant Invasions: General Aspects and Special Problems. Amsterdam: SPB Academic.
- Kruckeberg, A. R. 1951. Intraspecific variability in the response of certain native plant species to serpentine soil. *Am. J. Bot.* 38:408–419.
- Kruckeberg, A. R. 1954. The ecology of serpentine soils—a symposium, III: plant species in relation to serpentine soils. *Ecology* 35:267–274.
- Kruckeberg, A. R. 1967. Ecotypic response to ultramafic soils by some plant species of northwestern United States. *Brittonia* 19:133–151.
- Kruckeberg, A. R. 1985. California Serpentine: Flora, Vegetation, Geology, Soils and Management Problems. Berkeley: University of California Press.
- Lambert, G. and J. Kashiwagi. 1978. Soil survey of Napa County, California. Washington, DC: U.S. Department of Agriculture, Soil Conservation Service and University of California Agricultural Experimental Station.
- Lechowicz, M. J. and G. Bell. 1991. The ecology and genetics of fitness in forest plants. II. Microspatial heterogeneity of the edaphic environment. *J. Ecol.* 79:687–696.
- Lee, C. E. 2002. Evolutionary genetics of invasive species. *Trends Ecol. Evol.* 17:386–391.
- Li, Y., T. Fahima, A. B. Korol, J. Peng, M. S. Roder, V. Kirzhner, A. Beiles, and E. Nevo. 2000. Microsatellite diversity correlated with ecological-edaphic and genetic factors in three microsites of Wild Emmer Wheat in North Israel. *Mol. Biol. Evol.* 17(6):851–862.
- Lin, S. L. and L. Wu. 1994. Effects of copper concentration on mineral nutrient uptake and copper accumulation in protein of copper-tolerant and nontolerant *Lotus purshianus* L. *Ecotoxicol. Environ. Saf.* 29: 214–228.
- Mack, R. N. 1989. Temperate grasslands vulnerable to plant invasion: characteristics and consequences. Pages 155–179 in J. A. Drake, H. A. Mooney, F. diCasteri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson, eds. *Ecology of Biological Invasions: A Global Perspective*. Chichester, UK: J. Wiley.
- Mack, R. N. 1996. Predicting the identity and fate of plant invaders: emergent and emerging approaches. *Biol. Conserv.* 78:107–121.
- MacNair, M. R., V. E. MacNair, and B. E. Martin. 1989. Adaptive speciation in *Mimulus*: an ecological comparison of *M. cupripilus* with its presumed progenitor, *M. guttatus*. *New Phytol.* 112:269–279.
- Matkin, A. O. and P. A. Chandler. 1957. The U.C.-type soil mixes. Pages 68–85 in K. F. Baker, ed. *The U.C. System for Producing Healthy Container-Grown Plants*. Berkeley: University of California, Agricultural Experiment Station.
- McNeilly, T. 1968. Evolution in closely adjacent plant populations, III: *Agrostis tenuis* on a small copper mine. *Heredity* 23:99–108.
- Mehlich, A. 1984. Mehlich 3 soil extractant: a modification of Mehlich 2 extractant. *Commun. Soil Sci. Plant Anal.* 15:1409–1416.
- Metcalf, S. E., D. Fowler, R. G. Derwent, M. A. Sutton, R. I. Smith, and J. D. Whyatt. 1999. Spatial and temporal aspects of nitrogen deposition. Pages 15–50 in S. J. Langran, ed. *The Impact of Nitrogen Deposition on Natural and Semi-natural Ecosystems*. Dordrecht, The Netherlands: Kluwer Academic.
- Moyle, P. B. and T. Light. 1996. Fish invasion in California: do abiotic factors determine success? *Ecology* 77:1666–1670.
- Murphy, D. D. and P. R. Ehrlich. 1989. Conservation of California's remnant grasslands. Pages 201–211 in L. F. Huenneke and H. A. Mooney, eds. *Grassland Structure and Function: California Annual Grasslands*. Dordrecht, The Netherlands: Kluwer Academic.
- Orians, G. H. 1986. Site characteristics favoring invasions. Pages 133–148 in H. A. Mooney and J. A. Drake, eds. *Ecology of Biological Invasions of North America and Hawaii*. New York: Springer-Verlag.
- Proctor, J. 1999. Toxins, nutrient shortages and droughts: the serpentine challenge. *Trends Ecol. Evol.* 14:334–335.
- Proctor, J. and S.R.J. Woodell. 1975. The ecology of serpentine soils. *Adv. Ecol. Res.* 9:255–366.
- Pysek, P., K. Prach, and P. Smilauer. 1995. Relating invasion success to plant traits: an analysis of the Czech alien flora. Pages 39–48 in P. Pysek, K. Prach, M. Rejmanek, and M. Wade, eds. *Plant Invasions: General Aspects and Special Problems*. Amsterdam: SPB Academic.
- Rechinger, K. H. 1970. Flora des Iranischen Hochlandes und der umrahmenden Gebirge: Persien, Afghanistan, Teile von West-Pakistan, Nord-Iraq, Azerbaijan, Turkmenistan. Graz, Austria: Akademische Druck- u. Verlagsanstalt.
- Rejmánek, M. 1989. Invasibility of plant communities. Pages 369–388 in J. A. Drake, H. A. Mooney, F. diCasteri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson, eds. *Ecology of Biological Invasions: A Global Perspective*. Chichester, UK: J. Wiley.
- Rejmánek, M. and D. M. Richardson. 1996. What attributes make some plant species more invasive. *Ecology* 77:1655–1661.
- Rice, K. J. and R. N. Mack. 1991. Ecological genetics of *Bromus tectorum*, III: the demography of reciprocally sown populations. *Oecologia (Berl.)* 88:91–101.
- Sambatti, J.B.M. and Rice, K. J. 2006. Local adaptation, patterns of selection, and gene flow in the California serpentine sunflower (*Helianthus exilis*). *Evolution* 60(4):696–710.
- Sambatti, J.B.M. and Rice, K. J. 2007. Functional ecology of ecotypic differentiation in the California serpentine sunflower (*Helianthus exilis*). *New Phytologist* 175:107–119.
- Scherer-Lorenzen, M., A. Elend, S. Nollert, and E. D. Schulze. 2000. Plant invasions in Germany: general aspects and impact of nitrogen deposition. Pages 351–368 in H. A. Mooney and R. J. Hobbs, eds. *Invasive Species in a Changing World*. Washington, DC: Island Press.
- Shapiro, A. M. 2002. Revisiting the pre-European butterfly fauna of the Sacramento Valley, California. *J. Res. Lepid.* 41:31–39.
- Simberloff, D. 1995. Introduced species. Pages 323–336 in W. A. Nierenberg, ed. *Encyclopedia of Environmental Biology*. Volume 2. San Diego, CA: Academic.
- Sommer, S. G. and E. S. Jensen. 1991. Foliar absorption of atmospheric ammonia by ryegrass in the field. *J. Environ. Q.* 20:153–156.
- Thomson, D. M. 2007. Do source-sink dynamics promote the spread of an invasive grass into a novel habitat? *Ecology* 88:3126–3134.
- Vlamis, J. and H. Jenny. 1948. Calcium deficiency in serpentine soils as revealed by absorbent technique. *Science* 107:549–541.
- Walker, R. B. 1954. The ecology of serpentine soils—a symposium, II: factors affecting plant growth on serpentine soils. *Ecology* 35: 259–266.
- Wedin, D. A. and D. Tilman. 1996. Influence of nitrogen loading and species composition on the carbon balance of grasslands. *Science* 274: 1720–1723.
- Weiss, S. B. 1999. Cars, cows, and checkerspot butterflies: nitrogen deposition and management of nutrient-poor grasslands for a threatened species. *Conserv. Biol.* 13(6):1476–1486.
- Weiss, S. B. 2006. Impacts of Nitrogen Deposition on California Ecosystems and Biodiversity. Sacramento: California Energy Commission, PIER Energy-Related Environmental Research Publication CEC-500-2005-165.
- Westerbergh, A. and A. Saura. 1992. The effect of serpentine on the population structure of *Silene dioica* (Caryophyllaceae). *Evolution* 46(5):1537–1548.
- Wild, H. and A. D. Bradshaw. 1977. The evolutionary effects of metalliferous and other anomalous soils in south-central Africa. *Evolution* 31:282–293.
- Wu, L. and A. L. Kruckeberg. 1985. Copper tolerance in two legume species from a copper mine habitat. *New Phytol.* 99:565–570.
- Zohary, D. 1965. Colonizing species in the wheat group. Pages 404–423 in H. G. Baker and G. L. Stebbins, eds. *The Genetics of Colonizing Species*. New York: Academic.

Received May 15, 2009, and approved March 20, 2010.