CONTENTS

NEW SPECIES

MIMICKING FIRE FOR SUCCESSFUL CHAPARRAL RESTORATION

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Abstract

Following disturbance, seed pre-treatment is essential for re-establishing many species with low germination rates. However, some seeds, such as those from chaparral plants, do not respond to common horticultural treatments. Instead, methods that mimic chaparral's natural succession cues (e.g., fire) should be used to improve seed germination and restoration success. Fire effects, such as heat, charate, leachate, smoke, and/or liquid smoke, are effective in breaking long-term seed dormancy in many chaparral plants. The challenge is to break seed dormancy in a cost- and time-efficient manner that can be used in large-scale restoration projects. Results of our study show that short-term exposure (10 minutes to one hour) to liquid smoke and/or heat enhances seed germination of *Adenostoma fasciculatum* Hook. & Arn. (chamise), *Ceanothus cuneatus* (Hook.) Nutt. (buckbrush), and *Salvia mellifera* Greene (black sage). Chamise seeds treated with liquid smoke have the greatest percent increase of seed germination odds: 394%, from the control (P < 0.000). Buckbrush seeds treated with liquid smoke and heat have the greatest percent increase of seed germination odds: 953%, from the control (P < 0.000). Black sage seeds treated with heat have the greatest percent increase of seed germination odds: 354%, from the control (P < 0.000). Implementing these procedures in restoration may reduce the seed costs of certain species by nearly 90%.

Key Words: *Adenostoma fasiculatum*, *Ceanothus cuneatus*, chaparral restoration, fire effects, liquid smoke, *Salvia mellifera*, seed dormancy.

Chaparral is a major vegetation type that covers seven percent of California (Keeley and Davis 2007). Chaparral communities are impacted by recurrent fires, as well as mining, brush clearing, and other human activities. Restoration of resprouting shrub-dominated chaparral (as opposed to mere establishment of a vegetative cover) has proven challenging, especially in areas disturbed by mining. The introduced, invasive grass *Festuca perennis* (L.) Columbus & J. P. Sm. (Italian ryegrass) has often been used for revegetation and slope stabilization following disturbance, but it has been observed that this grass retards the natural establishment and succession of native chaparral shrubs (Barro and Conrad 1987, 1991; Janicki unpublished). Some investigators have found that the addition of organic material, compost, and/or mycorrhizal fungi significantly improves revegetation efforts on road-cuts, mines, or other disturbed areas where only decomposed granite remains (Claassen and Marler 1998; Claassen and Zasoski 1998; Curtis and Claassen 2007). Despite the availability of these tools, many chaparral restoration projects are unsuccessful for at least 20 years;

characteristic dominate shrubs are infrequent at restoration sites (Cione et al. 2002; Meira-Neto et al. 2011).

Many chaparral shrubs have very low germination rates unless exposed to fire or fire effects (Stone and Juhren 1951, 1953; Went et al. 1952; Sweeny 1956; Keeley 1987; Keeley and Fotheringham 1998). Common horticultural methods for breaking seed dormancy are not effective for dominant chaparral shrubs (Quick 1935; Stidham et al. 1980; Emery 1988). A promising restoration strategy has been demonstrated in South African fynbos, a homolog to California's chaparral. There, restoration researchers utilized seeds' natural responses to fire to enhance seed germination. (Baxter and Van Staden 1994; Dixon and Roche 1995; Dixon et al. 1995; Read et al. 2000; Matesanz and Valladares 2007). Chaparral restoration could also benefit from scientifically supported fire effects to pre-treat seeds. To improve restoration we should adapt known fire-effect treatments (liquid smoke or heat and/or charate) that increase seed germination for *Adenostoma fasciculatum* Hook. & Arn. (chamise), *Ceanothus cuneatus* (Hook.) Nutt. (buckbrush), and *Salvia mellifera* Greene (black sage) (Jager et al. 1996; Keeley 1987; Keeley et al. 2005).

We seek to improve chaparral restoration in the central Coast Range of California by

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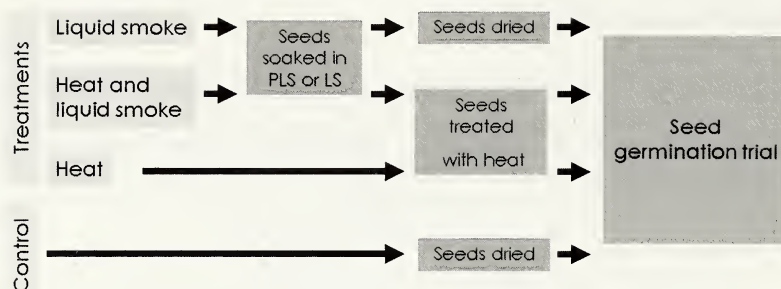
FIG. 1.   Experimental design schematic. LS = liquid smoke diluted with water. PLS = pure liquid smoke.

evaluating the potential of inexpensive and commercially available fire-effect treatments to increase seed germination. Our treatments differ from those used in other studies because we include exposure to heat and/or Wright's Hickory Seasoning (a commercial liquid smoke produced by B&G Foods, Inc.) and our sample sizes are more than 10 times as great (Keeley 1987; Keeley et al. 2005). We test the hypothesis that seed germination rates differ significantly between treatments and the control, and between treatment methods. We then quantify the changes treatments produce in germination rates and evaluate if the seed pre-treatments' percent increase of seed germination odds and their associated costs are beneficial to restoration.

METHODS

Seed Collection and Storage

S&S Seeds of Carpinteria, California hand collected chamise, buckbrush, and black sage seeds during fall 2006 and 2007 in southern California. Seed pods and stems were macerated with a de-bearding machine and separated by size and density with an air-screen machine. Trials 1–3 tested fall 2006 seeds for germination during winter 2006–2007 and fall 2007. Trial 4 tested fall 2007 seeds for germination during winter 2007–2008. Before germination tests, seeds were stored at room temperature in plastic mesh bags under ambient light conditions.

Seed Treatments

Thirty seeds at a time were placed onto unbleached coffee filters, tied with natural twine, and then submerged in Wright's Hickory Seasoning diluted with water in varied proportions (referred to as liquid smoke [LS] dilution hereafter) for 10 min (Jager et al. 1996; Keeley et al. 2005) (Fig. 1). We applied the temperature and heating periods that yield the highest germination in Keeley (1987): chamise, 70°C for one hr; buckbrush, 100°C for five min; black sage, 70°C for five min. To simulate the drying

process that occurs after hydroseeding, we dried samples in a forced-air convection oven at 30°C for one hr, unless the sample was designated for heat treatment. Only one treatment type was dried at a time in the oven to eliminate air contamination with LS. If a heat treatment was tested, heat was applied directly after soaking. Table 1 displays the treatment dilutions and/or heat levels and number of seeds for each treatment.

Seed Germination Trials

Following the methods of Keeley (1987), each set of 30 treated seeds was sown in 60 × 15 mm sterilized plastic Petri dishes lined with two layers of Whatman #1 filter paper. Two days after the treatments, seed germination was initiated by adding one and one-half to two ml of water to each Petri dish. Each dish was then placed inside a plastic bag to reduce evaporation and gas transfer between treatments, placed in a growth chamber, and cold stratified at ~4°C for one mo under ambient light conditions. The bag was then placed under a diurnal light schedule with temperatures ranging from 12°–18°C for eight wk. Every week, samples were randomly rearranged within the growth chamber to reduce environmental effects. After cold stratification, seeds were examined weekly for six wk for epicotyl emergence, which marks germination. Germinated seeds were recorded and then removed (Baskin and Baskin 1998).

Analysis

Data were analyzed with Minitab 15 Statistical Software (2007). For each species, a logistic regression model blocked by trial was used to assess the effects of treatments on germination rates. Model fit was assessed by Pearson, Deviance, and Hosmer-Lemeshow "goodness of fit" tests. Due to the large number of treatments compared, statistical significance was assessed using both Fisher and Bonferroni adjusted α-values based on the number of comparisons with $\alpha = 0.05$. Bonferroni-adjusted α-values for

TABLE 1. NUMBER OF SEEDS TESTED PER SPECIES, TRIAL, AND TREATMENT. Several replicates (30 seeds each) were included in each trial though the numbers of replicates per treatment and per trial were not necessarily similar. The control was present in every trial. The treatment names indicate the concentration of Wright's Hickory Seasoning liquid smoke diluted with water (if applied), the duration of soaking in liquid smoke if it exceeds 10 minutes (if applied), and heat (if applied) refers to heat treatments following Keeley (1987): chamise 70°C for one hour, buckbrush 100°C for five minutes, black sage 70°C for five minutes. LS = liquid smoke; PLS = pure liquid smoke.

Treatment/trial	Chamise					Buckbrush					Black sage				
	1	2	3	4	Total	1	2	3	4	Total	1	2	3	4	Total
control	90	150	150	150	540	90	150	—	150	390	90	60	120	150	420
heat	—	—	—	90	90	—	—	—	180	180	—	—	—	150	150
PLS	—	—	180	180	360	—	—	—	—	—	—	—	—	150	150
PLS heat	—	—	—	270	270	—	—	—	300	300	—	—	—	300	300
1:10 LS	—	—	—	150	150	—	—	—	—	—	—	—	—	150	150
1:10 LS heat	—	—	—	150	150	—	—	—	180	180	—	—	—	120	120
1:100 LS	90	90	120	120	420	90	210	—	—	300	90	90	150	150	480
1:100 LS heat	—	—	—	180	180	—	—	—	150	150	—	—	—	150	150
1:1000 LS	90	120	180	—	390	90	150	—	—	240	90	150	150	—	390
1:2000 LS	90	120	150	—	360	90	180	—	—	270	90	90	150	—	330
1 hr PLS	—	—	180	—	180	—	—	—	—	—	—	—	—	—	—
4 hrs PLS	—	—	180	—	180	—	—	—	—	—	—	—	—	—	—
18 hrs PLS	—	—	210	—	210	—	—	—	—	—	—	—	—	—	—
27 hrs PLS	—	—	180	—	180	—	—	—	—	—	—	—	—	—	—
30 hrs PLS	—	—	180	—	180	—	—	—	—	—	—	—	—	—	—
Total	360	480	1710	1290	3840	360	690	—	960	2010	360	390	570	1320	2490

TABLE 2. RESULTS FOR CHAMISE. The tabulated values from left to right include the percent seed germination, change compared to the control (percent change in seed germination odds and 95% confidence interval for percent change in seed germination odds with all treatments compared to the control, and P-value), and significant similarities (Bonferroni-adjusted value for multiple comparisons and Fisher test). Bonferroni-adjusted value for multiple comparisons is α = 0.00048 with a group value of α = 0.05 and the comparisons are indicated with numbers. Fisher comparisons are based on α = 0.05 and indicated with letters. Groups sharing a common letter and/or number are not significantly different. The treatment names indicate the concentration of Wright's Hickory Seasoning liquid smoke (LS) diluted with water (if applied), the duration of soaking in LS if it exceeds 10 minutes (if applied), and heat (if applied) refers to heat treatments following Keeley (1987): chamise 70°C for one hour. LS = liquid smoke; PLS = pure liquid smoke; an asterisk (*) designates the recommended treatment; and double asterisks (**) designate the recommended treatment if hydroseeding.

| | | Change compared to control | | | Significant similarities | |
Treatment	Germination (%)	Change (%)	95% confidence interval (%)	P	Bonferroni-adjusted for multiple comparisons	Fisher test
control	4	—	—	—	3	a
1:2000 LS	0	−83	(−98, 34)	0.094	23	a
1:1000 LS	2	45	(−39, 246)	0.397	123	a
1:100 LS	8	125	(24, 309)	0.008	123	bcd
1:10 LS	17	109	(9, 300)	0.027	123	bcd
PLS	16	243	(96, 501)	0.000	1	bdef
heat	12	45	(−35, 223)	0.360	123	c
1:100 LS heat	17	109	(11, 291)	0.022	123	bcd
1:10 LS heat**	30	347	(145, 717)	0.000	12	f
PLS heat	20	161	(47, 363)	0.001	123	bde
1 hr PLS*	9	394	(122, 999)	0.000	12	ef
4 hrs PLS	7	294	(71, 807)	0.001	123	b
18 hrs PLS	0	−76	(−97, 90)	0.177	123	a
27 hrs PLS	1	−72	(−96, 122)	0.229	123	a
30 hrs PLS	0	—	—	—	123	a

multiple comparisons for chamise, buckbrush, and black sage were respectively α = 0.00048, α = 0.0018, and α = 0.0011.

RESULTS

Chamise

Nine treatments significantly increased percent odds of seed germination relative to the control (P < 0.027), whereas five treatments did not differ significantly from the control (P > 0.05) (Table 2). One hour pure liquid smoke (PLS) increased percent odds of seed germination the most (394%; 95% CI: 122% to 999%, P < 0.000). Other promising treatments included 1:10 LS dilution with heat, four-hour PLS, and PLS that respectively increased percent odds of seed germination by 347%, 294%, 243% (P < 0.000, 0.000, 0.001). Other treatment estimates ranged from a 161% increase (PLS with heat, P < 0.001) to a 83% decrease (1:2000 LS dilution) (P < 0.094) of seed germination odds. Three treatments (1:2000 LS dilution, 8-hour PLS, and 27-hour PLS) negatively affected germination though reductions were not significant (P < 0.094, 0.177, 0.229). The treatments with more than a 200% seed germination odds increase listed above (including one hour PLS, 1:10 LS dilution with heat, four-hour PLS, and PLS) are not significantly different from one another (P > 0.273).

Buckbrush

Three treatments significantly increased percent odds of seed germination relative to the control (P < 0.045), whereas three did not differ significantly from the control (P > 0.05) (Table 3). PLS with heat increased percent odds of seed germination the most (953%; 95% CI: 228% to 3281%, P < 0.000). Both heat and 1:10 LS dilution with heat increased percent odds of seed germination 267% (P < 0.045, 0.045). All other treatment estimates ranged from a 77% increase (1:1000 LS dilution) to a 31% decrease (1:100 LS dilution, P < 0.609) of seed germination odds. PLS with heat significantly increased percent odds of seed germination relative to both heat and 1:10 LS dilution with heat (P < 0.000, 0.002).

Black Sage

All treatments significantly increased percent odds of seed germination relative to the control (P < 0.044) (Table 4). Heat increased percent odds of seed germination the most (354%; 95% CI: 172% to 657%, P < 0.000). Other promising treatments include PLS with heat, 1:100 LS dilution with heat, 1:2000 LS dilution, 1:10 LS dilution and heat, and 1:100 LS dilution, which increased seed germination odds by 228%, 195%, 185%, 168%, and 138% respectively (P < 0.000,

TABLE 3. RESULTS FOR BUCKBRUSH. The tabulated values from left to right include the percent seed germination, change compared to the control and pure liquid smoke with heat (percent change in seed germination odds and 95% confidence interval for percent change in seed germination odds compared to the control and compared to pure liquid smoke with heat, P-value), and significant similarities (Bonferroni-adjusted value for multiple comparisons and Fisher test). No seeds germinated with 1:2000 liquid smoke therefore these results could not be compared to Change compared to the control or Change compared to pure liquid smoke with heat. Bonferroni-adjusted value for multiple comparisons is $\alpha = 0.0018$ with a group value of $\alpha = 0.05$ and the comparisons are indicated with numbers. Fisher comparisons are based on $\alpha = 0.05$ and are indicated with letters. Groups sharing a common letter and/or number are not significantly different. The treatment names indicate the concentration of Wright's Hickory Seasoning liquid smoke diluted with water (if applied) and heat (if applied) refers to heat treatments following Keeley (1987): $100°C$ for five minutes. LS = liquid smoke; PLS = pure liquid smoke; an asterisk (*) designates the recommended treatment.

Treatment	Germination (%)	Change compared to control			Change compared to PLS and heat			Significant similarities	
		Change (%)	95% confidence interval (%)	P	Change (%)	95% confidence interval (%)	P	Bonferroni-adjusted for multiple comparisons	Fisher test
control	1.03	—	—	—	−91	(−97, −69)	0.000	1	a
1:2000 LS	0.00	—	—	—	—	—	—	12	
1:1000 LS	0.83	77	(−80, 1455)	0.609	−83	(−98, 79)	0.140	1	abc
1:100 LS	1.67	24	(−47, 2094)	0.195	−68	(−96, 157)	0.287	12	abc
heat	6.67	267	(3, 1208)	0.045	−65	(−82, −33)	0.002	1	b
1:100 LS heat	1.33	−31	(−88, 318)	0.690	−93	(−98, −73)	0.000	13	a
1:10 LS heat	6.67	267	(3, 1208)	0.045	−65	(−82, −33)	0.002	13	b
PLS heat*	17.00	953	(228, 3281)	0.000	—	—	—	23	c

0.000, 0.000, 0.000, 0.000). The remaining three treatments only had relatively small percent increase of seed germination odds, which were less than 138% ($P < 0.044$). While heat significantly increased percent odds of seed germination over five treatments, it is not significantly different from all treatments ($0.0011 < P < 0.050$).

DISCUSSION

Short periods of exposure (10 minutes to four hours) to LS and/or heat significantly enhance seed germination of chamise, buckbrush, and black sage. The stimulatory effect of these treatments was retained when seeds were re-dried and stored for two days. Recommended seed treatments have the highest percent increase of seed germination odds and may be statistically significant. In the case of statistically similar treatments, cost, empirical seed germination, and practicality were taken into consideration. In addition, LS-only treatments are also recommended because large industrial ovens may not be readily available for heat treatments.

Chamise

The recommended treatment for chamise (among three similar treatments) is PLS for one hour because it has the highest estimate of percent increase of seed germination odds. For chamise, the power (probability of the procedure to find a significant difference among treatments with differences as subtle as those seen with our sample size) is only 52%. With our minimum number of seeds per treatment (150), we can only detect germination rate differences as large as 18–20% with 90–95% probability, respectively. To determine if the 1:10 LS dilution with heat treatment is statistically different from all other treatments, then 14 and 17 replications (420 and 510 seeds) would need to be completed for 90 and 95% power, respectively. While PLS for one hour is recommended, this treatment may not be best for hydroseeding because we observed a percent reduction in seed germination odds as soaking time increases. If hydroseeding, the recommended treatment is 1:10 LS dilution for 10 minutes with heat, which is only significantly different from the control and PLS for one hour (Table 2).

Buckbrush

The recommended treatment for buckbrush is PLS with heat. No LS-only treatments significantly increased seed germination odds; therefore, no other treatments are recommended ($P \geq 0.195$). These statistical findings differ from Keeley's (1987), whose data did not show charate addition to be statistically different from the control. However, Keeley's (1987) data for charate addition and $100°C$ for five minutes is

TABLE 4. RESULTS FOR BLACK SAGE. The tabulated values from left to right include the percent seed germination, change compared to the control and heat (percent change in seed germination odds and 95% confidence interval for percent change in seed germination odds with all treatments compared to the control and compared to heat, P-value), and significant similarities (Bonferroni-adjusted value for multiple comparisons and Fisher test). Bonferroni-adjusted value for multiple comparisons is $\alpha = 0.0011$ with a group value of $\alpha = 0.05$ treatments and the comparisons are indicated with numbers. Fisher comparisons are based on $\alpha = 0.05$ and are indicated with letters. Groups sharing a common letter and/or number are not significantly different. The treatment names indicate the concentration of Wright's Hickory Seasoning liquid smoke diluted with water (if applied) and heat (if applied) refers to heat treatments following Keeley (1987): 70°C for five minutes. LS = liquid smoke; PLS = pure liquid smoke; an asterisk (*) designates the recommended treatment; and double asterisks (**) designate the recommended treatment if no oven is available.

Treatment	Germination (%)	Change compared to control			Change compared to heat			Significant similarities	
		Change (%)	95% confidence interval (%)	P	Change (%)	95% confidence interval (%)	P	Bonferroni-adjusted for multiple comparisons	Fisher test
control	8	—	—	—	—	—	—	1	a
1:2000 LS**	12	185	(63, 397)	0.000	−78	(−87, −63)	0.150	23	bcd
1:1000 LS	7	87	(4, 234)	0.036	−37	(−67, −18)	0.008	123	cd
1:100 LS	15	138	(53, 271)	0.000	−59	(−79, −21)	0.006	23	cd
1:10 LS	22	77	(2, 207)	0.044	−47	(−67, −17)	0.000	12	c
PLS	26	120	(28, 277)	0.004	−61	(−76, −36)	0.004	123	cd
heat*	42	354	(172, 657)	0.000	—	—	—	3	b
1:100 LS heat	32	195	(75, 398)	0.000	−35	(−59, 4)	0.074	23	bcd
1:10 LS heat	30	168	(54, 368)	0.001	−41	(−64, −2)	0.043	23	cd
PLS heat	34	228	(106, 420)	0.000	−28	(−52, 8)	0.113	3	bd

five times greater than the control. Statistical differences in our experiments can be attributed to larger sample sizes.

Black Sage

The recommended treatment for black sage is heat. For black sage, heat produced the greatest percent increase of seed germination odds. The probability of detecting differences between treatments was only 30%. As a result, we cannot conclude that the heat-only treatment increased seed germination odds relative to the other treatments, even though it had the largest observed percent increase of seed germination odds. The minimum number of seeds per treatment (150) can detect germination-rate differences only as large as 18–20% with 90–95% probability, respectively. To determine if heat is statistically different from all other treatments, 26 and 32 replications (780 and 960 seeds) would be required to detect an effect size of 8% with 90 and 95% certainty, respectively. If an oven is not available, then the alternative recommended treatment is 1:2000 LS dilution. 1:2000 LS dilution had the next highest percent change in seed germination odds when a treatment did not include heat, but this treatment was also not significantly different from others (Table 4).

Cost of Treatments

Seed pre-treatment is most economically beneficial when seeds have very low germination rates without treatment and large germination rates after treatment, and when the seed costs are high and the cost of treatment is low. Therefore, it is necessary to compare the cost of pre-treatments, both in terms of material and human resources, to the money saved from increased seed germination odds. The pre-treatments would be economically viable only if the resulting increase in seed germination odds decreased seed cost and if the pre-treatments cost less than the seed cost avoided. The pre-treatments would be most cost effective on plants such as chamise and buckbrush, whose seed germination odds increase dramatically from 4–18% and 10–57%, respectively. For these examples, one pound of treated seed would be equivalent to more than four or five pounds of untreated seeds. Savings are calculated based on the cost of one pound of native seeds from S&S Seeds in 2009 ($37), labor for one hour ($14), cost of supplies (LS varies based on concentration: $2.00 per treatment for PLS to $0.14 for 1:2000 LS dilution). Pre-treating chamise, buckbrush, and black sage may save an estimated $112, $337, and $115, respectively, by making one pound of seed equivalent to four or five pounds (95% CI: $38–$249, $68–$1198,

$48–$227) (P < 0.000, 0.000, 0.000). These seed pre-treatments are economically beneficial and should be used in restoration projects.

Conclusion

Establishing dominant shrubs, such as the ones studied here, is integral for both short-term and long-term restoration success. In the short-term, there is literally a "race between rates of shrub recovery" and non-native annual grass colonization (Keeley 2004) since shrubs are excluded by these grasses if they don't colonize the site early on (Shultz et al. 1955). In the long term, shrub establishment will build post-fire resilience and decrease the risk of catastrophic failure due to lack of seed bank and resprouting shrubs following an inevitable future fire (Meira-Neto et al. 2011). Unfortunately, many restoration sites in both chaparral and chaparral-like shrublands throughout other Mediterranean regions fail to establish shrubs (Cione et al. 2002; Meira-Neto et al. 2011). Our proposed seed treatments are one step to improve shrub colonization in California's chaparral. These treatments in coordination with other techniques to increase shrub establishment and survivorship will set a trajectory for long-term restoration success.

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EFFECTS OF FIRE AND FIRELINE DISTURBANCE ON THE PLANT COMMUNITY IN A SOUTHERN CALIFORNIA ECOLOGICAL RESERVE

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Abstract

Native plants in most California ecosystems are adapted to fire, but altered fire regimes and disturbance from firefighting activity, such as the construction of firebreaks or firelines, can change plant community composition and the ratio of native to nonnative species. In October 2007, a wildfire burned 710 acres through a chaparral/grassland mosaic on an ecological reserve, providing an opportunity to quantify fire and fireline disturbance impacts on native and nonnative species under differing disturbance conditions. In the spring of 2012 we sampled the plant community in three adjacent sites, focusing on *Centaurea melitensis*, which is a common nonnative invader after fire in California chaparral. The first site was burned and bulldozed, the second site was burned but not bulldozed, and the third site was not burned or bulldozed. The first site had also been sampled in the spring of 2008. After four years within the burned fireline site, the mean relative cover of *C. melitensis* decreased from 72% to 28%, but its density increased, and there were increases in the covers of nonnative annual grasses, litter, and native plants. Among the three sites in 2012, both of the burned sites had higher density and cover of *C. melitensis* and lower relative cover of annual grasses than the unburned site. The only site with notable native perennial presence was the burned fireline. The results of our study suggest that the recruitment of *C. melitensis* and some native species is promoted by fire. In the absence of additional disturbance by firelines, persistence of these taxa is limited by competition from nonnative annual grasses.

Key Words: California chaparral, *Centaurea melitensis*, disturbance, fire, firelines, invasive plants, Mediterranean ecosystems, nonnative annual grasses.

Fire has been a presence for thousands of years in southern California, from prehistoric infrequent lightning ignitions (Keeley and Fotheringham 2001) to Native American burning (Keeley 2002) to the relatively frequent anthropogenic fires of the present (Keeley and Fotheringham 2001). Although most native plants in California ecosystems are adapted to fire, fire frequency in many areas has increased beyond the extent of the natural regime, facilitating the recruitment of nonnative invaders (Hobbs and Huenneke 1992), supporting their persistence (Haidinger and Keeley 1993), and engendering the exclusion of native species (Keeley and Brennan 2012). Because of the threats to property, safety, and native biodiversity, California has an active approach to fire management, with practices such as the use of firebreaks or firelines that promote disturbances to plant communities. The disturbance effects of the construction and maintenance of firebreaks can promote nonnative plant colonization (D'Antonio et al. 1999; Merriam et al. 2006). The interaction of the effects of disturbance from firebreaks or firelines with impacts of frequent fire would be expected to additionally promote the colonization of nonnative annual species (Merriam et al. 2006).

The Sedgwick Reserve in the Santa Ynez Valley of Santa Barbara County, California, is part of the University of California Natural Reserve System. The land was used primarily for cattle grazing from the early 19th century until the site became a reserve in 1997. The Reserve supports coastal sage scrub, chaparral, native grassland, valley oak savanna, and other native vegetation communities but, perhaps due to the heavy disturbance associated with cattle grazing, these native communities have been invaded in some places by nonnative species. Wildfire had been excluded from the Reserve for at least 100 years when, in October 2007, a wildfire burned 710 acres through a chaparral/grassland mosaic on the Reserve. Protective firelines had been established at Sedgwick many years before. The Sedgwick Fire provided an opportunity to quantify fire and fireline disturbance impacts on native and invasive species under differing disturbance conditions.

Centaurea melitensis L. (Asteraceae) is a weedy annual forb that is native to the Mediterranean Basin and an aggressive invader in California shrublands and grasslands (Moroney and Rundel 2013). It is commonly observed after fire in California chaparral (Keeley et al. 2005). It can be dominant in disturbed areas, and has been found to out-compete native species (Moroney et al. 2011). In a comparative study of the demographics of *C. melitensis* in its native and

invasive ranges, a dense population of *C. melitensis* was found and surveyed in a burned fireline on the Sedgwick Reserve in the spring following the Sedgwick Fire (Moroney and Rundel 2013). We returned to the site four years later to quantify the changes in cover and density of *C. melitensis* and the associated plant community in the area disturbed by fire and the fireline. We also compared the cover and density of *C. melitensis* and the associated community composition in this site to an adjacent burned site with no fireline, and to an undisturbed (unburned, ungraded) site. Of particular interest was the comparative behavior of *C. melitensis* with nonnative annual grasses, which appear to competitively displace *C. melitensis* in California sites (Moroney and Rundel 2013).

The objectives of this study were to examine the relationship of disturbance events to patterns of native and nonnative dominance by asking the questions: (1) Does the native chaparral/grassland community recover in a burned fireline, or do nonnative species, *C. melitensis* in particular, persist and dominate?, and; (2) Does the post-fire community differ in sites with and without firelines, and do those sites differ from an undisturbed site? This was an opportunistic study with no replication of sites, so the results should be interpreted with this limitation in mind.

METHODS

Study Species

Centaurea melitensis is an annual thistle that is native to the western Mediterranean Basin, but has been dispersed by humans and is invasive globally. It is a problem pest in California because it threatens the health of livestock and the persistence of native plants and animals (DiTomaso and Gerlach 2000; Moroney et al. 2011). It has been in California since at least 1797 (Hendry 1931). *Centaurea melitensis* is one of the most common nonnative plants in the first five years after fire in chaparral and coastal sage scrub of southern California, with an average density of >16,000 individuals ha^{-1} in chaparral sites and >285,000 individuals ha^{-1} in sage scrub sites (Keeley et al. 2005).

Study Sites

The Sedgwick Reserve, University of California Natural Reserve System (34°42′47.7″N, 120°02′00.7″W) contains a mix of vegetation types including chaparral, coastal sage scrub, native and nonnative grasslands, and valley oak savanna. The recorded fire history for the Reserve begins in 1912, and there have been no fires recorded on the Reserve until the 2007 Sedgwick Fire (S. Alderete, Santa Barbara

County Fire Department, personal communication). Prior to the establishment of the Natural Reserve on the site the land was used for cattle grazing. We sampled three sites located on the Paso Robles Formation with a Shedd silty clay loam soil.

The first of the three sites (Burned, Fireline) was located along a ridge that was both burned and bulldozed during the 2007 Sedgwick Fire. A bulldozer cleared a one-blade width (12 ft) fireline on the ridgeline after the fire burned through the area to create access to the rest of the fire. This fireline was constructed several years before the Sedgwick Fire and had been intermittently maintained (S. Alderete, Santa Barbara County Fire Department, personal communication). In the spring following the fire (2008), we sampled the vegetation on the Burned, Fireline in association with a previous study that compared the density and dominance of *C. melitensis* in its native and invasive ranges (Moroney and Rundel 2013). We sampled this site again in the spring of 2012. The second site (Burned, No Fireline), sampled in the spring of 2012, was located along the same ridge immediately adjacent to the Burned, Fireline. This site burned in the Sedgwick Fire but was not disturbed by bulldozing. The third site (No Burned, No Fireline), also sampled in the spring of 2012, was 300 m south of the Burned, Fireline on the adjacent and parallel ridge, with a similar elevation, slope, and aspect. This site was not burned or disturbed in the Sedgwick Fire.

The two survey years, 2008 and 2012, had 739 mm and 577 mm of precipitation, respectively, during the rainy season (Lisque weather station, Sedgwick Reserve, 34.72449N, −120.0635W).

Sampling

In June 2008, sampling was conducted in the Burned, Fireline site. In June 2012, the same site was resampled, and the two additional sites were also sampled using two-stage systematic sampling (Elzinga et al. 1998). Ten transects were placed at randomly selected points within each 10 m increment of a 100 m baseline that followed the ridgeline. A series of 1 m × 0.2 m plots were placed at regular intervals along the transects starting at a randomly selected point. To determine population density of *C. melitensis*, individuals were counted within each plot. We estimated the percent cover of each of the following groups: *C. melitensis*, nonnative annual grasses, all nonnative species (including *C. melitensis* and annual grasses), all native species, litter, bare ground, and rock. Plot totals were averaged per transect. All taxa present in the plots were recorded.

TABLE 1. THE PRESENCE OF TAXA IN THE SAMPLE PLOTS REPORTED AS THE PERCENTAGE OF PLOTS IN EACH SITE. AF = Annual forb, S = Shrub, G = Geophyte, PG = Perennial grass, AG = Annual grass.

| Species | Life-form | Percentage of plots | | | |
| | | 2008 | 2012 | 2012 | 2012 |
		Burned, Fireline	Burned, Fireline	Burned, No Fireline	No Burned, No Fireline
Native					
Adenostoma fasciculatum Hook. & Arn.	S	20	5	0	0
Amsinckia sp.	AF	0	0	5	15
Artemisia californica Less.	S	10	20	0	0
Calochortus sp.	G	25	0	0	0
Ceanothus sp.	S	35	5	0	0
Daucus pusillus Michx.	AF	0	0	10	0
Dichelostemma capitatum (Benth.) Alph. Wood	G	10	0	0	0
Galium sp.	AF	5	0	0	0
Hazardia squarrosa (Hook. & Arn.) Greene	S	0	0	0	20
Deinandra fasciculata (DC.) Greene	AF	0	0	25	0
Lupinus sp.	AF	0	0	30	0
Navarretia sp.	AF	0	0	30	0
Plantago erecta E. Morris	AF	0	0	10	0
Salvia mellifera Greene	S	0	5	0	0
Sisyrinchium bellum S. Watson	G	0	0	5	0
Stipa sp.	PG	15	40	5	15
Native species richness		7	5	8	3
Nonnative					
Anagallis arvensis L.	AF	70	35	25	0
Avena sp.	AG	0	15	100	100
Bromus sp.	AG	5	95	85	90
Carduus pycnocephalus L.	AF	0	5	0	10
Centaurea melitensis L.	AF	95	85	85	30
Erodium sp.	AF	35	45	60	30
Hordeum murinum L.	AG	0	25	25	30
Lactuca serriola L.	AF	0	0	5	25
Nonnative species richness		4	7	7	7
Total species richness		11	12	15	10

Statistical Analyses

To compare differences in the Burned, Fireline site between the sampling years 2008 and 2012, we performed a multivariate analysis using Hotelling's T^2 test on the following variables: relative cover of *C. melitensis*, relative cover of annual grass, relative cover of native plants, relative native species richness, percent cover of rock, percent cover of litter, and percent cover of bare ground. The multivariate test was followed by separate linear regressions for each variable. Relative cover was calculated as the percent cover of the target group divided by the total vegetative cover of all species in a plot. These variables were arcsine-square root transformed to stabilize the variance and then back-transformed to proportions for interpretation. The difference in *C. melitensis* density between years was analyzed with a Poisson regression with robust standard errors.

To compare differences in the three sites in 2012 (Burned, Fireline, Burned, No Fireline, and No Burned, No Fireline), we used the same analytical approach as above, substituting MANOVA for Hotelling's T^2 in the multivariate analysis. The linear regressions were followed by *post hoc* testing using multiple comparisons with bonferroni corrections to test for the differences in predicted means between pairs of sites. All statistical analyses were done using Stata statistical software (Stata, version 12.1, Statacorp, College Station, TX).

RESULTS

A total of 24 species were recorded in the plots over all sites and years collectively, including 16 native species and eight nonnative species. Native life forms included seven annual forb species, five shrub species, three geophytes, and one perennial grass. There were no native annual grasses. All of the nonnative plants were annuals, with five annual forb species and three annual grass species (Table 1). *Centaurea melitensis* was the most common species in all of the sites collectively (74% of the plots).

Fireline Between Years

There was a significant difference in the relative cover composition of the community

TABLE 2. TWO POISSON REGRESSION MODELS WITH ROBUST STANDARD ERRORS COMPARING *CENTAUREA MELITENSIS* DENSITY WITHIN THE BURNED, FIRELINE BETWEEN YEARS AND BETWEEN YEARS AMONG SITES. 2008 is the reference year in the first model, and the Burned, Fireline is the reference site in the second model. *P < 0.001.

Source	Coefficient	X^2	P
Burned, Fireline between years			
Year	0.677	3.881	0.049
Constant	2.5	107.537	*
Sites within year			
Site 2	0.347	0.846	0.356
Site 3	−2.736	15.761	*
Constant	3.174	170.825	*

FIG. 1. Density box plots of *C. melitensis* measured in four sites at the Sedgwick Reserve. The two boxes on the left represent sites within a bulldozed fireline, with data measured in 2008 and 2012. The two boxes on the right represent two sites adjacent to the fireline, but not bulldozed, one burned site and one unburned site, with data measured in 2012.

within the Burned, Fireline in 2012 compared to 2008 (2-group Hotelling's T^2, F = 14.495, P = 0.0001). This difference was due to a decrease in the relative cover of *C. melitensis*, an increase in the relative cover of annual grasses, an increase in the relative cover of native plants, and an increase in the percent cover of litter (Table 2). The density of *C. melitensis* increased despite the decrease in relative cover (Fig. 1). There was no change in native species richness.

The number of plots with native shrubs, geophytes, and annual forbs decreased in four years, but the number of plots with native perennial grasses increased (Table 1). In 2008, the most common natives were shrub seedlings, but the most common group in 2012 was perennial grasses. All of the shrub species recorded in 2008 were still present in 2012 and the number of shrub species found within the Burned, Fireline increased from three to four. Overall, native species recovery was positive with an increase in native species relative cover and no significant change in native species richness.

Sites Within Year

The three sites (Burned, Fireline, Burned, No Fireline, and No Burned, No Fireline) differed significantly in community relative cover composition (Pillai's trace; $F_{2,27}$ = 44; P < 0.0001). The No Burned, No Fireline site had lower relative cover and density of *C. melitensis* and higher relative cover of annual grasses than both the Burned, Fireline site and the Burned, No Fireline site (Table 3, Fig. 1). The Burned, Fireline had higher percent cover of both rock and bare ground than either of the other two sites. The percent cover of litter was significantly higher in the Burned, No Fireline site than the Burned, Fireline site, but not different from the No Burned, No Fireline site (Table 3). There was no difference among the sites in relative cover of natives or in native species richness.

All of the native species in the Burned, Fireline were perennials, with four shrub species and one perennial grass species. The native species in the Burned, No Fireline site were mostly annual forbs, with one perennial grass, one geophyte, and no shrubs. In the No Burned, No Fireline site, the natives included one annual forb species, one shrub species, and one perennial grass (Table 1).

Discussion

Four years after the disturbances of fire and bulldozing, the mean relative cover of *Centaurea melitensis* decreased significantly, from 72% to 28%, within the Burned, Fireline. In contrast, the cover of annual grasses increased in four years from almost zero to a mean cover of 6%. Litter also increased significantly, from a mean cover of 10% in 2008 to 29% in 2012. Despite the decrease in relative cover of *C. melitensis*, the density remained the same. The same number of individuals germinated and survived, but they were smaller in size. This could have been due to the reduction in water availability in 2012 compared to 2008, or to competition with annual grasses that were not present in 2008. This suggests that even after severe disturbances such as fire and bulldozing that reduce the cover of annual grasses, these grasses can quickly regain dominance and displace annual forbs.

The differences in the three sites in 2012 were most dramatic in the relative cover and frequency of *C. melitensis*. While both of the Burned sites had more than 25% cover and 85% frequency of

TABLE 3. SEVEN LINEAR REGRESSION MODELS FOR THE EFFECT OF YEAR WITHIN THE BURNED, FIRELINE ON EACH OF THE FOLLOWING VARIABLES: *C. melitensis* DENSITY, THE RELATIVE COVER OF *C. melitensis*, ANNUAL GRASSES, NONNATIVE PLANTS, NATIVE PLANTS, RELATIVE NATIVE RICHNESS, AND THE PERCENT COVER OF LITTER, ROCK, AND BARE GROUND. The coefficients are predicted values for each year. The constant is the intercept. The reference year is 2008. *$P < 0.001$.

Source	Coefficient	t	P
Relative cover of *C. melitensis*			
Year	−0.547	−5.86	*
Constant	1.066	16.13	*
Relative cover of annual grass			
Year	0.5	8.35	*
Constant	0.017	0.41	0.689
Relative cover of native plants			
Year	0.347	2.84	0.011
Constant	0.228	2.65	0.016
Relative native richness			
Year	−0.018	−0.14	0.889
Constant	0.463	5.13	*
Percent cover of rock			
Year	−0.082	−2	0.061
Constant	0.185	6.38	*
Percent cover of litter			
Year	0.235	3.59	0.002
Constant	0.318	6.87	*
Percent cover of bare ground			
Year	−0.05	−0.51	0.618
Constant	0.667	9.54	*

C. melitensis, the 2012 No Burned, No Fireline site had only 5% cover and 30% frequency. This suggests that the disturbance caused by fire, regardless of the additional clearing by bulldozer, opens colonization sites sufficiently for *C. melitensis* to establish. The increased frequency and cover of annual grasses in the Burned, Fireline site after four years suggests that propagules from nearby unburned patches of annual grass colonize cleared sites over time. The lower cover of *C. melitensis* in the No Burned, No Fireline site may be linked to the increase in annual grass cover and associated litter over time, as their relative covers seem to have a somewhat inverse relationship. Once seeds are present, annual grasses germinate and grow tall earlier in the season than *C. melitensis*, possibly blocking out light and preempting germination potential. Litter accumulation may also suppress germination by limiting light and changing the temperature and moisture availability on the soil surface (Carson and Peterson 1990).

Of the three sites sampled in 2012, the Burned, Fireline had the lowest relative cover of annual grasses and the highest relative cover of *C. melitensis*. This site also had the lowest nonnative relative cover and the highest native relative cover. This may be related to the depth of the seed banks of annual grasses and *C. melitensis*. Smaller seeds are generally shallower in the soil than heavier seeded species, and thus more vulnerable to mortality from fire (Bond et al. 1999). If heavier, more compact *C. melitensis* seeds are buried deeper in the soil, while lighter grass seeds stay nearer the soil surface, then both the fire intensity and the depth of the bulldozer blade might have been factors in the reduction of annual grasses and the persistence of *C. melitensis*. High intensity, warm-season fires can kill annual grass seeds on the surface of the soil and increase the cover of native species (Meyer and Schiffman 1999). Furthermore, the bulldozer might have cleared surface seeds, exposing the deeper *C. melitensis* seeds to the surface. Alternatively, clearing the litter may have been the more important effect of bulldozing and fire. With barriers to germination removed, *C. melitensis* and native seeds in the seed bank would have had an opportunity to recruit. The disturbances of fire and bulldozing might reduce annual grasses and recover forbs and shrubs in the short term as long as the seed bank is deep enough and remains intact.

Woody plant canopy closure (i.e., native shrubs) has been shown to be the most important direct factor in explaining alien plant dominance in southern California chaparral and sage scrub sites within five years after fire (Keeley et al. 2005). The only site with substantial woody plant recruits four years after fire was the Burned, Fireline, with no shrubs in the Burned, No Fireline site, and the No Burned, No Fireline site supporting only a few small individuals of one shrub species, *Hazardia squarrosa* (Hook. & Arn.) Greene. In 2008, the shrubs recorded in the Burned, Fireline were seedlings, as the soil surface had been graded, removing all mature shrubs that might have been present. Four years after the fire, shrubs growing in the Burned, Fireline were still relatively small, and annual plant cover was high, suggesting that none of the shrubs in the Burned, Fireline were large enough to close the canopy sufficiently to shade out annual plants.

Fire frequency is an important determinant of the relative success of native versus nonnative species in chaparral. In sites that burn at intermediate fire frequencies, total species diversity is typically highest in the first few years following fire (Keeley and Fotheringham 2003). In sites that have burned at high frequency, nonnative annuals dominate after fire, but in sites that have not burned for several decades, native annuals dominate after fire (Haidinger and Keeley 1993). At Sedgwick Reserve fire has been absent for at least 100 yr. However, in the first four years after a fire, nonnative annuals dominated. Perhaps

the disturbance from past grazing has been a factor in determining the present composition of the community and the high relative cover of nonnative species. Due to sampling design limitations, our results must be interpreted with caution. However, our data can be useful to management of disturbed areas. The results indicate that in these sites, fire promoted native species diversity, and the Burned, Fireline had the most native perennials. Multi-year monitoring of the community is important to assess the fate of early colonizers after such disturbances. The results of our study suggest that the recruitment of *C. melitensis*, along with some native species, is promoted by fire. Over time, its abundance is limited by competition, not from woody native species, but from another group of nonnative invaders, Mediterranean annual grasses.

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SENEGALIA BERLANDIERI, S. CRASSIFOLIA, AND S. RENIFORMIS HYBRIDS (FABACEAE: MIMOSOIDEAE) IN CENTRAL AND NORTHERN MEXICO

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Abstract

Principal component analyses (PCA) and principal coordinate analyses (PCoA) suggest that *Senegalia berlandieri* (Benth.) Britton & Rose hybridizes with *S. crassifolia* (A. Gray) Britton & Rose, the resulting hybrid being *S.* × *anisophylla* (S. Watson) Britton & Rose. This uncommon hybrid is reported from the states of Coahuila, Durango, and San Luis Potosí, Mexico. In addition, PCA and PCoA suggest that *S. berlandieri* hybridizes with *S. reniformis* (Benth.) Britton & Rose. The resulting hybrid, *S. berlandieri* × *reniformis*, also is infrequent, being restricted to the state of Querétaro, Mexico. The morphological features of both probable F_1-hybrids are highly variable. The backcrosses to each respective parent were also examined. The hybrid between *S. berlandieri* and *S. reniformis* (**Senegalia** × **zamudii** Seigler, Ebinger, & Glass) is described.

Key Words: Fabaceae, Mimosoideae, principal component analysis, *Senegalia*.

Among New World species of the genus *Senegalia*, which consists of 110 species in tropical and subtropical areas ranging from the southwestern United States south to Argentina (Seigler et al. 2006), hybrids are uncommon. Those hybrids that we have encountered in our monographic study of this genus mostly involve species apparently related to *S. berlandieri* (Benth.) Britton & Rose and are restricted to central and northern Mexico and the adjacent southwestern United States (Britton and Rose 1928; Turner 1959; Correll and Johnston 1970; Johnston 1975; Maslin and Stirton 1997; Glass and Seigler 2006; Seigler et al. 2006; Seigler et al. 2012). The present study was undertaken to examine the morphological differences and affinities of hybrids and hybrid populations involving *S. berlandieri* and the related species *S. crassifolia* (A. Gray) Britton & Rose and *S. reniformis* (Benth.) Britton & Rose in central and northern Mexico. We consider *Acacia sororia* Standl., Contr. U.S. Natl. Herb. 20:186. 1919 (=*Senegalia sororia* [Standl.] Britton & Rose, N. Amer. Fl. 23:108. 1928) to be a synonym of *S. reniformis*.

Materials and Methods

Two separate analyses were conducted: one including *Senegalia berlandieri*, *S. crassifolia*, and their probable hybrid [*S.* × *anisophylla* (S. Watson) Britton & Rose]; and another including *S. berlandieri*, *S. reniformis*, and their apparent hybrid (*S. berlandieri* × *S. reniformis*). These analyses were based on herbarium specimens of the putative parents and hybrids from central and northern Mexico (Appendix 1). Specimens of these species and their hybrids collected by the authors and from several herbaria were separated into groups based on overall morphological similarity, scored for 10 characters (Appendix 2), and the data analyzed by principal component analysis (PCA) and principal coordinate analysis (PCoA). Three or more measurements were made for each continuous character of each specimen and plotted to confirm that gaps in the data exist.

A PCA to identify groupings of the specimens examined was carried out. For these analyses, the data were first standardized and a correlation matrix, eigenvalues, and eigenvectors were calculated using NTSYS-pc verson 2.1 (Rohlf 2000). Eigenvectors were scaled by the square root of λ. The axes were rotated and the resulting loading values graphically represented as both two- and three-dimensional plots (Figs. 1 and 2).

To carry out the PCoA, Gower's resemblance coefficients were calculated (Legendre and Legendre 1983; Podani 1999) with Program Gower6 (BASIC software for calculation of Gower's coefficients; made available by T. A. Dickinson, Royal Ontario Museum). The nature of each character was designated as binary, multistate, or quantitative descriptors, and all characters were weighted equally. The data matrix was transformed by the DCENTER algorithm using distances squared and eigenvectors and eigenvalues calculated with NTSYS-pc verson 2.1 (Rohlf

Fig. 1. Three-dimensional plot for the principal component analysis using 10 characters (Appendix 2) of 16 specimens of *Senegalia berlandieri* (B01–B16), 16 specimens of *S. crassifolia* (C01–C16), and 16 specimens of probable hybrids (*S.* × *anisophylla*) (A01–A16).

2000). Eigenvectors were scaled by the square root of λ. The resulting loading values were graphically represented as both two- and three-dimensional plots.

Results

Senegalia berlandieri and *S. crassifolia*

A PCA and a PCoA based on Gower's similarity coefficients using 10 characters (Appendix 2) proved to be similar. Specimens of *S. berlandieri* (16), *S. crassifolia* (16), and *S.* × *anisophylla* (16) listed in Appendix 1 were used in these analyses. In the PCA, the first three principal components accounted for 96% of the

total variance. Leaflet pairs/pinna, pinna pairs/ leaf, and leaflet length in mm (characters 5, 3, and 7) were most important for determining the component score of the first axis; leaflet shape, leaflet width in mm, and leaflet venation (characters 6, 8, and 9) were most important for determining the second axis. The species used in this analyses represented distinct groupings in both the PCA and PCoA. The results show that the parental species were well separated from each other, and that the putative hybrids were spatially located between the respective parental types. Putative backcrossed individuals to each of the parental species were positioned between each parental species and the probable F_1-hybrids (Fig. 1).
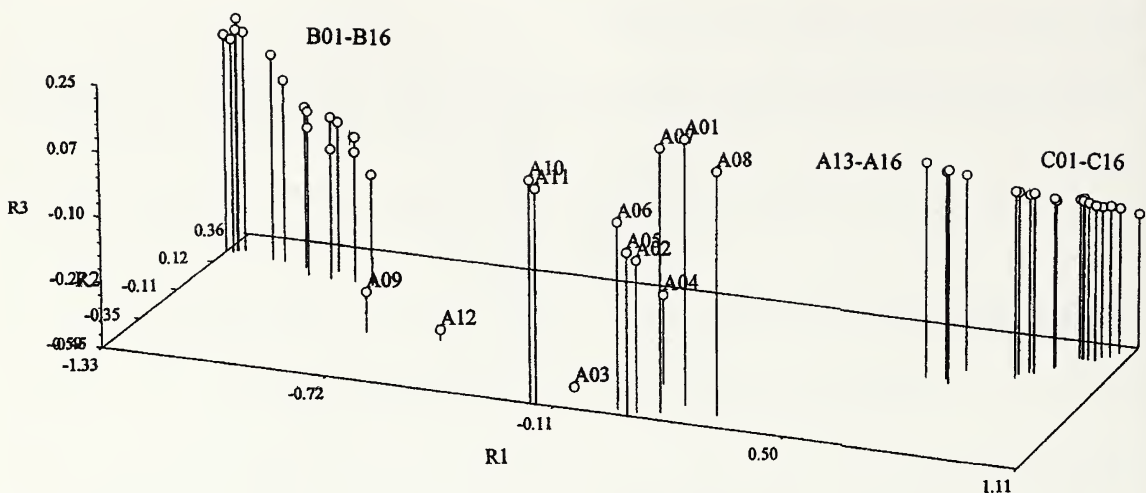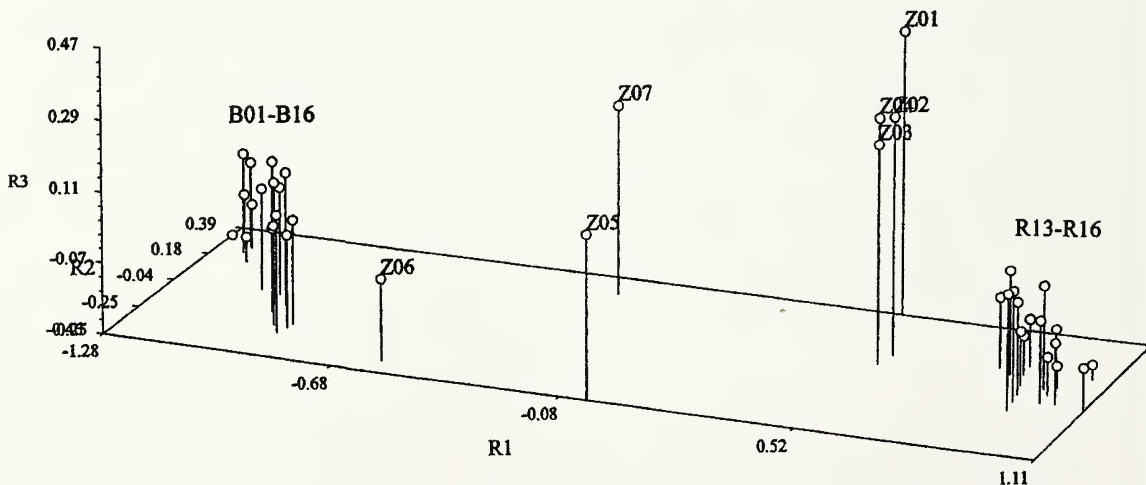

Fig. 2. Three-dimensional plot for the principal component analysis using 10 characters (Appendix 2) of 16 specimens of *Senegalia berlandieri* (B01–B16), 16 specimens of *S. reniformis* (R01–R16), and 7 specimens of probable hybrids (*S.* × *zamudii*) (Z01–Z06).

Senegalia berlandieri and *S. reniformis*

A PCA and a PCoA based on Gower's similarity coefficients proved to be similar. All specimens of *S. berlandieri* (16), *S. reniformis* (16), and *S. berlandieri* × *reniformis* (7) listed in Appendix 1 were used in these analyses. In the PCA, the first three principal components accounted for 96% of the total variance. Leaflet length in mm, leaflet shape, and leaflet pairs/pinna (characters 7, 6, and 5) were most important for determining the component score of the first axis; leaf length in mm, pinna length in mm, and leaflet venation (characters 2, 4, and 9) were most important for determining the second axis. The species used in these analyses represented distinct groupings in both the PCA and PCoA. The results indicate that the parental species were well separated from each other and the F_1-hybrid spatially located between them. Apparent backcrossed individuals were present between each parental species and probable F_1-hybrids, respectively (Fig. 2).

DISCUSSION

Senegalia berlandieri and *S. crassifolia*

Of these taxa, *Senegalia berlandieri* has the most extensive distribution, occurring in south central and southern Texas, south into the states of Chihuahua, Coahuila, Durango, Guanajuato, Hidalgo, Nuevo León, Querétaro, San Luis Potosí, Tamaulipas, and Zacatecas, Mexico. *Senegalia crassifolia*, in contrast, has a more restricted range, occurring in the states of Coahuila, Durango, San Luis Potosí, Tamaulipas, and Zacatecas, Mexico, and is considered to have a conservation status of "vulnerable" (Rico Arce 2007). The hybrid, *S.* × *anisophylla*, is restricted to areas where the parental species overlap in distribution in Coahuila, Durango, San Luis Potosí, and Zacatecas, Mexico, and has been considered to have a conservation status of "vulnerable" (Rico Arce and Griffiths 2002) although recognized as a hybrid between *S. berlandieri* and *S. crassifolia* (Johnston 1975).

Senegalia × *anisophylla* can easily be separated from both *S. berlandieri* and *S. crassifolia* using some of the characteristics listed in Appendix 2. The most obvious and commonly used characteristics include: leaves with 1 pinna pair in *S. crassifolia*, 2–4 pairs in *S.* × *anisophylla*, and 7–19 pairs in *S. berlandieri*; and leaflets 1–rarely 2 pairs/pinna in *S. crassifolia*, 5–9 pairs/pinna in *S.* × *anisophylla*, and 30 or more pairs in *S. berlandieri*. Occasional backcrossed individuals that are somewhat more difficult to identify were encountered. Two specimens (A09, A12) probably represent backcrosses of *S.* × *anisophylla* to *S. berlandieri* (Fig. 1). Backcrosses of this type

differ from the F_1-hybrid in that they have 5–7 pinna pairs per leaf, 12–25 leaflet pairs per pinna, and oblong leaflets. Apparent backcrosses between *S.* × *anisophylla* and the other parental type, *S. crassifolia* (A13, A14, A15, A16), differ from the F_1-hybrid by having 2–3 pinna pairs per leaf, 2–4 leaflet pairs per pinna, and large oval, orbicular, to obovate leaflets, some exceeding 25 mm in length. *Senegalia crassifolia* specimens, in contrast, have leaves with 1 pinna pair and usually 1 pair of leaflets/pinna.

Senegalia berlandieri and *S. reniformis*

Senegalia reniformis has a quite restricted range; we have only seen specimens from the states of Hidalgo and Querétaro, Mexico (Glass and Seigler 2006). The hybrid, *S. berlandieri* × *S. reniformis,* has only been found in the state of Querétaro, Mexico, where the authors have collected specimens of the hybrid in locations where one or both parents were present in the same area.

Senegalia berlandieri × *S. reniformis* is easily separated from both *S. berlandieri* and *S. reniformis*. The most obvious characteristic is that there are 1 or rarely 2 pairs of leaflets/pinna in *S. reniformis*, 3–16 pairs/pinna in the hybrid, and 30 or more pairs in *S. berlandieri*. Although useful for recognition when available, inflorescence structure was not used in the analyses as few specimens were in flower. *Senegalia berlandieri* has globose inflorescences, and *S. reniformis* has spicate inflorescences, whereas those of the hybrid are short spicate and less than twice as long as wide. Most specimens of **S.** × **zamudii** Seigler, Ebinger, & Glass were collected from areas where *S. berlandieri* and *S. reniformis* occur sympatrically. In Figure 2, two specimens (Z05, Z07) probably represent F_1-hybrids. These specimens have oblong leaflets that average 10 mm in length with 4–10 leaflet pairs/pinna. Occasionally, apparent backcrossed individuals are encountered. Specimen Z06 between the F_1-hybrid and *S. berlandieri* has smaller leaflets that are similar to those of *S. berlandieri* and up to 15 pairs of leaflets/pinna. Apparent backcrosses between the F_1-hybrid and *S. reniformis* (Z01, Z02, Z03, Z04) differ from the F_1-hybrid by having 3–4 leaflet pairs per pinna, and large oval, orbicular, to obovate leaflets, some leaflets exceeding 15 mm in length (Fig. 2). *Senegalia reniformis* specimens, in contrast, have leaves with 1–2 pairs of leaflets/pinna. Based on these specimens, a proposed new hybrid is described. This hybrid is named after Dr. Sergio Zamudio Ruiz (Instituto de Biología, Facultad de Ciencias, Universidad Nacional Autónoma de México, presently at the Centro Regional del Bajío, Instituto de Ecología, Pátzcuaro, Michoacán), who has collected specimens of this new species and published extensively on the flora of this area of Mexico.
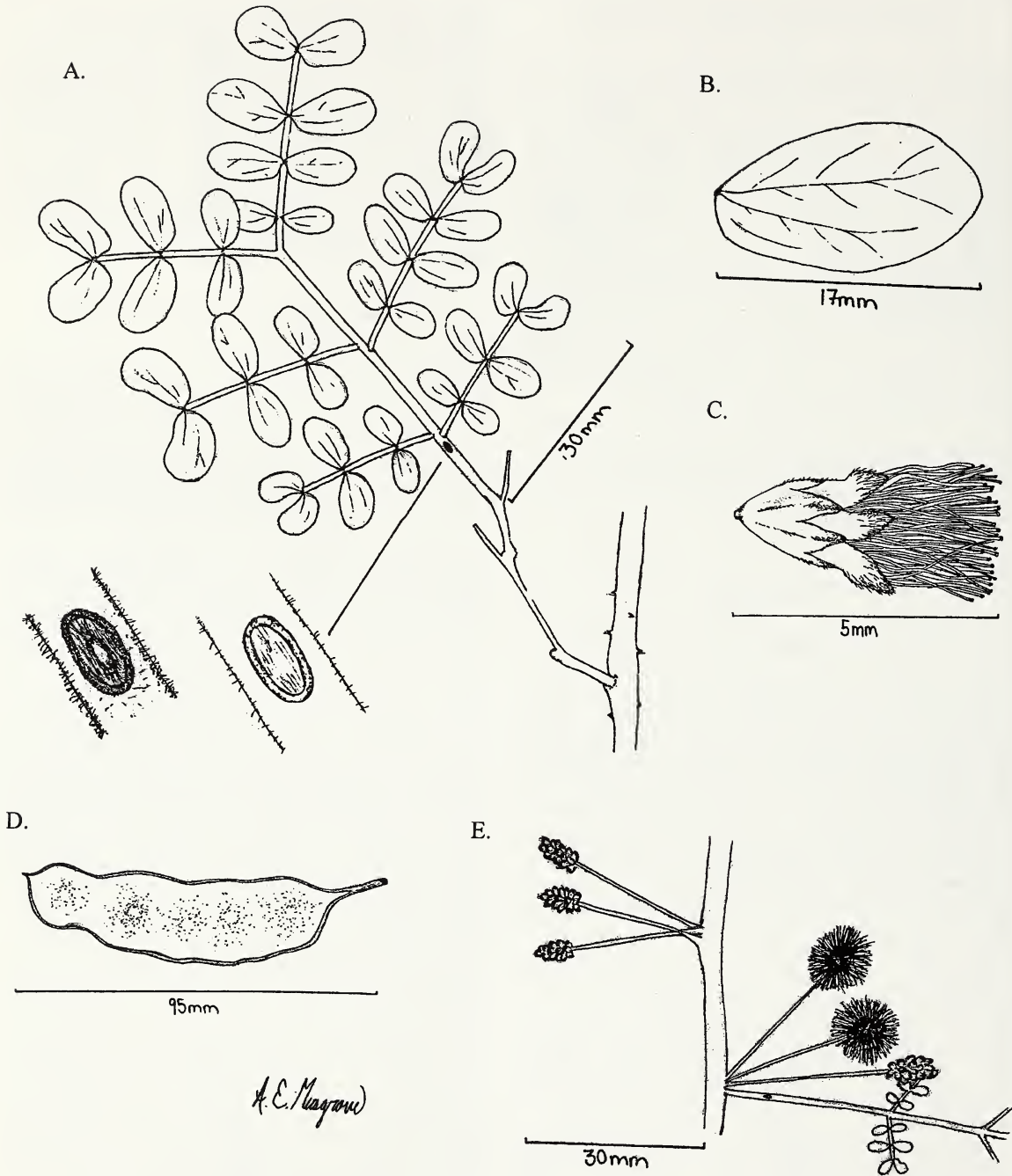
Fig. 3. *Senegalia zamudii* Seigler, Ebinger & Glass, A: Leaf with petiolar glands (*S. Zamudio 247858*). B: Leaflet (adaxial surface) (*S. Zamudio 247858*). C: Flower (*S. Zamudio 994930*). D: Fruit (*S. Zamudio 247858*). E. Clustered inflorescences with associated leaves and prickles (*S. Zamudio 247858*).

TAXONOMIC TREATMENT

Senegalia × zamudii Seigler, Ebinger, & Glass, nothomorph nov. (Fig. 3).—TYPE: MEXICO, Querétaro, Cañón del Río Extorax entre El Platano y El Timbre, alt. 900 m, 12 Dec 1999, *S. Zamudio, E. Esparza & E. Zamudio 11241* (holotype: MEXU, photo ILL).

Senegalia × zamudii Seigler, Ebinger & Glass differs from other *Senegalia* species by shrubby habit, leaf size (40–90 mm), oval to reniform stipules, a solitary orbicular petiolar gland (0.8–2.5 mm long) usually located between the leaflets of the lowermost pinna pair, 2 to 6 pairs of pinnae per leaf, 3 to 16 pairs of leaflets per pinna, inflorescence a spike 10–20 mm long, peduncles

15–30 mm long, and yellow to pink sessile flowers.

Shrub or small **tree** to 4 m tall. **Bark** dark brown, rough; twigs maroon to dark reddish brown to dark brown, straight, terete, glabrous to puberulent; short shoots absent; prickles usually reddish brown, flattened, straight to slightly curved, woody, 1–6 × 1–5 mm at the base, usually puberulent, persistent, scattered along the twig, commonly absent. **Leaves** alternate, 40–90 mm long; stipules green, oval to reniform, symmetrical, flattened, straight, herbaceous, 4–10 × 4–12 mm near the middle, glabrous, deciduous; petioles terete to shallowly grooved adaxially, 6–30 mm long, glabrous to puberulent; petiolar gland solitary, usually located between the lowest pinna pair, sessile, orbicular, 0.8–2.5 mm long, apex depressed, glabrous; rachis shallowly grooved adaxially, 10–35 mm long, mostly lacking glands; pinnae 2–6 pairs per leaf, 20–60 mm long, 10–30 mm between pinna pairs; paraphyllidia 0.3–0.8 mm long, commonly absent; petiolule 3–15 mm long; leaflets 3–16 pairs per pinna, opposite, 1–10 mm between leaflet pairs, oblong to obovate to reniform, 8–25 × 2–18 mm, glabrous to puberulent on both surfaces, lateral veins mostly obvious, 1–5 veins from the base, base oblique and usually obtuse, margins not ciliate, apex obtuse, midvein subcentral. **Inflorescence** a loosely 35- to 60-flowered cylindrical spike, 10–20 × 11–15 mm wide, usually 1–2 from the leaf axils or in terminal racemose clusters, the main axis to 150 mm long; peduncles 15–30 × 0.4–0.7 mm thick, puberulent; receptacle not enlarged; involucre a single small bract located on the upper half of the peduncle, deciduous; floral bracts linear, 0.9–1.5 mm long, ciliate, early deciduous. **Flowers** sessile, yellow to pink; calyx 5-lobed, 1.7–2.3 mm long, puberulent; corolla 5-lobed, 2.3–3.1 mm long, puberulent, lobes one-quarter the length of the corolla; stamen filaments 4.5–6.5 mm long, distinct; anther glands absent; ovary glabrous, on a stipe to 0.6 mm long. **Legumes** tan to light brown, straight to slightly curved, elliptic in cross section, not constricted between the seeds, oblong, 60–100 × 18–28 mm wide, coriaceous, lightly reticulately striated, densely puberulent, eglandular, dehiscent along both sutures; stipe 7–20 mm long; apex obtuse, short beaked. **Seeds** uniseriate, no pulp, dark brown, orbicular to oblong, somewhat flattened, 10–13 × 6–9 mm, smooth to minutely pitted; pleurogram U-shaped, 2–3 mm across. **Flowers:** October–January. **Distribution:** A species of xeric scrublands and tropical low deciduous forests on calcareous soil at an elevation of 1000–2000 m in the state of Querétaro, Mexico.

Specimens Examined

MEXICO. QUERÉTARO. 1 km E of Peña-miller, alt. 1160 m, *C. Glass, G. Glass & O. Téllez 380* (ILL); 6 km N of jct. Hwy. 120 to Jalpán and road to Peñamiller, 29 Jan 2004, *D. S. Seigler, C. Céspedes & J. Seigler 15864B* (EIU, ILL); 6 km N of jct. Hwy. 120 to Jalpán and road to Peñamiller, 29 Jan 2004, *D. S. Seigler, C. Céspedes & J. Seigler 15865* (EIU, ILL); 6 km N of jct. Hwy. 120 to Jalpán and road to Peñamiller, 29 Jan 2004, *D. S. Seigler, C. Céspedes & J. Seigler 15866* (EIU, ILL); pasture, 4.8 km N of San Pablo, 3 Jun 1991, *D. S. Seigler, J. E. Ebinger, H. Clarke & K. Readel 13662* (EIU, ILL); Brecha San Pablo Tolimán-Higuerillas (km 10), alt. 2000 m, 12 Jul 1977, *S. Zamudio 298* (MEXU); Brecha Peñamiller-Aldama, 5 km al Peñamiller, alt. 1580 m, 7 Oct 1977, *S. Zamudio 699* (MEXU).

Key to the Species and Hybrids Examined

(The differences between *Senegalia zamudii* and the parental species are reviewed in the Discussion.)

1. Most leaves with 7–15 pinna pairs; most pinnae with 30–55 pairs of leaflets . . . . *Senegalia berlandieri*
1′ Most leaves with fewer than 7 pinna pairs; pinnae with 1–25 leaflet pair(s)
  2. Leaflets large, many more than 20 mm long; pinnae with 1 (rarely 2) leaflet pair(s)
    3. Leaves with 1 pinna pair; inflorescence globose . . . . *Senegalia crassifolia*
    3′ Leaves with 1–4 pinna pairs; inflorescence a spike. . . . . . . *Senegalia reniformis*
  2′ Leaflets mostly smaller, most less than 20 mm long; pinnae with 3 or more leaflet pairs.
    4. Inflorescence globose . . . .*Senegalia* × *anisophylla*
    4′ Inflorescence a short spike about 2 × longer than wide . . . . *Senegalia* × *zamudii*

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APPENDIX 1

SPECIMENS USED IN SCORED PRINCIPAL COMPONENT (PCA) AND PRINCIPAL COORDINATE (PCoA) ANALYSES

Senegalia × *anisophylla*: MEXICO. COAHUILA: 11 km N of Ahuichila, Cañón de Ahuichila, alt. 1250–1500 m, 15 Jun 1972, *F. Chiang, T. L. Wendt & M. C. Johnston 7812* (NY); Sierra de Jimulco, 3 km N of Mina San José, 8 km NE of Estación Otto, alt. 1800–3138 m, 27 Sep 1972, *F. Chiang, T. L.Wendt & M. C. Johnston 9539* (NY); Sierra de Jimulco, 3 km N of Mina San José, 8 km NE of Estación Otto, alt. 1800–3138 m, 27 Sep 1972, *F. Chiang, T. L.Wendt & M. C. Johnston 9539a* (NY); 5 km SW of La Rosita (San Miguel el Alto), alt. 1300 m, 29 Jun 1973, *M. C. Johnston, T. L. Wendt & F. Chiang 11510* (MO); 5 km SW of La Rosita (San Miguel el Alto), alt. 1300 m, 29 Jun 1973, *M. C. Johnston, T. L. Wendt & F. Chiang C. 11511* (MO); Mountains, cañones near Jimulco, 14 May 1885, *C. G. Pringle 163* (NY); Sierra de Parras en el Ejido Chupaderos, alt. 1500 m, 28 May 1981, *A. Rodríguez & M. A. Carranza s.n.* (MU). DURANGO: 8 mi N of Cuencamé, 27 Jun 1977, *J. D. Dwyer 14253A* (MO); Estación Microndas "Sapioris," about 30 km SW of Gómez Palacio on road toward Durango, alt. 1400–1500 m, 25 Mar 1973, *M. C. Johnston, T. L. Wendt & F. Chiang C. 10397* (MO); Estación Microndas "Sapioris," about 30 km SW of Gómez Palacio on road toward Durango, alt. 1400–1500 m, 25 Mar 1973, *M. C. Johnston, T. L. Wendt, F. Chiang C. & J. Henrickson 10398* (MO); just S and SE of Estación Microondas "Sapioris," about 20 km NW of Estación Chocolate, alt. 1450–1500 m, 13–14 Aug 1973, *M. C. Johnston, T. L. Wendt & F. Chiang C. 12200* (MO). SAN LUIS POTOSÍ: Dirt road to Los Anoles near border of Tamaulipas, 9 km S of El Huisache, alt. 1450 m, 3 Jun 1997, *C. Glass & G. Glass 428* (ILL); dirt road to Los Anoles near border of Tamaulipas, 9 km S of El Huisache, alt. 1450 m, 3 Jun 1997, *C. Glass & G. Glass 430* (ILL); 2 km SE of Huizache junction and about 5 km WSW of El Huizache, alt. 1400 m, 19 May 1973, *M. C. Johnston, T. L. Wendt & F. Chiang C. 11119* (MO); 2 km airline SE of Huizache Junction, alt. 1400 m, 19 May 1973, *M. C. Johnston, T. L. Wendt & F. Chiang C. 11120* (MO); E de Núñez, km 84 carretera San Luis-A. Morelos, alt. 1600 m, *J. Rzedowski 5548* (F).

Senegalia berlandieri: MEXICO. COAHUILA: Sierra Mojada Mountains, 20 Apr 1892, *M. E. Jones 195* (DS); Jimulco, 9 Apr 1886, *C. G. Pringle 867* (MIN); Ejido el Capulín, 10 km al SW de Parras de la Fte. Mpio. Parras, alt. 2050 m, 6 Mar 1983, *A. Rodríguez, M. A. Carranza & A. Orta 81* (ILL). GUANAJUATO: 10 km al SE de Xichú, alt. 1000 m, 4 Feb 1997, *E. Pérez & S. Zamudio 3561* (MEXU). NUEVO LEÓN: Road to Galeana from Linares, alt. 630 m, 4 Jun 1997, *C. Glass & G. Glass 435* (ILL). QUERÉTARO: El Platano, alt. 1000 m, 30 Nov 1992, *R. Fernández N. 4839* (ASU); El Carnicero, alt. 1380 m, *E. González 1439* (MEXU); below lookout on road to Jalpán (second pull-off), 10 Jun 2005, *D. S. Seigler, B. R. Maslin & C. Céspedes 16066* (ILL). SAN LUIS POTOSÍ: 17 km W of Tamuín, 21 Dec 1990, *D. S. Seigler, J. E. Ebinger, H. Clarke & C. Gratton 13226* (ILL). TAMAULIPAS: Rancho Las Aguilas, Carretera Soto la Marina–Aldama, 10 Mar 1992, *J. L. Mora-López 141* (MEXU); Victoria, alt. 320 m, 1 Feb–9 Apr 1907, *E. J. Palmer 30* (F); vicinity of Victoria, alt. 320 m, 1 Feb–9 Apr 1907, *E. J. Palmer 124* (MO); 4.5 mi SW of Ciudad Victoria along road to Jaumave, alt. 1450 ft., 6 Apr 1955, *I. L. Wiggins 13355* (SD). UNITED STATES. TEXAS. Hidalgo Co: Santa Ana National Wildlife Refuge, 14 Apr 1977, *J. C. Solomon 2746* (MO). Val Verde Co.: 5 mi W of Langtry, 13 Apr 1963, *A. C. Koelling 837* (ILL); 3 mi W of Langtry, 1 Apr 1954, *O. E. Sperry 2970* (ILL).

Senegalia crassifolia: MEXICO. COAHUILA: 30 km al poniente de Parras, brecha Parras-Viesca, Dec 1993, *M. A. Carranza, J. Luna & S. Comparán 2006* (TEX); 12 km N of Ahuichila, Cañón de Ahuichila, alt. 1300 m, 15 Jun 1972, *F. Chiang, T. L. Wendt & M. C. Johnston 7808* (MO); NE edge of Cerro Bola, alt. 1150 m, 6 Jul 1972, *F. Chiang, T. L. Wendt & M. C. Johnston 8286* (MO); Sierra de Jimulco and up to 3 km N of Mina San Jose, alt. 1800–3138 m, 27 Sep 1972, *F. Chiang, T. L. Wendt & M. C. Johnston 9538* (MO); 18 km S de Parras de la Fuente, alt. 1400 m, 16 Sep 1982, *A. Orta, M. A. Carranza, and A. Rodríguez 64* (TEX); Torreón, 13–20 Oct 1898, *E. J. Palmer 474* (MO); hills near Jimulco, Apr–May 1885, *C. G. Pringle 49* (WIS); Hwy. 40 at roads to San Pedro and Matamoros, 14 Jul 1975, *D. S. Seigler & G. Holstein 9233* (ILL); 37 mi W of Paila on Hwy. 40, 28 May 1983, *D. S. Seigler, J. Kramer & E. Carreira 12014* (ILL); mountain pass of La Peña, Nov 1852, *G. Thurber 829* (MO). DURANGO: Estación Microndas "Sapioris" about 30 km SW of Gómez Palacio on hwy. toward Durango, alt. 1400–1500 m, 25 Mar 1973, *M. C. Johnston, T. L. Wendt & F. Chiang*

10406 (MO); 5.1 mi S of El Refugio, alt. 4000 ft, 21 Jul 1977, *E. Lehto, D. J. Pinkava, B. Parfitt & T. Reeves 21670* (NY). SAN LUIS POTOSÍ: 3 mi SE of Presa de Guadalupe, 1250 m, 24 Nov 1962, *R. Moran 10019* (SD); 1 km E de El Huizache, alt. 1310 m, 22 Jul 1983, *L. Rico & J. L. Contreras s.n.* (CM). TAMAULIPAS: SW of Tula, alt. 4400 ft, 26 Nov 1966, *H. D. Ripley & R. C. Barneby 14770* (NY). ZACATECAS: Sierra del Yeso, almost due W of La Presa de los Angeles, alt. 1400–1500 m, 30 Jun 1973, *M. C. Johnston, T. L. Wendt & F. Chiang C. 11532* (MO).

Senegalia reniformis: MEXICO. QUERÉTARO: Hwy. 120, S of Jalpán, 1 km E of Peñamiller, alt. 1160 m, 23 May 1997, *C. E. Glass, G. Glass, J. T. Carreón & J. Ramírez 382* (ILL); rocky north facing slope N of Cerro Gordo, alt. 1860 m, 23 May 1997, *C. E. Glass, G. Glass, J. T. Carreón & J. Ramírez 387* (EIU, ILL); rocky north facing slope N of Cerro Gordo, alt. 1860 m, 23 May 1997, *C. E. Glass, G. Glass, J. T. Carreón & J. Ramírez 389* (EIU, ILL); Hwy. 120 N of Higuerillas, km marker 92, *C. Glass, G. Glass, J. T. Carreón & J. O. B. Ramírez 397* (ILL); 7 km S of Peña Blanca on Hwy. 120, 29 Jan 2004, *D. S. Seigler, C. Céspedes & J. Seigler 15861* (EIU, ILL); 6 km N of jct. Hwy 120 to Jalpán and road to Peñamiller, 29 Jan 2004, *D. S. Seigler, C. Céspedes & J. Seigler 15862* (EIU, ILL); 6 km N of jct. Hwy 120 to Jalpán and road to Peñamiller, 29 Jan 2004, *D. S. Seigler, C. Céspedes & J. Seigler 15864A* (ILL); N of jct. of road to Peñamiller on Mexico Hwy. 120, the road to Jalpán, 3 Jun 1991, *D. S. Seigler, J. Ebinger, H. Clarke & K. Readel 13669* (EIU, ILL); 4 km N of jct. of road to Peñamiller on Hwy. 120, the road to Jalpán, *D. S. Seigler, J. Ebinger, H. Clarke & K. Readel 13675* (EIU, ILL); 4 mi N jct. of road to Peñamiller on Hwy. 120, road to Jalpán, 3 Jun 1991, *D. S. Seigler, J. Ebinger, H. Clarke & K. Readel 13676* (EIU, ILL); 20 mi N of Vizarrón on Hwy. 120, 10 June 2005, *D. S. Seigler, B. R. Maslin & C. Céspedes 16064* (ILL); below lookout on road to Jalpán (second pull-off), 10 Jun 2005, *D. S. Seigler, B. R. Maslin & C. Céspedes 16067* (ILL); below lookout on road to Jalpán (second pull-off), 10 Jun 2005, *D. S. Seigler, B. R. Maslin & C. Céspedes 16068* (ILL); below lookout on road to Jalpán (second pull-off), 10 Jun 2005, *D. S. Seigler, B. R. Maslin & C. Céspedes 16069* (ILL); 6–7 km al S de Tolimán, 16 May 1978, *S. Zamudio R. 713* (MEXU); 1 km al N de Peñamiller, alt. 1515 m, 25 May 1977, *S. Zamudio R. 2094* (MEXU).

Senegalia × zamudii: Specimens listed under specimens examined after the description of *S. × zamudii.*

APPENDIX 2

CHARACTERS SCORED FOR THE PRINCIPAL COMPONENT ANALYSES (PCA) AND PRINCIPAL COORDINATE ANALYSES (PCoA) OF THE *SENEGALIA BERLANDIERI*/*S. CRASSIFOLIA* COMPLEX, AND THE *S. BERLANDIERI*/*S. RENIFORMIS* COMPLEX

1. Petiole gland position (Glp) 1 = near middle of petiole, 2 = base of first pinna pair.
2. Leaf length in mm (Lfl).
3. Pinna pairs/leaf (Pip).
4. Pinna length in mm (Pil).
5. Leaflets pairs/pinna (Len) 1 = 30–55, 2 = 3–29, 3 = 1–2.
6. Leaflet shape (Les) 1 = linear to oblong, 2 = obovate, oblanceolate to reniform.
7. Leaflet length in mm (Lel).
8. Leaflet width in mm (Lew).
9. Leaflet venation (Lev) 1 = not obvious, 2 = obvious.
10. Venation arrangement (Ven) 1 = pinnate, 2 = palmate.

GIBBERELLIC ACID INDUCES ASYMBIOTIC GERMINATION OF THE OBLIGATE MYCOHETEROTROPH *PTEROSPORA ANDROMEDEA* (ERICACEAE)

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Abstract

Studies of the Monotropoideae (monotropes; Ericaceae), a monophyletic group of non-photosynthetic, mycoheterotrophic, and often rare or endangered plants, have been limited by the inability to propagate them. Monotropes associate with specific fungal hosts, and the only previously known method of seed germination was induction by host fungi or closely related fungi. In order to overcome very low monotrope seed germination rates and to facilitate further study and conservation efforts, we developed a method using gibberellic acid (GA) to induce asymbiotic germination. *Pterospora andromedea* Nutt. (Monotropoideae, Ericaceae) and *Sarcodes sanguinea* Torr. (Monotropoideae, Ericaceae) seeds from California were exposed to their fungal symbiont or to agarose infused with 0–1 mM GA and then scored for germination. Continuous exposure to 0.5 mM GA for two months induced 75% *P. andromedea* germination, compared to only 21% with its host fungus, *Rhizopogon salebrosus* A.H. Sm. (Basidiomycota). Even short GA exposure (one or three days) significantly enhanced germination (69% and 90%, respectively). The highest germination rate was observed with exposure to 0.5 mM GA for three or 14 d. The closely related *S. sanguinea* required a three-month exposure to GA and even then produced far lower germination rates (~1%). Nevertheless, this is the only known method of inducing monotrope germination without the presence of a specific fungal symbiont. In the case of *P. andromedea*, exogenous GA stimulates germination at rates far higher than that achieved with its fungal symbiont. Application of GA to induce monotrope germination may be used to examine the early stages of mycoheterotroph development, to improve assays for seed viability, and potentially to aid conservation efforts.

Key Words: Gibberellic acid, monotropes, mycoheterotroph, *Pterospora*, *Sarcodes*, seed germination.

Mycoheterotrophic plants are non-photosynthetic parasites of fungi, and they are represented by over 400 species in 87 genera (Leake 1994). Some mycoheterotrophs such as the Monotropoideae are epiparasites that indirectly parasitize surrounding plants through their mycorrhizal fungi in a tripartite symbiosis. In the classical ectomycorrhizal symbiosis, a photosynthetic plant fixes carbon from the atmosphere and trades a portion of its carbon to a fungus growing on its roots in exchange for mineral nutrients. Epiparasites also form associations with mycorrhizal fungi, but these mycoheterotrophs receive carbon from rather than donate carbon to their mycorrhizal fungal partner. Thus, epiparasitic plants reverse the normal flow of carbon found in typical mycorrhizal interactions (Björkman 1960) and represent an extreme in the continuum of plant–fungal interactions within mycorrhizal symbioses (Smith and Read 2008).

The Monotropoideae (Ericaceae, hereafter monotropes) have drawn scientific interest since the birth of mycorrhizal studies (Frank 2004 translation of 1885 paper), and with the advent of molecular techniques, monotropes continue to inspire new lines of investigation (Berch et al. 2005; Merckx et al. 2009; Braukmann and Stefanović 2012; Ogura-Tsujita et al. 2012). Individual monotrope species have been found to be highly specialized on single genera, species groups, or species of ectomycorrhizal fungi (Bidartondo and Bruns 2001, 2002, 2005). The monotropes as well as many other epiparasitic plants are often rare or endangered (Wallace 1975; Wogen and Lippert 1998; Schori 2002; Brown et al. 2003; Lok et al. 2009) and represent uniquely difficult conservation targets due to their dependence on specific host fungi and the autotrophic plants with which their fungi associate.

Our study utilized material from California *Pterospora andromedea* Nutt. populations to investigate seed germination in this monotypic species. *Pterospora andromedea* has a range spanning the continental United States, southern Canada, and Mexico (Wallace 1975). However, this broad range consists of two discontinuous populations. The Eastern population, with a recorded range from southeastern Canada through the northeastern United States, is rare and in many locales endangered (Schori 2002).

The Western population ranges from Mexico north to Canada and east to the Rocky Mountains, and within at least parts of this western range the plant can be locally abundant. Throughout its range, *P. andromedea* associates with host fungi in the genus *Rhizopogon* subgenus *Amylopogon* (Basidiomycota). In the West, *R. salebrosus* A.H. Sm. or *R. arctostaphyli* A.H. Sm. appear to be the primary hosts (Bidartondo and Bruns 2002), and there is a single report with *R. ellenae* A.H. Sm. (Dowie et al. 2011). In eastern North America, Hazard et al. (2011) found that a related, but undescribed, *Rhizopogon* species serves as the host for *P. andromedea*. This eastern species is less common than *Rhizopogon* in western forests and may be limiting the range and frequency of *P. andromedea* in the East (Hazard et al. 2011).

Evolution by angiosperms of diverse mechanisms for maintaining dormancy reflect adaptations to particular environmental conditions (Finch-Savage and Leubner-Metzger 2006). A requirement for the presence of its host fungus is one such adaptation that enables *P. andromedea* to avoid breaking dormancy under unfavorable conditions. *Pterospora andromedea* has inflorescences up to a meter tall and is one of the largest monotropes. However, *P. andromedea* has tiny, dust-like seeds that contain few nutritional resources, and seedlings are unlikely to survive for long without a suitable host fungus (Bakshi 1959; Bruns and Read 2000). Bakshi (1959) failed to germinate seeds under a wide variety of temperature, storage, and nutrient conditions, including planting the seeds in soil collected from the root zone of *P. andromedea* and from soil collected from the root zone of *Picea pungens* Engelm.. He used a tetrazolium method to determine seed viability and reported that no seeds older than nine weeks appeared viable (Bakshi 1959). Using just fungal cultures isolated from the plants, Bruns and Read (2000) discovered that seeds could be induced to germinate at low levels even when substantially older than nine weeks. Then, using a broader sampling of fungi, they demonstrated that only members of the *Amylogogon* subgenus of *Rhizopogon* induced germination. Each mature plant demonstrates even greater host specificity and only associates with a single species within the same subgenus of fungi identified by the germination experiments (Bidartondo and Bruns 2002; Hazard et al. 2011).

A complex balance of hormones controls seed germination and the termination of dormancy in plants (Kucera et al. 2005). The importance of gibberellins (GAs) and their activity as promoters of seed germination is well documented in model systems (Koornneef et al. 2002; Sun and Gubler 2004). GA has been applied to many non-model plants for conser-

vation (Li et al. 2007; Ortega-Baes and Rojas-Aréchiga 2007; Flores et al. 2008; Zeinalabedini et al. 2009; Mattana et al. 2012; Kandari et al. 2012) and restoration (Commander et al. 2009; Turner et al. 2012). However, the efficacy of GA on monotrope germination has not been examined. The inability to grow *P. andromedea* from seed severely limits propagation efforts as well as further experimental work. Here we present the only known method for asymbiotic germination of *P. andromedea* seeds using gibberellic acid (GA), as well as evidence that GA may be used to germinate other monotropes such as *Sarcodes sanguinea* Torr.

MATERIALS AND METHODS

Fungal Strains and Seed Collections

Pterospora andromedea seeds and roots were collected from Blodgett Forest, a University of California research station (38°54′N, 120°39′W, elev. ~1370 m) situated in the Sierra Nevada foothills near Georgetown, CA. In order to identify the fungal host of individual *P. andromedea* plants, small root fragments were collected in summer (August 2004, July 2005, and August 2008), after emergence of inflorescences. Roots were stored on ice or at 4°C prior to DNA extraction. Genomic DNA was extracted from colonized rootball tissue using the XNAP RED-Extract-N-Amp™ Plant PCR Kit (Sigma-Aldrich, St. Louis, MI), and the internal transcribed spacer (ITS) region from the host fungus was PCR amplified using primers ITS1F and ITS4B (Gardes and Bruns 1993). PCR products were sequenced at the UC Berkeley DNA Sequencing Facility using ABI chemistry. Sequences were identified as either *R. salebrosus* or *R. arctostaphyli* by matching to sequences of known specimens in the GenBank database (Bidartondo and Bruns 2001, 2002). Mature *P. andromedea* seeds from 21 of these fungal host-typed plants were collected after seed set in November 2004, September 2005, and October 2008 and stored at 4°C. Only *P. andromedea* seeds from plants associated with *R. salebrosus* in the field were used in this work.

All seed germination experiments involving the host fungus used *R. salebrosus* strain TDB-379, which was isolated from *P. andromedea* roots, and grown on Modified Melin Norkrans (MMN) medium with 1.5% agar (Bruns and Read 2000).

Mature *Sarcodes sanguinea* seeds were collected in August 2008 from eight plants near the USDA Forest Service work station (37°03′N, 119°9′W, elev. 1375 m) near Dinkey Creek, CA in the Sierra National Forest. All seeds were stored at 4°C prior to use.
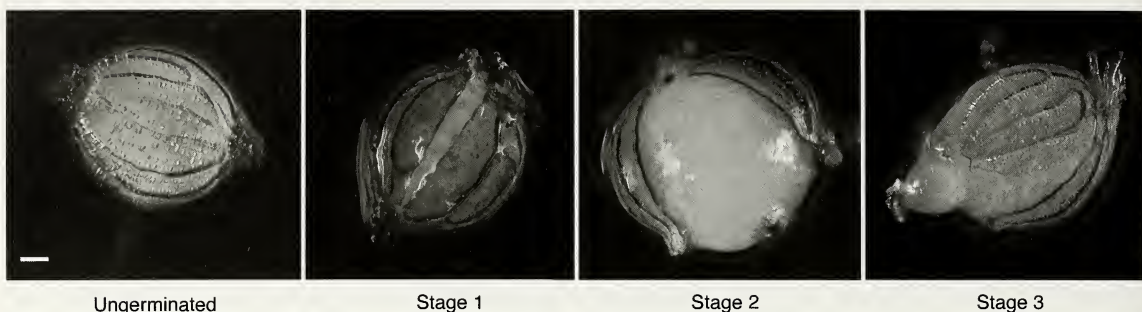
FIG. 1. Stages of *Pterospora andromedea* seed germination. All seeds were de-winged and placed on agarose with gibberellic acid. Ungerminated seeds have intact seed coats. Stage one seeds have cracked seed coats. Stage two seeds have imbibed and swelled. Stage three seeds have visible radicle emergence. Scale bar denotes 100 um.

Gibberellic Acid Assays

Wings were removed from *Pterospora andromedea* seeds less than one year after collection. Seeds were surface sterilized by gentle agitation for 20 min in saturated calcium hypochlorite with a drop of Tween 80, then filtered onto sterile Whatman paper, and rinsed twice with sterile water (Bruns and Read 2000). Seeds were plated onto 2% water agar and monitored for one week for contamination. Contaminated seeds were excised and discarded. Seeds were manually transferred to 0.8% agarose with 0.01, 0.1, 0.5, or 1 mM filter-sterilized GA (Sigma-Aldrich, St. Louis, MI), or to agarose without GA as a disruption control. Seeds exposed to *R. salebrosus* were placed just ahead of the growing mycelial front. After two months, germination was assessed according to the stages described by Bruns and Read (2000) (Fig. 1). Experiments used at least 100 seeds of each germination treatment (exposure to *R. salebrosus*, or combination of GA concentration and time exposed to GA) per replicate.

Statistical Analysis

Percent germination was calculated for replicates of each combination of germination treatment, time, and stage of germination. For experiments with continuous GA exposure, one-way ANOVAs were run for stage three and total germination, with treatment condition as the independent variable. For experiments where seeds were exposed to GA and then transferred to plain agarose, two-way ANOVAs were done for percent total germination and stage three germination. The factors were GA concentration and time of GA exposure, with Tukey HSD tests on the time factor. Statistical analyses were done with JMP software version 5.0.1a for Mac (SAS Institute, Inc, Cary, NC).

RESULTS

Continuous exposure to GA induced germination in *P. andromedea* (Fig. 2). Germination

treatment (either GA concentration or exposure to host fungus, *R. salebrosus*) had a significant effect (one-way ANOVA, P < 0.0001) on both total and stage three percent germination (Table 1). According to Tukey HSD tests, there was a significant decrease in stage three germination with GA concentrations over 0.1 mM, even though total germination increased. Optimal total germination response of 75 ± 10% (mean ± SD) germination occurred with 0.5 mM GA, which was significantly higher than 0% germination on agarose alone, germination with 0.01 mM GA (0.8 ± 2.4%), or germination with the host fungus, *R. salebrosus* (21 ± 12%). Stage three germination, indicated by radicle emergence, was highest with 23 ± 14% germination on 0.1 mM GA. Stage three germi-
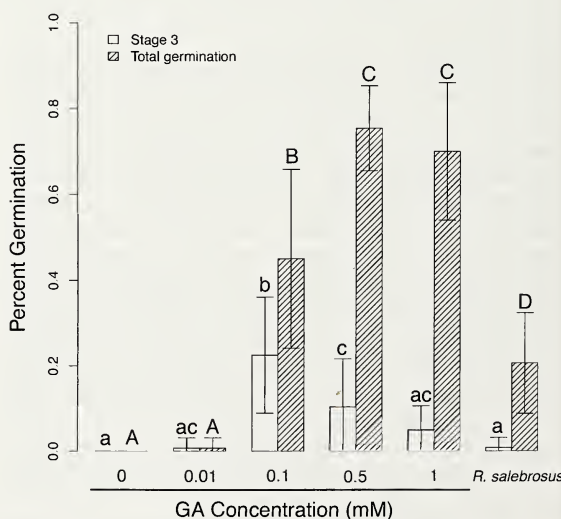

FIG. 2. Gibberellic acid induces *Pterospora andromedea* seed germination better than its host fungus, *Rhizopogon salebrosus*. Error bars indicate standard deviations. Lower case and capital letters respectively indicate significance levels based on Tukey HSD tests for stage three (radicle emergence) and total germination, with treatment condition as the independent variable and a 95% confidence.

TABLE 1. RESULTS OF ONE-WAY ANOVAS DETAILING THE EFFECTS OF CONTINUOUS EXPOSURE FOR TWO MONTHS TO GA ON PERCENT TOTAL GERMINATION AND STAGE THREE GERMINATION OF *PTEROSPORA ANDROMEDEA* SEEDS.

	Total germination				
Source	df	Sum of squares	Mean square	F	P
Germination treatment	5	4.561	0.912	59.394	<0.0001
Error	48	0.737	0.015		

	Stage 3 germination				
Source	df	Sum of squares	Mean square	F	P
Germination treatment	5	0.321	0.064	12.368	<0.0001
Error	48	0.249	0.005		

nation induced by *R. salebrosus* was significantly lower (0.9 ± 2.4%).

A short exposure to GA (Fig. 3) was sufficient to induce *P. andromedea* germination and outperformed continuous exposure for stage 3 germination (Fig. 2). Time on GA, GA concentration, and the interaction of time and concentration significantly affected total and stage three percent germination (two-way ANOVA, P < 0.0001, Table 2). Tukey HSD tests indicated that three days of exposure to 0.5 mM GA was not significantly different from a 14-day exposure while still showing an improvement over a one-day exposure. Three days of exposure to 0.5 mM GA led to 90 ± 0% total germination response and 68 ± 8% stage three germination. Two weeks of GA exposure produced 93 ± 11% stage three germination. Parallel treatments with 0.1 mM GA showed significantly less germination for one- (2 ± 4%) and three- (8 ± 8%) day exposures, while a two-week exposure produced 72 ± 11% stage three and 77 ± 11% total germination. After two weeks of GA exposure, total germination, but not stage three germination, was significantly different between 0.1 and 0.5 mM GA. The total germination responses to each of the three GA exposure times were significantly different from each other. Stage three germination with 14 d of GA exposure was significantly different from just one or three days' exposure.

Sarcodes sanguinea seeds failed to respond to GA concentrations of 0.01, 0.1, 0.5, and 1 mM after two months. However, after three months low levels of germination occurred with 0.5 mM and 1 mM GA (1 ± 1% and 1 ± 0.7%, respectively). In the presence of *R. salebrosus*, 42 ± 14% of the seeds germinated. All germination was stage three.

DISCUSSION

We utilized *P. andromedea*'s germination response to GA to produce an improved method to assay seed viability and to enable further studies and conservation efforts using *P. andromedea* seeds. Continuous exposure to GA led to far higher germination response than with *R. salebrosus*, *P. andromedea*'s host fungus (Fig. 2). Gibberellic acid–induced germination was also higher than the most *P. andromedea* germination observed by Bruns and Read (2000) of 26 ± 21% (SD). The ability of GA to germinate seeds well beyond nine weeks old indicates that it is a more accurate determination of seed viability than the tetrazolium method applied by Bakshi (1959). However, while continuous exposure to increasing concentrations of GA did lead to higher overall germination response, increased GA concentrations also had less stage three germination (Fig. 2), suggesting either inhibition by or toxicity of GA.

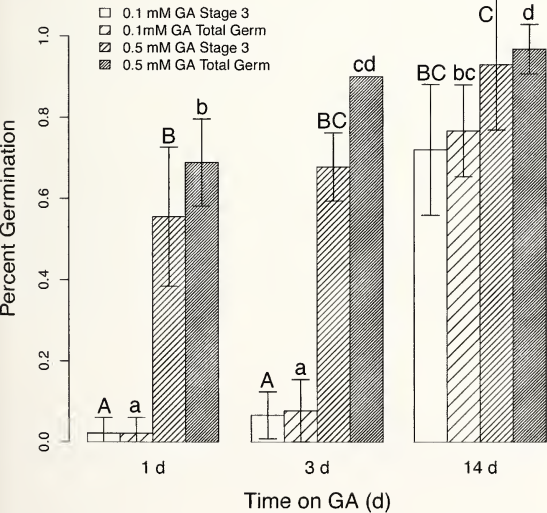This suppressive effect of continuous exposure to GA at higher concentrations was ameliorated

FIG. 3. Short exposure to gibberellic acid induces *Pterospora andromedea* seed germination. Seeds were exposed to gibberellic acid (GA) and then transferred to unamended agarose. Error bars indicate standard deviations. Lower case and capital letters respectively indicate significance levels based on Tukey HSD tests for stage three (radicle emergence) and total germination.

TABLE 2. RESULTS OF TWO-WAY ANOVAS DETAILING THE EFFECTS OF SHORT EXPOSURE TO GA (1 D, 3 D, OR 14 D) ON PERCENT TOTAL GERMINATION AND STAGE THREE GERMINATION OF *PTEROSPORA ANDROMEDEA* SEEDS.

Source	df	Sum of squares	Mean square	F	P
Total germination					
Time exposed to GA	2	1.12	0.560	90.789	<0.0001
GA concentration	1	1.703	1.703	276.253	<0.0001
Time x concentration	2	0.455	0.228	36.910	<0.0001
Error	18	0.111	0.006		
Stage 3 germination					
Time exposed to GA	2	1.389	0.695	36.723	<0.0001
GA concentration	1	1.093	1.093	57.800	<0.0001
Time x concentration	2	0.199	0.0995	5.267	0.0159
Error	18	0.341	0.019		

by exposing seeds to GA for shorter periods followed by transfer to plain agarose. A concentration of 0.1 mM GA required two weeks of GA exposure to get more than 10% germination. Just one day with 0.5 mM GA induced over 4.5 times as much total germination as interaction with *R. salebrosus*, and most of this germination was stage three. Three days of exposure to 0.5 mM GA produced nearly 90% total germination, and two weeks led to nearly all seeds reaching stage three germination. To our knowledge, GA is not known to inhibit germination at higher concentrations. For instance, Fennimore and Foley (1998) found ~90% germination of *Avena fatua* L. after exposure to 10 mM GA.

Sarcodes sanguinea exhibited low germination response to up to 1 mM GA. The seeds were viable, as demonstrated by their germination in the presence of *R. salebrosus*, at a rate very close to the 46 ± 22% found by Bruns and Read (2001). *Pterospora andromedea* seeds are far smaller and have more delicate seed coats than those of *S. sanguinea*. The low germination in *S. sanguinea* could be due to a different porosity or composition of the seed coats or lower sensitivity to GA.

Bruns and Read (2000) found that in vitro, *P. andromedea* germination did not require direct contact with the host fungus, suggesting that a diffusible substance induces germination. The fact that gibberellins were first isolated from a fungus (*Fusarium fujikuroi* Nirenberg) and have since been identified as a secondary metabolite in many other fungi (Bömke and Tudzynski 2009) might lead one to think that GA is the diffusible substance observed by Bruns and Read (2000). However, this is unlikely for two reasons. First, in order for GA to be the diffusible substance, one would expect it to be limited to *R. salebrosus* and *R. arctostaphyli* in order to explain the observed specificity. Yet, as mentioned above, GA is known to be produced by a wide range of unrelated fungi. Second, if GA were the diffusible signal from *Rhizopogon*, one would expect *P. andromedea* and *S. sanguinea* to respond to it in similar ways, yet their sensitivity to it is quite different and uncorrelated with their response to the unknown diffusible substance(s) from *Rhizopogon*. For these reasons, it seems more likely that the chemical signal of *Rhizopogon* either triggers the endogenous gibberellin pathway in *P. andromedea* or works by some independent pathway.

Gibberellic acid–induced germination of *P. andromedea* seeds will clearly provide a useful tool for assessing the viability of seed lots, but whether it can be applied to help establish seedlings is yet to be determined. The main problem is that the next developmental steps are likely to require a compatible association with *Rhizopogon*, its host fungus, which in nature is mutualistically associated with pine roots. Under Petri dish conditions, growth of *Rhizopogon* is much more limited, and germinating *P. andromedea* seeds rarely develop beyond stage three, even when induced to germinate by its host fungus (Bruns and Read 2000). Thus, in order to test whether further development is possible it will probably require a three-organism system to be assembled, and this feat has yet to be achieved with any member of the Monotropoideae. Further work to incorporate GA into a practical conservation plan for *P. andromedea* and other monotropes may require field experiments.

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CLIMATE CHANGE VULNERABILITY ASSESSMENT OF RARE PLANTS IN CALIFORNIA

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Abstract

We assessed the vulnerability to climate change of 156 rare plant species. The species were selected from the 1625 rare species in California to comprise eight rarity types, classified according to range size, population size, and habitat specificity. For each of the 156 species, we first assigned a climate change vulnerability score using life history attributes and species distribution models, as specified by the Climate Change Vulnerability Index (CCVI) of NatureServe. The resulting CCVI scores were extremely vulnerable (n = 2), highly vulnerable (n = 40), moderately vulnerable (n = 57), presumed stable (n = 32), increase likely (n = 16), and insufficient evidence (n = 9). *Piperia yadonii* Rand, Morgan & Ackerman and *Mimulus purpureus* A. L. Grant were the species scored as extremely vulnerable. There was no correlation of the CCVI scores with rarity type, suggesting that climate change vulnerability cannot be inferred by simple categorizations based on geographic range and habitat preference. Second, we conducted a follow-up species distribution model sensitivity analysis that showed that the modeling results were highly dependent upon both model algorithm and choice of predictor variables. However, 60 of the 156 species were predicted to have declines in climatic suitability, regardless of modeling technique. Third, as an independent assessment of vulnerability, we calculated the topographic complexity around known occurrences of each species. Species in topographically dissected landscapes may be less vulnerable to climate change because they can find suitable climates locally as climate changes. We found that topographic complexity varied substantially, even within a single CCVI score level, and therefore provides unique information on vulnerability. Our results can be used to guide monitoring, management, and conservation plans for rare plant species.

Key Words: California, climate change, NatureServe, rare plants, vulnerability.

Climate change may negatively impact the flora of California, a biodiversity hotspot with over 2000 endemic plant species (Myers et al. 2000). A changing climate may reduce and extirpate populations (Pounds et al. 2006), cause species to migrate north and upslope (Parmesan 1996; Kelly and Goulden 2008; Loarie et al. 2009), advance flowering times, promote species invasion, increase disturbance (e.g., fire), and cause community reorganization (Walther et al. 2002; Burkett et al. 2005). Several tools have been developed to identify which species and habitats are most imperiled by the negative impacts of climate change (Schnieder et al. 2007; Williams et al. 2008; Heller and Zavaleta 2009; EPA 2009; Byers and Norris 2011; Glick et al. 2011; Schlesinger et al. 2011), under the assumption that the world will continue to warm in the near term, even if emissions are immediately reduced (IPCC 2007). By identifying species or habitats most at risk from effects of climate change, conservation and management efforts can be targeted to reduce these impacts, such as by protecting existing habitat or through assisted migration (Hunter 2007; McLachlan et al. 2007).

Vulnerability assessments provide a standardized method to assess sensitivity to climate change that is time-efficient, repeatable, and is directly comparable across species. Investigators can use vulnerability assessments to rank a list of species with regard to their relative expected sensitivity to shifts in climate (Gardali et al. 2012). Most studies are focused upon individual species; however, recent work has also considered the vulnerability of landscapes (Klausmeyer et al. 2011). For example, topographically complex landscapes may provide refugia or paths for movement to more suitable areas under changing temperature and moisture regimes (Hunter et al. 1988; Beier and Brost 2010). Moreover, understanding how regional and local processes interact to create spatial heterogeneity in climate may help predict the direction and rate of climate change (Ackerly et al. 2010). Further, assessments of geophysical diversity (i.e., the number of bedrock types) may be a useful alternative to species-level assessments, since high levels of geological diversity are often associated with habitat heterogeneity and species diversity (Anderson and Ferree 2010).

Species-level vulnerability assessments are typically based on intrinsic life history traits, species distribution models (SDMs), or both. The trait-

based approach identifies and scores species attributes relevant to avoiding or tolerating climate change, such as movement ability (i.e., dispersal rates) or sensitivity to changes in temperature or moisture. The sum of these scores represents the species' overall vulnerability to climate change. Trait-based indices were largely developed with animals as a primary focus. For example, the International Union for Conservation of Nature (IUCN) analyzed the life history, ecology, behavior, physiology, and genetic makeup of "red list" animal species to assess a species vulnerability to climate change (Foden et al. 2009).

A second set of tools used to assess vulnerability to climate change is SDMs (Pearson and Dawson 2003; Loarie et al. 2008; Stralberg et al. 2009). Typically, point occurrence data for a species are used to create a statistical model of climatic suitability using historical (often 30-year-mean) climate data. This model is then used to predict the species' contemporary range, based on a grid of historical climate, and the species' future range, based on a grid of predicted future climate. Finally, the change in predicted range size and the amount of range overlap is calculated. Species with large range reductions and/or low range overlap are considered to be more vulnerable than species with small range reductions and/or high range overlap. However, there are a large number of modeling techniques used to describe climatic suitability, and differences in model algorithms and assumptions can greatly influence the quality of model predictions (Araújo and New 2007).

A leading example of combining species traits and SDMs into a single vulnerability analysis comes from NatureServe (Arlington, VA), a non-profit organization whose mission is to provide the scientific basis for effective conservation action. NatureServe developed the Climate Change Vulnerability Index (CCVI) to serve as a standardized methodology for assessing vulnerability to climate change at the species level (Young et al. 2012). The CCVI consists of a Microsoft Excel document with four main sections: Section A—direct exposure to changing temperature and precipitation; Section B—indirect exposure to climate change, including sea level rise, natural and human barriers, and land impacts from climate mitigation; Section C—sensitivity factors (hereafter referred to as "life history traits"); and Section D—modeled response to climate change.

Our goal was to assess the vulnerability of California rare plant species to climate change and to evaluate the application of the Nature-Serve CCVI method to rare plants. Rarity is a major feature of California's botanical heritage. The California Native Plant Society (CNPS) Rare Plant Program, which works in coordination with the California Department of Fish and Game's (CDFG) Natural Diversity Database,

recognizes 1625 plant taxa as rare or endangered, as of March 1, 2011. While many of the 1625 taxa are subspecies and varieties, and thus the words "taxa" and "taxon" are appropriate than "species," we use "species" throughout the text for simplicity. There are 26 California Rare Plant Rank 1A—presumed extinct in California; 1132 Rank 1B—rare or endangered in California and elsewhere; and 492 Rank 2—rare or endangered in California, but more common elsewhere (CNPS 2001). These rare species may have narrow ranges, small population sizes, or narrow habitat preferences (or all of the above) for natural or anthropogenic reasons (CNPS 2001). The potential impacts of climate change were not a factor considered by CNPS when assigning rare plant ranks; thus, which of the 1650 species will be most vulnerable to climate change has been largely uninvestigated.

Climate-only SDMs suggest California plants may be in trouble: 66% will experience 80% reductions in range size within a century (Loarie et al. 2008). In addition, plants may be unable to adjust their ranges fast enough to spatially track shifting climates (Loarie et al. 2009). It is possible that rare species may be even more sensitive to climate change, given their limited geographic ranges and small population sizes. Or, perhaps they will be less sensitive to climate change, given their specialized ecologies. These attributes also make it more difficult to accurately model rare species than common species. Given our conservation concerns, it is our hope to create a meaningful vulnerability ranking for rare species and to identify which spatial and life history factors contribute most to that vulnerability.

Due to the large number of rare plants in California, we sought to determine whether the level of climate change vulnerability could be inferred for certain groups of rare plants based on rarity type, life history traits, or biogeographic affinity. Our work can be divided into three complementary parts. First, for a subset of the 1650 rare plants (n = 156), we compiled a set of life history attributes and created distribution models to rank vulnerability as specified by the CCVI of NatureServe. Second, we conducted a SDM sensitivity analysis to determine how choice of model algorithm and predictor variables influenced distribution model predictions of habitat suitability in future climates. Third, we calculated an index of vulnerability based on topographic complexity around known occurrences.

METHODS

Species Selection

To create a list of focal species that was representative of California rare plant species as a whole, we first classified each of the 1625 species

TABLE 1. TYPES OF RARITY. The types of rarity, modified from Rabinowitz (1981), come from intersecting range size (small or large), population size (small or large), and habitat specificity (habitat specialist or generalist). For each category, the number of species in our sample and an example species is provided. While only seven of the eight groups are "rare," species with relatively large ranges, large populations, and generalist habitat preferences among our sample are still relatively rare with respect to the average species in the flora. Thus, we used all eight groups for our selection.

	Large range		Small range	
Population size	Habitat generalist	Habitat specialist	Habitat generalist	Habitat specialist
Large populations	n = 28 *California macrophylla*	n = 25 *Streptanthus morrisonii*	n = 24 *Mimulus purpureus*	n = 17 *Allium tuolumnense*
Small populations	n = 24 *Lilium parryi*	n = 15 *Calochortus plummerae*	n = 17 *Taraxacum californicum*	n = 6 *Monardella stebbinsii*

into one of the eight types or forms of rarity (Rabinowitz 1981) (Table 1). Following Rabinowitz's (1981) definitions, only seven of the eight groups are "rare," because the combination "large range, large population, and habitat generalist" is considered common. However, since our sample pool was made up of only rare species, even the species within this pool with large ranges, large populations, and generalist habitat preferences were rare relative to the average species in the flora. Thus, we sampled across all eight groups to obtain our subset of 156 species (Appendix 1). Nomenclature for these species follows the CNPS Inventory (2001).

We used information from the California Natural Diversity Data Base (CNDDB) to attribute each species with the three variables required for rarity type classification, as follows: (1) range size—total area of species range based on a minimum convex polygon encompassing mapped occurrences from the CNDDB; (2) population size—the median population number of individuals, extracted from the comment field of CNDDB; and (3) habitat specificity—substrate affinity, extracted from the habitat field of CNDDB. For range size and population size, species were designated as large or small based on their value relative to the median of the distribution of values. We then randomly selected species from each of the eight rarity types (Table 1). Our list of 156 species includes 139 California Rare Plant Rank 1Bs, 13 Rank 2 s, and three Rank 3 s. While rank 3 s are not nominally rare and thus do not contribute to the 1625 described above, we included three of these species to see if they had remarkably different vulnerability scores.

Climate Change Vulnerability Index (CCVI)

CCVI overview. The NatureServe CCVI (release 2.01) assesses 24 climate change vulnerability risk factors, placed in four categories: direct exposure, indirect exposure, life history traits, and modeled response. To complete the CCVI, we collected information on the distribution,

natural history, and conservation status of rare species from CDFG, CNPS, and NatureServe. We then conducted a literature review, mapped species distributions, and modeled responses to climate change. Biologists and botanists were consulted to fill data gaps as needed for particular species. Collected data and sources for each species are available online at www.dfg.ca.gov/biogeodata/.

CCVI Section A: Direct exposure (two factors). Direct exposure was scored based on the percentage of the species' range that falls into NatureServe's recommended categories of projected changes of temperature or moisture. The temperature change categories (decreasing in severity) were $>3.1°C$, $2.8–3.1°C$, $2.5–2.7°C$, $2.2–2.4°C$, and $<2.2°C$; the moisture change categories (decreasing in severity) were <-0.119, $-0.097–-0.119$, $-0.074–-0.096$, $-0.051–-0.073$, $-0.028–-0.050$, and >-0.028. Climate data (Fig. 1a–d) and projections for the year 2080 were derived by The Nature Conservancy and downloaded from their Climate Wizard (Model: Ensemble Average, emission scenario [ES] A2; www.climatewizard.org). Temperature change was the predicted change in annual temperature by 2080, calculated over the range of the species in California. Moisture change was the predicted net change in moisture based on the Hamon AET:PET Moisture Metric, calculated over the range of the species in California. Additional climate data was acquired for the modeled response (Section D) and SDM sensitivity analysis (II) from WorldClim, as described below.

CCVI Section B: Indirect exposure (four factors). Indirect exposure evaluated landscape configuration factors that may affect the vulnerability of a species to climate change: Exposure to sea level rise, distribution relative to natural barriers, distribution relative to anthropogenic barriers, and predicted impact of land use changes resulting specifically from human responses to climate change. To evaluate these factors, we compared the distribution of the known occurrences of each species with a map of
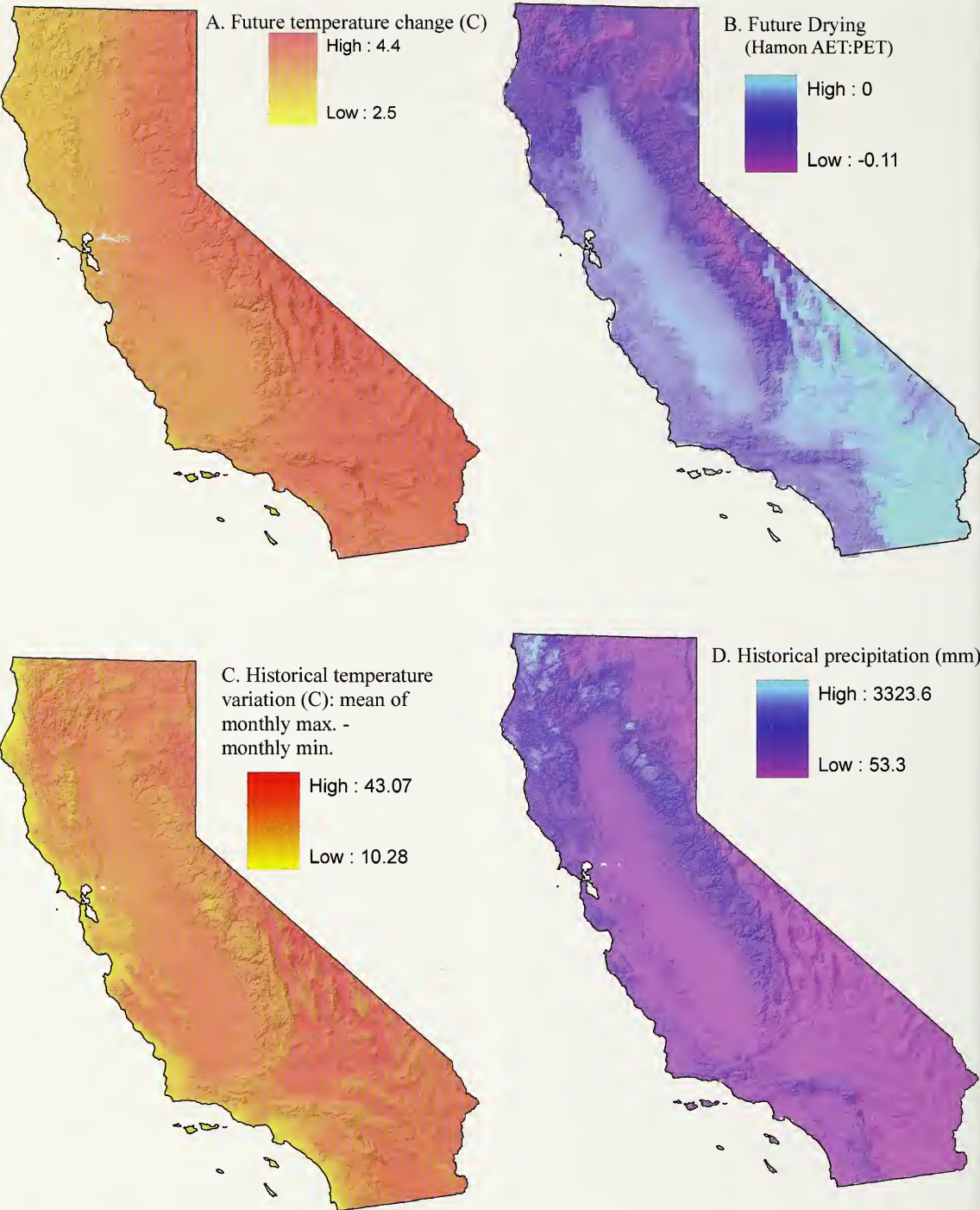
FIG. 1. Map of future temperature change (a), future drying (b), historical temperature variation (c), and historical annual precipitation (d).

predicted sea level rise (Strauss et al. 2012), topographic maps that depicted landscape features, and maps of proposed renewable energy (e.g., solar power stations, wind farms, geothermal wells; California Department of Fish and Game 2011). For sea level rise, the percent of the

species' range occurring in areas subject to sea level rise were placed into five broad categories (decreasing in vulnerability): (1) >90%, (2) 50–90%, (3) 10–49, (4) <10, and (5) predicted increase in extent (intertidal species whose habitat may increase with sea level rise). For barriers,

TABLE 2. LIFE HISTORY TRAITS USED IN DETERMINING CLIMATE CHANGE VULNERABILITY INDEX (CCVI) IN THIS STUDY. Assumptions and data sources are listed for each determining factor.

Factor	Assumption	Data source
Dispersal and movements	Lower dispersal ability leads to high vulnerability.	Dispersal mechanisms from scientific literature and expert opinion.
Predicted sensitivity to temperature and moisture changes	Narrow historical climate exposure and special microclimatic preferences leads to high vulnerability.	Historical temperature and precipitation variation from Climate Wizard. Physiological hydrological niche and physiological thermal niche from scientific literature and expert opinion.
Dependence on a specific disturbance regime	Dependence on a particular disturbance regime leads to high vulnerability.	Adaptation and affinity for fire and flood-prone habitats from scientific literature and expert opinion.
Restriction to uncommon geological features or derivatives	Habitat specialization leads to high vulnerability.	Substrate affinity from CNDDB. SSURGO soil data from the NRCS.
Reliance on interspecific interactions	Dependence on other species (facilitation, pollinators, and seed dispersers) leads to high vulnerability.	Literature and expert opinion.
Genetics	Low genetic diversity leads to high vulnerability.	Not scored for any species due to insufficient information.
Phenological response	Shorter bloom period leads to high vulnerability.	CNPS's Rare Plant Inventory bloom-period database.

each species was placed into one of four categories (decreasing in vulnerability): (1) Barriers completely surround the current distribution, (2) barriers border the current distribution incompletely but will likely impair distributional shits, (3) barriers border the current distribution incompletely but will be unlikely to impair distribution shifts, and (4) significant barriers do not exist. For renewable energy, each species was placed into one of four categories (decreasing in vulnerability): The likelihood that a species' natural history or range may be (1) very likely to conflict with mitigation-related land-use changes, (2) likely to conflict with land-use changes, (3) likely to benefit from land-use changes, or (4) very likely to benefit from land-use changes.

CCVI section C: life history traits (16 factors). The life history traits were grouped into the following categories: dispersal/movement, sensitivity to temperature or moisture, disturbance-dependence, geologic restriction, interspecific interactions, genetic diversity, and phenology (Table 2). Each species was scored by assessing whether its life history traits would be expected to decrease, somewhat decrease, neutral, somewhat increase, increase, or greatly increase its vulnerability to climate change. If information was not available for a particular factor, it was scored as unknown. Guidance on how to rank each factor was provided by NatureServe. Ranks for ten factors in this group were required or the vulnerability index returned a score of "Insufficient Evidence."

CCVI Section D: Modeled response (two factors). We modeled the change in range size

and range overlap of predicted future range with predicted current range using the Maxent algorithm, a statistical model that uses machine learning (Phillips et al. 2006; Elith and Leathwick 2009).

The spatial centroid of each CNDDB mapped occurrence record was used. The records of the CNDDB have been carefully curated by the staff of CDFG, yet uncertainty in the exact locations likely remains, contributing an unknown, but likely small, amount of variation to the model results presented here. Another limitation is that occurrences outside of CA are omitted; however, visual examination of the distributions of our focal species suggests that only ~10% have distributions that may cross into Oregon or Baja California, Mexico. We used a dataset acquired from WorldClim (Hijmans et al. 2005) comprising four climate variables (annual temperature, annual precipitation, seasonality of temperature, and seasonality of precipitation) for current conditions (mean 1950–mean 2000) and for future conditions (called "2080," but data are means for 2070–2100; Global Circulation Model [GCM] CGCM3.1, ES A1B) at 1 km^2 resolution. We fit a Maxent model for current conditions and used the resulting model to predict climatic suitability, ranging from 0–1, for both current and future conditions; background points were selected randomly. Maxent was run using the default "auto features" mode, allowing the use of linear, quadratic, product, threshold, and hinge features. These continuous surfaces were then converted to binary (suitable/unsuitable) using a threshold determined as the value that maximizes the kappa, a statistical measure of the agreement

TABLE 3. CLIMATE CHANGE VULNERABILITY INDEX SCORE DESCRIPTIONS.

Index scores	Descriptions
Extremely vulnerable (EV)	Abundance and/or range extent within geographical area assessed extremely likely to substantially decrease or disappear by 2050.
Highly vulnerable (HV)	Abundance and/or range extent within geographical area assessed likely to decrease significantly by 2050.
Moderately vulnerable (MV)	Abundance and/or range extent within geographical area assessed likely to decrease by 2050.
Presumed stable (PS)	Available evidence does not suggest that abundance and/or range extent within the geographical area assessed will change (increase/decrease) substantially by 2050. Actual range boundaries may change.
Increase likely (IL)	Available evidence suggests that abundance and/or range extent within geographical area assessed is likely to increase by 2050.
Insufficient evidence (IE)	Available information about a species' vulnerability is inadequate to calculate an index score.

between predictions and observations, and the AUC values were calculated (Cohen 1960; Jiménez-Valverde 2011). Change in range size was calculated as the total area predicted as suitable in the future (t_2) minus the total area predicted as suitable in the present (t_1), divided by total area predicted as suitable at t_1. Range overlap was calculated as the total area predicted to be suitable at t_1 and t_2, divided by the total area predicted as suitable at t_1. The geographic extent of all models was California. This may overestimate range loss when a species' new range is predicted to be outside of California.

CCVI risk factor score. The natural history and distributional information for each species was entered into the CCVI Excel calculator to obtain scores for each species. The output was one of six vulnerability scores: extremely vulnerable (EV), highly vulnerably (HV), moderately vulnerable (MV), presumed stable (PS), increase likely (IL), and insufficient evidence (IE; Table 3). All vulnerability index scores were calculated with and without modeled response to climate change (Section D).

Statistical analysis of CCVI predictors. To identify which of the factors were most strongly associated with the resulting vulnerability scores, we evaluated the distribution of risk factor scores against the distribution of CCVI scores across all of our species. Factors that were frequently scored as increasing or decreasing vulnerability should show up as significant predictors of the distribution of CCVI scores, while factors that were infrequently scored as increasing or decreasing vulnerability should not. We converted the CCVI scores and factor ranks to their numeric equivalents, then regressed the CCVI score vs. each of the factors from these sections. We did not test for a relationship of CCVI with dietary versatility, genetic variation, or genetic bottlenecks, because no species were scored for those factors. Tests varied in the number of species included because we did not have information on all life history traits for all species (i.e., when the factors were marked as unknown). We also compared the CCVI score with California Rare Plant Rank and rarity type using two one-way ANOVAs. Finally, we tested if range size change or range overlap was related to California Rare Plant Rank and rarity type using four one-way ANOVAs.

SDM Sensitivity Analysis

For each of the 156 species, we ran 22 additional SDMs to estimate the sensitivity of range predictions to modeling algorithms and choice of predictor variables. Our 23 models (all run in Maxent unless stated otherwise) were: 1) 19 climate variables (bioclim); 2) four climate variables (described above); 3–14) four climate variables, with different GCM*ES combinations (GCMs included BCCR-BCM2.0, CSIRO-Mk3.0, INM-CM3.0, and MIROC3.2 [medres]; ESs included A2, AB, and B1); 15) 19 climate variables with soil type; 16) 19 climate variables with soil properties (pH, organic matter, and clay); 17) four climate variables with soil type; 18) four climate variables with soil properties (pH, organic matter, and clay); 19) four climate variables, with a customized geographic extent for each species; 20) four climate variables with an equal number of presences and psuedo-absences; 21) four climate variables, with Random Forest; 22) four climate variables, with random forest, and with a customized geographic extent for each species; 23) four climate variables, with the boosted regression tree model. Soil type data came from the Geologic Map of California (Jennings et al. 2010), which we simplified into seven "soil types" (gabbro, granite, limestone, sandstone, serpentine, shale, and volcanic) and rasterized to 1 km^2 resolution. Soil property data were obtained from the Natural Resources Conservation Service (NRCS) soil survey geographic database (SSURGO) and rasterized to 1 km^2. The customized geographic extents were determined by intersecting the point occurrence data with the Jepson Ecoregions (Hickman 1993);

A. *Eriogonum twisselmannii*   B.*Limosella australis*
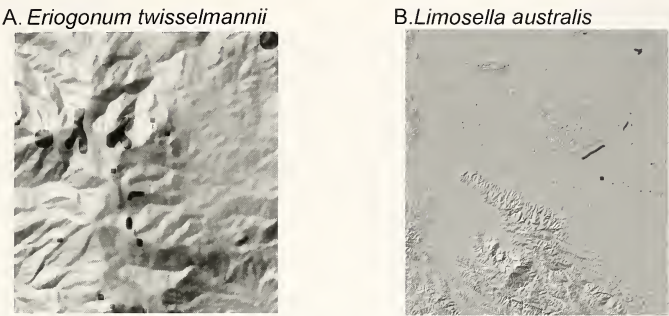

FIG. 2.   Illustration of topographic complexity. (a) *Eriogonum twisselmannii* had an anomaly score of −0.61 and a topographic complexity (standard deviation of elevation) of 27.3. (b) *Limosella australis* had an anomaly score of −0.64 and a topographic complexity score of 0.51.

for each species, the predictor raster surfaces were cropped to the shape of the ecoregions that contained the species.

To compare the model predictions, we calculated an "anomaly score" for each species and each model. For a given species, at each known occurrence, an anomaly value was calculated as the predicted suitability in the present (t_1) subtracted from the predicted suitability in the future (t_2). The mean of the anomaly values across all occurrences was the "anomaly score" for each species. A negative anomaly score meant that suitability in the future was predicted to be lower than current suitability.

There are two main advantages of using an anomaly score to compare model predictions for our SDM sensitivity analysis, rather than using the conventional metrics of change in range size or range overlap. First, the anomaly score can be derived without converting continuous predicted surfaces to binary, the latter of which requires determining a threshold above or below which a particular location is considered suitable or unsuitable. For rare species, it is especially difficult to choose a meaningful threshold, given the limited number of point occurrences available for evaluation of the prediction errors made at various threshold values (Hijmans 2012). Second, anomaly scores are based on climate suitability change only at known occurrences, while range size and overlap consider the entirety of California. Most rare plant species occupy only a small portion of their range where specific habitat requirements are met, and managers are most concerned with how climate suitability will change where the species actually occurs. Evaluating change in suitability over the entire range of the species requires assumptions about habitat occupancy and movement that may not be met by many rare plant species. Furthermore, using the anomaly score meant that predictions were only necessary for known occurrences, making our sensitivity analysis computationally feasible.

We asked if the anomaly score was significantly related to the model type, within species, using a two-way ANOVA. Tukey's HSD tests were used for post-hoc means separation by model type. We also examined the relationship of anomaly score and CCVI score using linear regression. Finally, we tested if the median anomaly score of each species was related to California Rare Plant Rank or rarity type using two one-way ANOVAs.

Topographic Complexity Analysis

As an index of "topographic complexity," we calculated the standard deviation of elevation (resolution = 30 × 30 m) within 100 m of each occurrence, and took the mean of those values per species. Topographic complexity measured at 1000 m was highly correlated with topographic complexity measured at 100 m (r = 0.94, P < 0.001), so just the 100 m buffer was used. A species in a topographically complex landscape was considered less vulnerable than a species in a topographically homogeneous landscape (Fig. 2). We asked if the topographic complexity score was significantly related to the CCVI score using linear regression. We also tested if the topographic complexity score was related to California Rare Plant Rank or rarity type using two one-way ANOVAs.

RESULTS

Climate Change Vulnerability Index

Of the 156 species assessed, 99 were determined to be vulnerable (extremely vulnerable, highly vulnerable, or moderately vulnerable) to climate change and 48 were determined to be stable or increasing (presumed stable or increase likely). The distribution of final scores was: extremely vulnerable (n = 2), highly vulnerable (n = 40), moderately vulnerable (n = 57), presumed stable (n = 32), increase likely (n = 16), and insufficient evidence (n = 9). *Piperia yadonii* Rand, Morgan & Ackerman and *Mimulus purpureus* A. L. Grant were the species scored as extremely vulnerable. All assessment scores and species attribute data

TABLE 4. TOP FIVE MOST VULNERABLE SPECIES AS DETERMINED BY CLIMATE CHANGE VULNERABILITY INDEX SCORE. For CCVI, IL = increase likely, PS = presumed stable, MV = moderately vulnerable, HV = highly vulnerable, EV = extremely vulnerable, and IE = insufficient evidence. CCVI (without D) is the CCVI score recalculated after excluding the species distribution model results. The global (G) and state (S) rankings are from the California Natural Diversity Data Base; G-rank is the global rank, reflecting global rarity, and S-rank is the state rank, reflecting state rarity. Both indices range from 1 to 5, with 1 being critically imperiled and 5 being secure. California Rare Plant Rank 1B is rare or endangered in California and elsewhere and Rank 2 is rare or endangered in California, but more common elsewhere. Federal listing is the status of the species according to the Endangered Species Act. Section D refers to the modeled response of the CCVI. CCVI index score definitions follow Table 3. *Limosella australis* may not be native to California.

Rank	Species	CCVI	CCVI (without D)	G-rank	S-rank	California Rare Plant Rank	Federal listing
Based on CCVI with Section D							
1	*Piperia yadonii* (Orchidaceae)	EV	HV	5	2	2	None
2	*Mimulus purpureus* (Phrymaceae)	EV	HV	2	2.2	1B	None
3	*Calliandra eriophylla* (Fabaceae)	HV	MV	5	2&3	2	None
4	*Limosella australis** (Scrophulariaceae)	HV	HV	4&5	2	2	None
5	*Taraxacum californicum* (Asteraceae)	HV	MV	2	2	1B	Endangered
Based on CCVI without Section D							
1	*Monolopia congdonii* (Asteraceae)	MV	EV	3	3	1B	Endangered
2	*Orcuttia viscida* (Poaceae)	HV	EV	1	1	1B	Endangered
3	*Pogogyne abramsii* (Lamiaceae)	MV	EV	1	1	1B	Endangered
4	*Symphyotrichum lentum* (Asteraceae)	HV	EV	2	2	1B	None
5	*Mimulus purpureus* (Phrymaceae)	EV	HV	2	2.2	1B	None

are reported in Appendix 1. The top five most vulnerable species, with and without Section D ("modeled response"), are listed in Table 4.

For the 156 species assessed, the final CCVI score was significantly related to just one of the factors that were used to calculate it: anthropogenic barriers (NatureServe factor B2b; $r^2 = 0.09$, $P < 0.001$, $n = 147$). Anthropogenic barriers were determined to limit the migration ability of 99 of the 156 species, and the presence of anthropogenic barriers was significantly related to overall climate change vulnerability. Although not significantly related to overall climate change vulnerability, two factors were found to increase vulnerability for the majority of rare plants assessed: land use change from human response to climate change was found to increase vulnerability for 80 species, and narrow temperature tolerance ("historical thermal niche") was also found to increase vulnerability for 80 species.

Overall climate change vulnerability was not significantly related to California Rare Plant Rank. For example, final CCVI scores for 1B species were spread rather evenly as highly vulnerable (n = 35), moderately vulnerable (n = 49), presumed stable (n = 30), and increase likely (n = 14). In addition, overall climate change vulnerability was not related to rarity type. Similarly, neither change in range size nor range overlap were significantly related to California Rare Plant Rank or rarity type.

SDM Sensitivity Analysis

The anomaly scores statistically differed by species and by model type (species $P < 0.001$; model type $P < 0.001$), where the models with the most positive anomalies (greatest increase in suitability) were those made with Maxent that included soils information, and the models with the most negative anomalies (greatest reduction is suitability) were those made with Random Forest.

The anomaly score and the CCVI score were significantly related ($r^2 = 0.54$, $P < 0.001$), where species scored as vulnerable also had low anomaly scores. This is not surprising, given the CCVI score included modeled response. In fact, the CCVI score calculated after excluding modeled response was not significantly related to the anomaly score. The anomaly score was not significantly related to California Rare Plant Rank or rarity type.

Topographic Complexity Analysis

Topographic complexity and the CCVI score were not significantly related. Topographic complexity was not significantly related to California Rare Plant Rank, but was significantly related to rarity type ($P < 0.001$), where habitat specialists occurred in locations with higher topographic complexity than habitat generalists.

DISCUSSION

We have three key results: (1) 2/3 of our focal species were scored as vulnerable to climate change, (2) SDM predictions were highly variable, and (3) topographic complexity may provide complementary information on climate change vulnerability.

Climate Change Vulnerability Index (CCVI)

Ninety-nine of our 156 species (63%) were vulnerable to climate change (scored as moderately vulnerable or worse). We present a list of the top five most vulnerable species (Table 4), an annotated species list (Appendix 1), and all the information we used to make our determinations (CCVI Excel workbooks and species profiles available online; CDFG 2011). We were unable to elucidate strong relationships between species characters and vulnerability. No significant relationship was found between the CCVI vulnerability rank and California Rare Plant Rank, plant rarity type (Rabinowitz 1981), or any species life history trait considered. This suggests that direct exposure to climate change based on projected changes to future temperature and precipitation conditions within a species' range was the strongest driver of vulnerability.

One vulnerability factor from the Indirect Exposure Section (landscape configuration) was significantly (but weakly) related to the CCVI scores: anthropogenic barriers. For 99 of the 156 species, the ability to migrate to track shifting climate will likely be impeded by man-made barriers. This may reflect the fact that many rare species are concentrated in coastal areas, where population density and associated fragmentation are extremely high (e.g., the San Francisco Bay Area and Los Angeles) (Stein et al. 2000). Coastal areas support "naturally rare" plant species that have evolved or survived over time in local refugia because of cool, aseasonal climates and a high level of soil heterogeneity. Other rare plants in coastal areas were once more common and have become "anthropogenically rare" due to high levels of development and habitat loss. Whether naturally or anthropogenically rare, if these species are unable to tolerate new climate conditions and cannot find refuge from novel, intolerable climates locally, the likelihood of dispersing to a more favorable, distant location is expected to be very low given man-made barriers. These species are prime candidates for assisted migration (McLachlan et al. 2007; Richardson et al. 2009; Vitt et al. 2010).

The general inability to predict the CCVI vulnerability scores using the indirect exposure and life-history traits reflects the high importance of direct exposure (projected changes to temperature and moisture within a species' range) in calculating the overall CCVI score. This is perhaps unsurprising, given that the indirect exposure and life-history traits are weighted by direct exposure in the calculation of the final CCVI score (Young et al. 2012). While this multiplicative approach makes it difficult to identify which risk factors are most important for a group of species, it is the appropriate approach for the CCVI, because a species with zero exposure to climate change should be considered invulnerable even if it has traits that make it sensitive to climate change, and vice versa.

We found the CCVI scores were independent of both California Rare Plant Rank and rarity type. This suggests that the rarest species, such as the California Rare Plant Rank 1B species or habitat specialists with small ranges and small population sizes, are not necessarily the most vulnerable to climate change. We also found no relationship of CCVI scores with other species attribute information, including plant life-cycle duration, plant growth form, and biogeographic affinity (results not shown). This is a desirable result, as it suggests that the CCVI scores contain novel information. This is perhaps the greatest strength of the CCVI: It represents a framework for thinking exclusively about climate change vulnerability. In developing the CCVI, a goal of NatureServe was to create an index that would be as independent as possible from existing rarity ranking indices. We suggest that the CCVI score can be viewed alongside of rarity scores (e.g., California Rare Plant Rank) to identify the most vulnerable *and* rarest species.

SDM Sensitivity Analysis

Our sensitivity analysis found that SDM predictions were highly variable. The range of anomaly scores per species was very large (Fig. 3), reflecting sensitivities to the choice of predictor variables and model algorithm (i.e., Maxent, Random Forest, and boosted regression trees). Further, for 90 of the 156 species, the *direction* of the anomaly (decreasing suitability or increasing suitability) was even variable (yellow bars of Fig. 3). One of the largest sources of variability in modeled response was the algorithm. In particular, Random Forest always produced the highest anomaly scores. Despite the high variability in anomaly scores, AUC values were uniformly high (mean = 0.988, median = 0.993, range = 0.921–1.00). These high AUC values suggest that all models are equally good, despite the fact that the models make radically different predictions about future climatic suitability. This is unsurprising, as AUC values tend to be inflated for species with narrow distributions, and therefore may not adequately
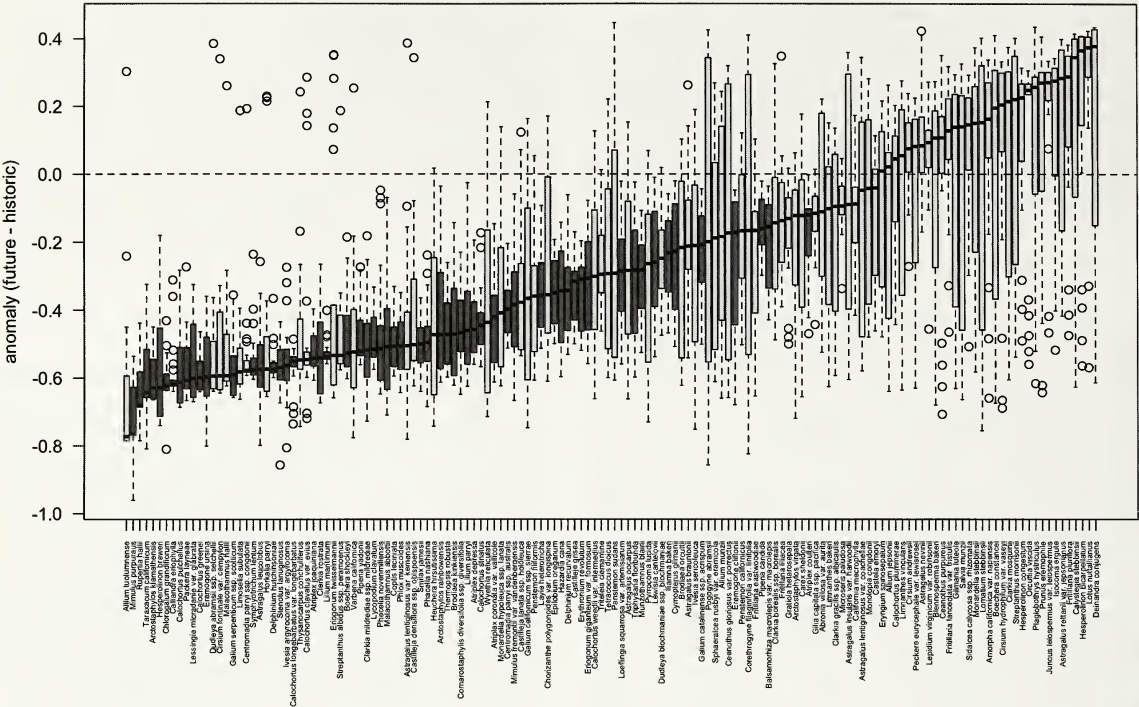
FIG. 3. Sensitivity analysis results, by species. The variation in anomaly score across 24 distribution models is represented with box plots, where open circles indicate statistical outliers. Dark grey boxes are those species whose distributions do not cross the horizontal dashed line. Light grey boxes are those species whose distributions do cross the horizontal dashed line.

capture differences in model success for rare plants (Lobo et al. 2007; Gogol-Prokurat 2011).

The variability in our modeled results is probably due in large part to working with rare species, which have few occurrences (the median number of occurrences for our species was 35) and many non-climatic factors that determine their distributions. This reflects the "rare species modeling paradox," which says that the species "most in need of predictive distribution modeling … are the most difficult to model" (Lomba et al. 2010). In other words, while it is extremely important to identify the climatic tolerances of rare species, given our conservation concerns, it is extremely difficult to make meaningful models of the climatic ranges based on the limited available information.

The variability of the modeled results is cause for concern because our CCVI scores include modeled results from just one of the 24 different models. When we excluded these modeled results from our CCVI scores, some of the CCVI scores moved up or down a score level (e.g., from highly vulnerable to moderately vulnerable or increase likely to presumed stable; see Table 4 and Fig. 4 for an example). In other words, the results of the single model used in the CCVI have a large impact on the final CCVI score, which is worrisome since modeled results are extremely

dependent on model algorithm and the choice of predictor variables. None of our species were scored as "increase likely" when we excluded the modeled results, despite that approximately half of the factors could be scored as decreasing vulnerability. Thus, the potential positive effects of climate change as measured by the CCVI were driven solely by increases in future range size predicted by SDMs. However, SDM results may be relatively reliable for predicting where suitable habitat will be in the future, compared to predicting declining suitability (Schwartz 2012). While recent advances in modeling techniques (i.e., consensus modeling, modeling clades instead of species, adding process models, factoring out spatial autocorrelation in occurrence data) may help create a model that better reflects the niches of plants, we expect that a quantitative modeling approach, in isolation, will never be sufficient to accurately predict the fate of rare species in the face of climate change.

Topographic Complexity Analysis

Our index of topographic complexity may help create a finer understanding of climate change vulnerability for our species. For example, 41 species are ranked as highly vulnerable, but they have a range of topographic complexity scores.
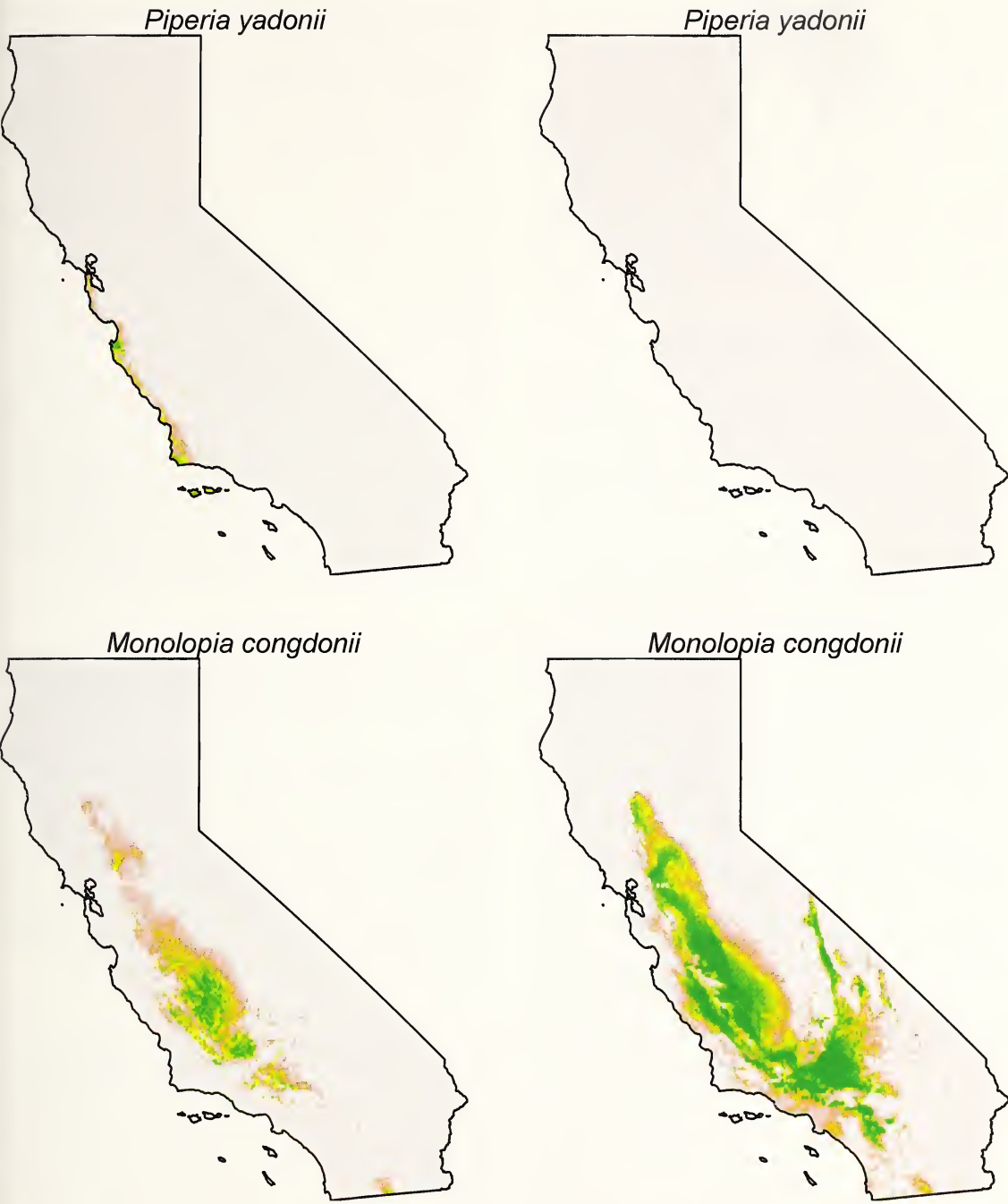
FIG. 4. Maps of the predicted current (left column) and future (right column) ranges for two vulnerable species. For *Piperia yadonii*, the predicted range loss causes the overall CCVI score to increase, from highly vulnerable to extremely vulnerable. For *Monolopia congdonii*, the predicted range gain causes the CCVI score to decrease, from extremely vulnerable to moderately vulnerable.

Thus, we can single out the highly vulnerable species that also have low topographic complexity scores as being especially vulnerable, especially if they have low dispersal ability, with the mechanistic expectation that the local topography will not be sufficient to buffer a species from region-wide climate change by providing local refugia. An additional benefit is that elevation data is available at higher resolution than climate variables, allowing for finer suitability predictions. Furthermore, topographically homogeneous places have been predicted to have faster

velocities of climate change, at least when compared at the worldwide scale (Loarie et al. 2009). That said, the relationship between local landscape features and climate is complex and is just beginning to be described (Dobrowski 2011). Moreover, the interactions among topography, soils, soil water capacity, and microclimate on plant performance remains poorly described, despite the fact that our observations suggest plants are extremely sensitive to such interactions, at least in California and, more generally, in the mid-latitudes.

CCVI for Rare Plants

NatureServe's CCVI is an excellent structure and transparent clearinghouse for information regarding climate change vulnerability. To our knowledge, it considers the most exhaustive list of extrinsic and intrinsic factors that may influence vulnerability, and also allows input of model-based results. Further, it is in use by many different groups, allowing for comparison of results. However, we've identified several problems with the CCVI as it applies to plants.

We were able to process only one species per eight-hour workday, a rate far too slow and expensive for most agencies to use for all the listed species in California. Our approach of subsetting a larger list based on rarity type had the advantage of possibly identifying particular combinations of range size, population size, and habitat specialism that cross-walk to climate change vulnerability, thus saving us the need to complete the CCVI for the remaining species. However, we found rarity type had no predictive power for the CCVI scores, and thus a detailed species-level analysis seems necessary to rank species with regards to climate change vulnerability. An alternative or complementary approach is to conduct other types of assessments, including vulnerability of landscape features (topography and connectivity) and habitats. These assessments can be completed relatively easily, and the results are perhaps more reliable, given that the connection of vulnerability scores to landscape features and habitats is less tenuous than the connection of vulnerability scores to species distributions and species ecologies. For example, most conservationists might agree that a well-connected landscape is less vulnerable to climate change than a fragmented landscape, but fewer might agree that a species with three pollinators is less vulnerable to climate change than a species with only one pollinator.

Some attributes that are important to plant vulnerability are missing, including mating system (selfing vs. out-crossing) and pollinator specificity and efficiency. We recommend that different "flavors" of the CCVI be released in the future, at least one for animals and one for plants. Also, it is nearly impossible to complete the scoring for a given plant species, because information is simply lacking. When information is lacking, the guidelines often recommend scoring the species as neutral, while "unknown" is often the more appropriate score. Also, some of the scoring guidelines are too simplistic. For example, soil endemics are scored as more vulnerable to climate change than soil generalists, while this remains an under-addressed research question (Damschen et al. 2012). A related issue is that soil specificity should be assessed as a natural barrier; currently, it is only considered a life history trait. Finally, while the CCVI accounts for species interactions in a general sense, it does not explicitly take into account invasive species, which have major impacts on California plant diversity. Invasive species can become more virulent or less virulent depending on temperature and precipitation changes, and can greatly affect a species' native habitat. For example, a recent study showed that climate shifts could increase the dominance of exotic species (Sandel and Dangremond 2012).

Conclusions

The information produced in our vulnerability assessments will be useful in identifying the most vulnerable rare plant species to climate change, which can then be carefully monitored. Moreover, vulnerability assessments are an excellent way to identify knowledge gaps and to form new hypotheses about species distributions and climatic tolerances. Viewing multiple sources of information together, including the CCVI vulnerability score, rarity ranking, topographic complexity, and a range of SDM results may give a broader picture of the overall vulnerability of a rare plant species to climate change.

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APPENDIX 1

TAXON ATTRIBUTES

For CCVI (IL = increase likely, PS = presumed stable, MV = moderately vulnerable, HV = highly vulnerable, EV = extremely vulnerable, and IE = insufficient evidence). Positive anomaly = increase in climatic suitability, negative anomaly = decrease in climatic suitability. Topographic complexity is the standard deviation of elevations within 100 m of each occurrence. Range size change = ([future−present/present]). Range overlap is the sum of area predicted to be suitable future and present, divided by the sum of area predicted as suitable at present. For rarity type g = geographic range size (l = large, s = small), p = population (l = large, s = small, h = habitat specificity (s = specialist, g = generalist).

Taxon	Family	CCVI (with D)	CCVI (without D)	Anomaly	Topographic complexity	Range size change	Range overlap	Rarity type	CA Rare Plant Rank
Abronia alpine	Nyctaginaceae	IE	HV	NA	12.16	NA	NA	gsplhs	1B
Abronia villosa var. aurita	Nyctaginaceae	IE	MV	−0.11	5.47	26.6	71.44	glpshg	1B
Agrostis blasdalei	Poaceae	IE	MV	NA	7.93	NA	NA	glpshg	1B
Allium jepsonii	Alliaceae	IL	PS	0.02	18.38	816.02	98.1	gsplhs	1B
Allium munzii	Alliaceae	HV	HV	−0.18	10.34	86.81	68.79	glplhg	1B
Allium tuolumnense	Alliaceae	PS	PS	−0.77	11.85	−99.28	0	gsplhs	1B
Amorpha californica var. napensis	Fabaceae	IL	PS	0.16	16.61	237.29	99.44	glpshg	1B
Arctostaphylos klamathensis	Ericaceae	HV	PS	−0.63	18.15	−100	0	glplhs	1B
Arctostaphylos rainbowensis	Ericaceae	HV	MV	−0.47	15.34	−76.05	19.63	glpshs	1B
Arctostaphylos virgata	Ericaceae	MV	PS	−0.12	15.34	68.31	68.31	gspshg	1B
Astragalus braumonii	Fabaceae	IL	PS	0.28	12.07	1762.4	99.99	glplhs	1B
Astragalus insularis var. harwoodii	Fabaceae	PS	PS	−0.51	7.37	46.32	49.9	gsplhg	2
Astragalus lentiginosus var. coachellae	Fabaceae	MV	MV	−0.58	10.07	−45.36	6.26	glpshg	1B
Astragalus lentiginosus var. kernensis	Fabaceae	MV	MV	−0.21	16.85	321.35	26.02	glpshs	1B
Astragalus leucolobus	Fabaceae	IL	IL	−0.09	2	912.13	92.96	glpshg	1B
Astragalus nevinii	Fabaceae	IL	PS	−0.05	2	213.28	94.39	glpshg	1B
Astragalus oocarpus	Fabaceae	IL	PS	0.08	NA	896.57	91.77	gspshg	1B
Astragalus rattanii var. jepsonianus	Fabaceae	MV	PS	−0.28	11.05	−90.24	8.82	glpshg	1B
Atriplex coronata var. vallicola	Chenopodiaceae	HV	MV	−0.46	1.92	−98.62	0	glplhg	1B
Atriplex coulteri	Chenopodiaceae	HV	MV	−0.54	3.69	−94.3	0.27	glplhg	1B
Atriplex depressa	Chenopodiaceae	HV	HV	−0.42	4.18	−87.55	8.54	glplhg	1B
Atriplex joaquinana	Chenopodiaceae	MV	MV	−0.12	5.79	−35.7	27.03	glpshg	1B
Balsamorhiza macrolepis var. macrolepis	Asteraceae	MV	MV	−0.15	12.07	−12.82	40.22	glplhs	1B
Blennosperma bakeri	Asteraceae	PS	HV	0.11	0.48	224.14	99.44	glpshg	1B
Boechera constancei	Brassicaceae	IL	PS	0.2	16.34	215.52	97.21	gspshs	1B
Boechera shockleyi	Brassicaceae	HV	HV	−0.53	18.73	−58.99	4.02	glpshs	2
Brodiaea kinkiensis	Themidaceae	MV	NA	−0.47	NA	−45.12	38.66	gsplhg	1B
Brodiaea orcuttii	Themidaceae	HV	HV	−0.22	7.06	−57.77	36.89	glplhs	1B
California macrophylla	Geraniaceae	MV	PS	−0.55	18.17	−33.13	2.02	glpshs	1B
Calliandra eriophylla	Fabaceae	HV	MV	−0.62	3.51	−86.1	0	glpshg	2
Calochortus clavatus var. avius	Liliaceae	MV	PS	−0.6	15.04	−72.63	1.68	gsplhg	1B
Calochortus greenei	Liliaceae	MV	HV	−0.55	2.57	28.38	16.27	glplhg	1B
Calochortus longebarbatus var. longebarbatus	Liliaceae	PS	PS	−0.09	9.06	45.86	69.68	glplhg	1B
Calochortus plummerae	Liliaceae	PS	HV	0.05	18.04	135.12	64.99	glpshs	4
Calochortus pulchellus	Liliaceae	HV	MV	−0.61	20.99	−100	0	gspshg	1B

APPENDIX 1. CONTINUED.

Taxon	Family	CCVI (with D)	CCVI (without D)	Anomaly	Topographic complexity	Range size change	Range overlap	Rarity type	CA Rare Plant Rank
Calochortus striatus	Liliaceae	IE	PS	NA	10	NA	NA	glpshg	1B
Calochortus weedii var. *intermedius*	Liliaceae	PS	PS	0.35	6.66	777.06	100	gspshs	1B
Calystegia purpurata subsp. *saxicola*	Convolvulaceae	PS	PS	-0.45	1.76	348.29	13.93	glplhg	1B
Calystegia stebbinsii	Convolvulaceae	MV	MV	-0.3	15.51	80.63	48.19	glplhs	1B
Carex sheldonii	Cyperaceae	MV	MV	-0.12	5.36	60.98	59.36	glplhg	2
Castela emoryi	Simaroubaceae	MV	PS	-0.5	10.13	-95.32	3.94	glplhs	2
Castilleja densiflora subsp. *obispoensis*	Orobanchaceae	PS	HV	-0.04	3.59	68.34	64.16	glpshg	1B
Castilleja grisea	Orobanchaceae	MV	PS	-0.32	NA	-46.31	45.01	gspshg	1B
Castilleja lanata subsp. *hololeuca*	Orobanchaceae	MV	PS	-0.38	NA	-73.38	14.48	glpshg	1B
Ceanothus gloriosus var. *porrectus*	Rhamnaceae	MV	PS	-0.17	11.13	9.9	45.97	gspshg	1B
Ceanothus purpureus	Rhamnaceae	IL	PS	0.11	14.55	144.83	62.28	glplhs	1B
Centromadia parryi subsp. *australis*	Asteraceae	MV	HV	-0.4	2.69	47.89	35.71	glplhg	1B
Centromadia parryi subsp. *congdonii*	Asteraceae	HV	MV	-0.58	3.82	-100	0	glplhg	1B
Chlorogalum grandiflorum	Agavaceae	HV	MV	-0.62	14.39	-73.18	0	gspshs	1B
Chorizanthe polygonoides var. *longispina*	Polygonaceae	HV	MV	-0.36	7.81	-66.91	23.6	glplhs	1B
Cirsium andrewsii	Asteraceae	PS	MV	0.08	14.78	103.46	90.99	glpshs	1B
Cirsium fontinale var. *campylon*	Asteraceae	HV	MV	-0.59	14.41	-92.19	3.1	gsplhs	1B
Cirsium hydrophilum var. *vaseyi*	Asteraceae	IL	PS	0.21	17.48	219.32	98.53	gspshs	1B
Clarkia borealis subsp. *borealis*	Onagraceae	IL	PS	-0.14	24.89	283.63	99.68	gsplhg	1B
Clarkia gracilis subsp. *albicaulis*	Onagraceae	MV	PS	-0.1	20.41	-1.32	4.67	glplhs	1B
Clarkia mildrediae subsp. *mildrediae*	Onagraceae	MV	PS	-0.52	27.34	-46.22	0.64	gsplhs	1B
Clarkia mosquinii	Onagraceae	IL	PS	0.22	23.87	842.67	100	gsplhg	1B
Clarkia rostrata	Onagraceae	MV	PS	-0.54	12.05	-78.14	0.02	glplhg	1B
Comarostaphylis diversifolia subsp. *diversifolia*	Ericaceae	MV	MV	-0.47	13.36	-56.44	2.91	glpshg	1B
Coptis laciniata	Ranunculaceae	MV	MV	-0.51	19.43	-85.03	13.6	glplhg	2
Corethrogyne filaginifolia var. *linifolia*	Asteraceae	MV	MV	-0.17	8.61	-18.55	48.86	gsplhg	1B
Cymopterus gilmanii	Apiaceae	HV	HV	-0.23	21.24	-49.55	30.96	glpshs	2
Deinandra conjugens	Asteraceae	PS	MV	0.38	8.5	536.77	99.64	glplhg	1B
Delphinium hutchinsoniae	Ranunculaceae	HV	MV	-0.57	24.74	-100	0	glpshg	1B
Delphinium recurvatum	Ranunculaceae	MV	PS	-0.34	2.52	-87.64	2.64	glplhg	1B
Dudleya abramsii subsp. *setchellii*	Crassulaceae	HV	MV	-0.6	16.71	-92.76	0.07	glplhs	1B
Dudleya blochmaniae subsp. *blochmaniae*	Crassulaceae	HV	MV	-0.25	8.79	-64.43	26.36	glplhs	1B
Dudleya parva	Crassulaceae	MV	HV	NA	19.14	NA	NA	glplhs	1B
Epilobium oreganum	Onagraceae	IE	PS	-0.35	14.24	-89.09	10.74	glpshs	1B
Eremogone cliftonii	Caryophyllaceae	MV	PS	-0.17	18.94	19.94	23.45	glplhs	1B
Eremogone ursina	Caryophyllaceae	HV	MV	-0.6	8.82	-65.31	0.03	gsplhg	2
Eriogonum giganteum var. *formosum*	Polygonaceae	MV	PS	-0.31	NA	-34.69	44.05	gspshg	1B
Eriogonum twisselmannii	Polygonaceae	MV	PS	-0.53	27.32	120.23	15.36	gsplhs	1B
Eryngium spinosepalum	Apiaceae	MV	PS	-0.31	20.28	-60.4	25.05	glplhg	1B
Erythronium revolutum	Liliaceae	PS	MV	0.01	2.55	447.4	96.34	glplhg	2
Fritillaria eastwoodiae	Liliaceae	MV	MV	-0.17	14.77	102.85	50.43	glplhg	3
Fritillaria lanceolata var. *tristulis*	Liliaceae	IL	PS	0.13	12.29	224.42	95.61	glpshs	1B
Fritillaria liliacea	Liliaceae	MV	MV	-0.14	9.34	-18.5	34.92	glplhs	1B

APPENDIX 1.   CONTINUED.

Taxon	Family	CCVI (with D)	CCVI (without D)	Anomaly	Topographic complexity	Range size change	Range overlap	Rarity type	CA Rare Plant Rank
Fritillaria pluriflora	Liliaceae	IL	PS	0.29	8.81	534.69	99.56	glplhs	1B
Galium californicum subsp. sierrae	Rubiaceae	HV	MV	−0.37	9.71	−11.08	10.24	gsplhs	1B
Galium catalinense subsp. acrispum	Rubiaceae	PS	PS	−0.21	NA	5.38	69.1	gspshg	1B
Galium serpenticum subsp. scotticum	Rubiaceae	MV	PS	−0.59	23.11	−89.14	0.63	glpshs	1B
Gilia capitata subsp. chamissonis	Polemoniaceae	MV	MV	NA	9.14	NA	NA	glplhg	1B
Gilia capitata subsp. pacifica	Polemoniaceae	PS	PS	−0.12	15.7	−36.27	60.29	glplhg	1B
Gilmania luteola	Polygonaceae	PS	MV	0.14	10.93	238.24	72.79	glplhg	1B
Gratiola heterosepala	Plantaginaceae	MV	MV	−0.13	1.79	80.04	55.28	glplhg	1B
Hazardia cana	Asteraceae	MV	PS	−0.34	NA	−68.95	26.2	gspshg	1B
Hesperevax sparsiflora var. brevifolia	Asteraceae	IE	PS	NA	NA	NA	NA	gsplhs	1B
Hesperolinon bicarpellatum	Linaceae	IL	PS	0.37	14.24	1760.49	99.99	glplhs	1B
Hesperolinon breweri	Linaceae	HV	MV	−0.63	19.09	−92.97	0.03	glplhs	1B
Hesperolinon congestum	Linaceae	PS	MV	0.23	11.55	193.2	98.58	gsplhs	1B
"Hesperolinon serpentinum"	Linaceae	IE	PS	NA	8.27	NA	NA	glplhg	1B
Heuchera hirsutissima	Saxifragaceae	HV	MV	−0.47	31.47	−95.67	0.42	glpshs	1B
Horkelia parryi	Rosaceae	MV	PS	−0.57	9.71	−73.03	0.11	glplhs	1B
Ilianna bakeri	Malvaceae	PS	MV	0.28	0.6	2093.41	100	gspshg	4
Isocoma arguta	Asteraceae	HV	MV	−0.56	9.03	−55.39	0	gspshg	1B
Ivesia argyrocoma var. argyrocoma	Rosaceae	MV	MV	−0.21	2.14	130.04	59.44	glplhs	1B
Ivesia sericoleuca	Rosaceae	PS	MV	0.27	1.86	473.82	100	gsplhg	1B
Juncus leiospermus var. leiospermus	Juncaceae	MV	PS	−0.36	10.68	−27.6	32.73	glplhg	1B
Layia heterotricha	Asteraceae	PS	HV	0.09	13.61	191.83	72.8	glpshg	1B
Lepidium virginicum var. robinsonii	Brassicaceae	HV	MV	−0.6	16.56	−90.55	0	glplhs	1B
Lessingia micradenia var. glabrata	Asteraceae	PS	PS	−0.26	35.35	79.78	58.78	gsplhs	1B
Lewisia cantelovii	Montiaceae	HV	MV	−0.54	5.79	−100	0	glpshg	1B
Lilium maritimum	Liliaceae	HV	MV	−0.46	20.46	−73.9	11.96	glpshg	1B
Lilium parryi	Liliaceae	PS	PS	−0.1	2.94	48.86	88.02	gsplhg	1B
Limnanthes bakeri	Limnanthaceae	HV	HV	−0.58	0.51	−74.57	9.24	gspshg	2
Limnanthes vinculans	Limnanthaceae	PS	MV	0.05	1.34	189.22	99.12	gspshg	1B
Limnosella australis*	Scrophulariaceae	MV	MV	−0.23	10.01	−26.14	69.1	glplhg	2
Loeflingia squarrosa var. artemisiarum	Caryophyllaceae	PS	MV	−0.29	1.36	91.98	65.3	glplhg	2
Lomatium stebbinsii	Apiaceae	PS	MV	0.15	12.3	314.06	87.31	gsplhs	1B
Lotus nuttallianus	Fabaceae	PS	HV	0.37	1.26	284.9	97.25	gspshg	1B
Lycopodium clavatum	Lycopodiaceae	MV	MV	−0.52	13.84	−76.28	21.76	gsplhg	4
Malacothamnus abbottii	Malvaceae	MV	MV	−0.51	9.17	−53.13	40.52	gsplhg	1B
Malacothamnus hallii	Malvaceae	HV	MV	−0.59	15.67	−99.79	0	glplhs	1B
Microseris paludosa	Asteraceae	PS	PS	−0.09	6.81	−6.28	55.98	glpshg	1B
Mimulus fremontii var. vandenbergensis	Phrymaceae	HV	MV	−0.39	7.87	−86.14	12.83	gspshg	1B
Mimulus purpureus	Phrymaceae	EV	HV	−0.76	4.91	−62.01	0	gsplhg	4
Monardella hypoleuca subsp. lanata	Lamiaceae	MV	EV	−0.04	3.7	247.14	98.47	glplhg	1B
Monardella stebbinsii	Lamiaceae	HV	MV	−0.41	16.07	−93.63	4	glplhg	1B
Monolopia congdonii	Asteraceae	PS	MV	0.15	37.36	261.98	100	gspshs	1B
Munzothamnus blairii	Asteraceae	MV	PS	−0.28	NA	−53.06	37	gspshg	1B

APPENDIX 1. CONTINUED.

Taxon	Family	CCVI (with D)	CCVI (without D)	Anomaly	Topographic complexity	Range size change	Range overlap	Rarity type	CA Rare Plant Rank
Orcuttia viscida	Poaceae	HV	EV	0.25	0.95	754.92	100	gsplhg	1B
Packera eurycephala var. *lewisrosei*	Asteraceae	MV	MV	0.08	25.51	472.34	75.63	gsplhs	1B
Packera layneae	Asteraceae	HV	MV	−0.61	10.8	−11.2	0.14	gspshs	1B
Penstemon californicus	Plantaginaceae	MV	MV	−0.17	11.95	−57.7	21.87	glplhg	1B
Penstemon filiformis	Plantaginaceae	IL	PS	−0.36	16.09	111.94	51.72	glplhs	1B
Penstemon sudans	Plantaginaceae	MV	MV	−0.29	12.9	34.72	75.15	gsplhg	1B
Phacelia argentea	Boraginaceae	IE	HV	NA	2.26	NA	NA	gsplhg	1B
Phacelia nashiana	Boraginaceae	MV	MV	−0.5	22.58	1.42	2.5	gsplhs	1B
Phacelia novenmillensis	Boraginaceae	MV	MV	−0.51	25.54	107.47	17.43	gspshg	1B
Phlox muscoides	Polemoniaceae	MV	PS	−0.51	12.05	−99.13	0.83	gsplhg	2
Piperia candida	Orchidaceae	MV	PS	−0.16	20.57	−30.99	56.98	glpshs	1B
Piperia yadonii	Orchidaceae	EV	HV	−0.52	8.97	−100	0	gsplhg	1B
Plagiobothrys hystriculus	Boraginaceae	PS	HV	0.26	0.26	2617.31	100	gspshg	1B
Pogogyne abramsii	Lamiaceae	MV	EV	−0.2	2.98	305.14	76.43	glplhg	1B
Prunus eremophila	Rosaceae	PS	HV	0.27	3.14	171.11	99.48	gspshs	1B
Pyrrocoma lucida	Asteraceae	PS	MV	−0.26	2.76	111.83	36.65	glplhg	1B
Rupertia hallii	Fabaceae	HV	MV	−0.68	16.8	−99.21	0	gsplhg	1B
Salvia munzii	Lamiaceae	MV	MV	0.14	13.86	−14.2	69.65	glpshg	2
Sidalcea calycosa subsp. *rhizomata*	Malvaceae	PS	MV	0.15	6.08	92.29	96.45	glplhg	1B
Smilax jamesii	Smilacaceae	MV	PS	−0.5	11.39	22.96	37.02	glpshg	1B
Sphaeralcea rusbyi var. *eremicola*	Malvaceae	PS	MV	−0.19	8.89	132.39	82.33	glpshs	1B
Stenotus lanuginosus	Asteraceae	HV	MV	−0.57	2.96	−52.78	0.9	gsplhg	2
Streptanthus albidus subsp. *peramoenus*	Brassicaceae	HV	HV	−0.53	17.7	−99.95	0.03	glplhs	1B
Streptanthus morrisonii	Brassicaceae	IL	PS	0.22	17.71	602.34	99.89	glplhs	1B
Symphyotrichum lentum	Asteraceae	HV	EV	−0.58	0.61	−39.16	2.01	glpshg	1B
Taraxacum californicum	Asteraceae	HV	MV	−0.64	7.59	−67	0	gspshg	1B
Tetracoccus dioicus	Picrodendraceae	HV	HV	−0.29	15.41	−59.52	35.55	glplhs	1B
Thermopsis robusta	Fabaceae	MV	HV	−0.47	18.41	−85.05	6.07	glpshs	1B
Thysanocarpus conchuliferus	Brassicaceae	MV	PS	−0.55	NA	−67.57	5.54	gspshg	1B
Trifolium polyodon	Fabaceae	PS	PS	−0.3	NA	40.95	88.69	gsplhg	1B
Triphysaria floribunda	Orobanchaceae	HV	HV	−0.28	9.11	−36.31	33.19	glplhs	1B
Triteleia clementina	Themidaceae	IE	MV	NA	7.84	NA	NA	gsplhg	1B
Verbena californica	Verbenaceae	MV	HV	−0.53	8.29	29.66	3.29	gsplhs	1B
Wyethia reticulata	Asteraceae	HV	PS	−0.44	9.71	−78.23	0	gsplhs	1B
Xylorhiza orcuttii	Asteraceae	MV	MV	NA	6.57	NA	NA	glpshg	1B

MORPHOLOGICAL AND ECOLOGICAL SEGREGATION OF TWO SYMPATRIC *LOMATIUM TRITERNATUM* (APIACEAE) VARIETIES IN MONTANA

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Abstract

The *Lomatium triternatum* complex is widespread in the Columbia River Basin. *Lomatium triternatum* (Pursh) J. M. Coult. & Rose var. *triternatum* and *L. triternatum* (Pursh) J. M. Coult. & Rose var. *anomalum* (M. E. Jones ex J. M. Coult. & Rose) Mathias are sympatric throughout much of their range and are reported to have similar fruit but different leaves. Plants of the two varieties repeatedly occur within 5–30 m of each other at an unusual site in northwest Montana, USA. We collected data on leaf and fruit morphological characters and habitat associations at this site to help address whether the proper taxonomic rank for these two taxa should be revised. Terminal leaflet shape and specific leaf area differed between the two varieties with little or no overlap. Fruit mericarp length and width also differed between the two varieties. These patterns are not consistent with treating *L. triternatum* var. *triternatum* and *L. triternatum* var. *anomalum* as sympatric, interbreeding, conspecific taxa. The two varieties of *L. triternatum* also occurred in different plant communities in spite of growing in close proximity: var. *anomalum* occurs with tall, leafy forbs, while var. *triternatum* is associated with xeric-adapted bunchgrasses and cushion-forming forbs. We conclude that the two varieties are better recognized as separate species.

Key Words: Apiaceae, Columbia Basin, *Lomatium triternatum*, Montana.

Lomatium is the largest North American genus in the Apiaceae with its main center of diversity in the Columbia Plateau and Intermountain West (Mathias 1938; Sun and Downie 2010). Analysis of molecular data suggests that *Lomatium* and other closely allied genera probably underwent rapid diversification during the late Tertiary (Sun et al. 2004). As a result, the genus is taxonomically difficult (Mathias 1938), with relatively few taxonomically informative morphological traits, numerous narrow endemic species (Darrach et al. 2010), and a good deal of morphological convergence (Sun and Downie 2010).

The *Lomatium triternatum* (Pursh) J. M.Coult. & Rose complex is widespread in the Columbia River Basin. The complex has been variously treated as seven species (Coulter and Rose 1900), two species consisting of seven varieties (Mathias 1938), and one species consisting of three varieties (Hitchcock et al. 1961; Cronquist et al. 1997). The complex is loosely united by the following characters: narrow involucel bracts, similar mericarp shape, and vaguely similar leaf shape. Hitchcock and Cronquist (1973), in the most recent treatment for the Pacific Northwest, use a tripartite classification with two subspecies: *L. t.* subsp. *triternatum* and *L. t.* subsp. *platycarpum* (Torr.) B. Boivin (= *L. simplex* [Nutt. ex S. Watson] J. F. Macbr.). Subspecies *triternatum* is composed of two varieties: var. *triternatum* and var. *anomalum* (M. E. Jones ex J. M. Coult. &

Rose) Mathias. Here we explore the taxonomic disposition of these two varieties. They are reported to have similar fruit but distinctly different leaves. Variety *triternatum* has bipinnate or biternate leaves with linear leaflets, while var. *anomalum* has bipinnate to tripinnate leaves with narrowly oblong leaflets. These two varieties are reported to be "wholly intergradient" (Cronquist et al. 1997), but no further information is provided. Variety *triternatum* occurs from southern Alberta and British Columbia to northern California and northern Utah, while var. *anomalum* is found sporadically from northwest Montana to eastern Washington south to southwest Oregon, across much of Idaho to northern Utah and southwest Wyoming (Cronquist et al. 1997; Consortium of Northwest Herbaria 2011).

Possession of similar morphological traits can often indicate a close phylogenetic relationship between species. Indeed, similar morphology, especially in the anatomy of reproductive structures, has long formed the basis of classical systematics (Stace 1980). However, similar morphology may actually be the result of convergent evolution rather than an indication of close phylogenetic relationship (Niklas 1997; Judd et al. 2008). Indeed, recent molecular studies show that convergent evolution has occurred in the Apiaceae, and fruit morphology in particular is reported to be a poor indicator of phylogenetic relatedness in the family (Downie et al. 2002).

Under the biological species concept, two species will rarely if ever interbreed to produce fertile offspring, but interbreeding is possible and likely in a zone of overlap between two subspecies or varieties of the same species (Mayr 1942; Stace 1980). Both *L.* var. *triternatum* and *L. t.* var. *anomalum* occur together in an unusual geologic setting in northwest Montana known as the Giant Ripple Marks. Plants of the two varieties repeatedly occur within 5–30 m of each other. The purpose of our study is to determine the degree to which these two taxa may intergrade ecologically and/or morphologically at this site in order to inform an independent assessment of their proper taxonomic rank.

Fig. 1.   Giant Ripple Marks geologic site in northwest Montana. Ripple marks are in the bottom of the valley; the ridges support *Lomatium triternatum* var. *triternatum* and have a light color from the leaves and flowers of *Eriogonum ovalifolium*. The dark areas between the ridges indicate more mesic vegetation and support *L. triternatum* var. *anomalum*.

STUDY SITE

We conducted our study in the Giant Ripple Marks at the north end of Camas Prairie Basin at an elevation of ca. 885 m, 8 km south of the town of Hot Springs on the Flathead Indian Reservation in Sanders Co., Montana (47°30.9′N, 114°35.0′W). The climate of this region is semi-arid with cold winters and hot summers. The most similar weather recording station to the study site is at Lonepine, 15 km to the north. The mean January and July temperatures are −5.2°C and 20.1°C, respectively. The average annual precipitation is 286 mm (NCDC 2012). The majority of the precipitation occurs from April through June.

The Giant Ripple Marks were formed when Glacial Lake Missoula drained during Pleistocene glacial retreats, and water poured south over passes at the north end of the Camas Prairie Valley. The water dumped its load of coarse sediments in two lines of enormous current ripples (Alt and Hyndman 1986). These ripple marks appear today as two series of low (5–20 m), parallel ridges roughly perpendicular to the main axis of the valley (Fig. 1). The vegetation of the Giant Ripple Marks is a mosaic of bunchgrass prairie on the well-drained ridges with graminoid and forb-dominated meadow vegetation and occasional vernal pools on the deeper, fine textured soils in the swales between the ridges. The tops and upper and middle slopes of the ripple mark ridges are dominated by the grasses *Pseudoroegneria spicata* (Pursh) Á. Löve, *Poa secunda* J. Presl, and *Elymus elymoides* (Raf.) Swezey and the cushion-forming forbs *Eriogonum ovalifolium* Nutt. and *Antennaria dimorpha* (Nutt.) Torr. & A. Gray. *Bromus tectorum* L. is an annual, exotic grass that is common particularly where the perennial grasses have declined due to grazing. Vegetation of the swales is currently dominated by introduced species such as *Poa pratensis* L. and *Potentilla recta* L. The most common native species in the swales include the grasses *Elymus elymoides* and *Poa secunda*

and the forbs *Lomatium triternatum* var. *anomalum*, *Artemisia ludoviciana* Nutt., and *Lupinus sericeus* Pursh.

METHODS

We located a 50-m transect across six haphazardly chosen ripple marks in early June 2009 so that approximately half of each transect was on the slope of the ridge, and the other half was in the swale at the bottom. We sampled the closest *Lomatium triternatum* plant to the transect line at 5-m intervals, providing 10 samples per transect and a total of 60 target plants. We classified each plant into either var. *triternatum* (narrow leaflet) or var. *anomalum* (broad leaflet) and measured the length and maximum width of the terminal leaflet of the lowest leaf for each plant in the field and then immediately placed the leaflet in a plant press. Senescent or damaged leaves were avoided. We dried collected leaves for 24 hr and weighed each one to the nearest mg.

Vegetation associated with each target plant was quantified by placing a 1-m^2 plot frame with the target plant in the center and estimating canopy cover of each vascular plant species into one of the following classes: 0.1%, 1%, 5%, 10%, 15%, etc. Native plot vegetation was ordinated using principal components analysis (PCA). Only species occurring in at least five plots were included in the analysis. Non-native species, such as *Agropyron cristatum* (L.) Gaertn. *Bromus tectorum*, and *Potentilla recta*, were common in some plots but were excluded from the analysis. Nomenclature follows Lesica (2012).

We collected mature fruits (mericarps) from haphazardly chosen plants of both *L. triternatum* taxa on June 18, June 24, and July 10, 2008. Length and width of randomly chosen mericarps
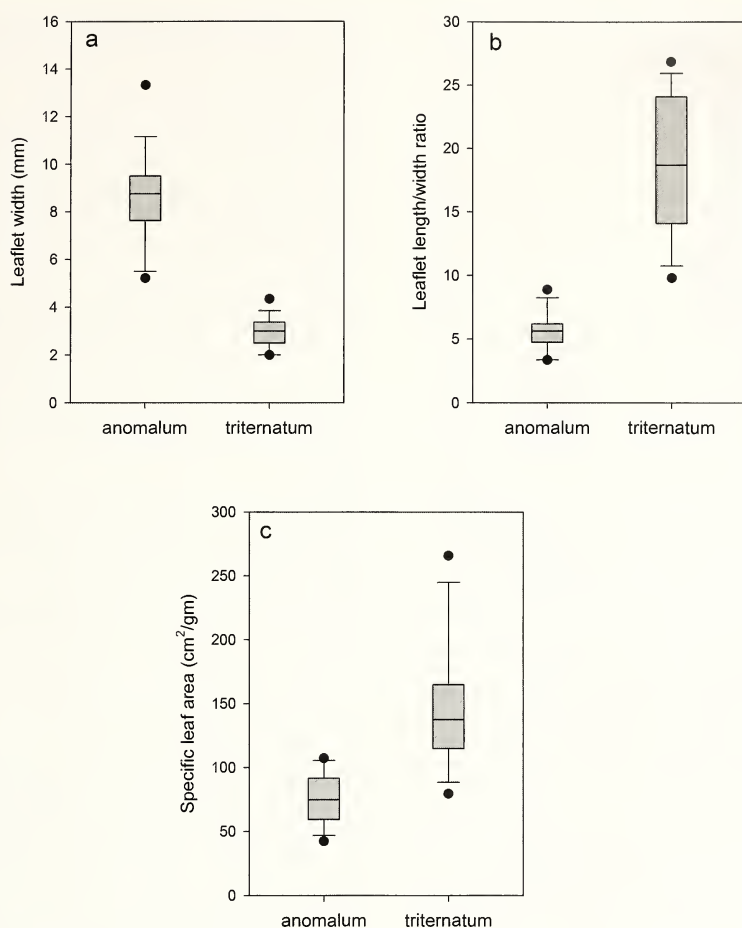
FIG. 2. Width (a), length/width ratio (shape) (b), and specific leaf area (c) for terminal leaflets of *Lomatium triternatum* var. *anomalum* and var. *triternatum*. The box represents the middle 50% of the scores with the vertical line the median; the upper and lower whiskers mark the range of values excluding outliers; the dots represent the 5th and 95th percentiles.

and their enclosed seed were measured to the nearest 0.1 mm with a dissecting microscope. Within-morphotype measurements did not differ among dates (P ≥ 0.15), so we combined measurements from different dates in our analyses to provide a sample of n = 40 for each taxon.

Leaf area (cm²) was measured on the dried leaf collections with a LI-COR 3100 area meter (LI-COR, Lincoln, NE). Surface area of each leaflet was measured three times and averaged. Specific leaf area (SLA) for each target plant was calculated as the ratio of the average of the three surface area measurements to leaf dry mass (cm²/g). We used two-sample t-tests to assess the difference in leaflet shape, specific leaf area, and fruit size and shape.

RESULTS

Shape of the terminal leaflets differed between the two varieties with little overlap. Leaflet length

did not differ between the two varieties (P = 0.11). However, leaflet width was significantly greater for *L. t.* var. *anomalum* compared to var. *triternatum* (P < 0.001; Fig. 2a), and length/width ratio for the terminal leaflet of var. *triternatum* was greater than 10 but less than 10 for var. *anomalum* (P < 0.001; Fig. 2b). Specific leaf area (SLA) also differed between varieties. Mean SLA was 148 cm²/g (SE = 9) and 76 cm²/g (±4) for var. *triternatum* and var. *anomalum*, respectively (t = 7.0, P < 0.001), and there was little overlap between the two varieties (Fig. 2c).

Some fruit characters also differed between the two varieties. Mean mericarp length was 7.0 mm (SE = 0.1) and 8.6 mm (±0.2) for var. *triternatum* and var. *anomalum*, respectively (t = 7.9, P < 0.001), and width was 4.2 mm (±0.1) and 4.8 mm (±0.1), respectively (t = 5.1, P < 0.001). However, fruit shape (length-width ratio) did not differ between the two varieties (P = 0.30). The ratio of the width of one side of the
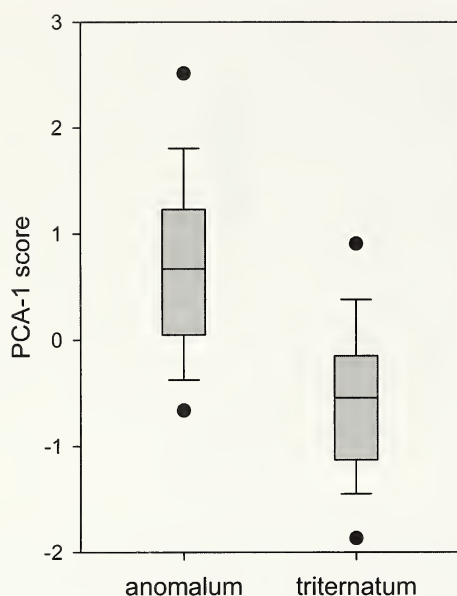
FIG. 3. First principal component analysis (PCA) scores for vegetation associated with *Lomatium triternatum* var. *anomalum* and var. *triternatum*. The box represents the middle 50% of the scores with the vertical line the median; the upper and lower whiskers mark the range of values excluding. The dots represent the 5th and 95th percentiles. Higher PCA scores were associated with more mesic vegetation.

mericap wing to the width of the enclosed seed was 0.56 (±0.02) and 0.49 (±0.03) for vars. *triternatum* and var. *anomalum*, respectively (t = 2.2, P = 0.028).

The two varieties of *Lomatium triternatum* occurred in different plant communities. The first axis of the PCA accounted for 17% of the total variation in the associated vegetation data. PCA 1 represented a gradient between xeric vegetation dominated by the grass *Pseudoroegneria spicata* and the cushion-forming forbs *Antennaria dimorpha* and *Eriogonum ovalifolium,* and a more mesic assemblage dominated by taller, leafier forbs including *Achillea millefolium* L., *Lupinus sericeus, Lomatium macrocarpum* (Torr. & A. Gray) J. M. Coult. & Rose, and *L. triternatum* var. *anomalum*. Twenty-seven plants of var. *triternatum* (84%) had a PCA-1 score <0, while 22 of var. *anomalum* plants (79%) had a score >0 (Fig. 3). Other axes were not interpretable.

DISCUSSION

The two *Lomatium* taxa discussed here were associated with different habitats at our study site. Plants assigned to var. *anomalum* were found only in swales dominated by tall, leafy forbs, while var. *triternatum* was common in more xeric, ridgetop and slope communities dominated by relatively sparse *Pseudoroegneria spicata* tussocks

and cushion-forming forbs. Different communities often host different congeners (Schluter 2000).

By definition infraspecific taxa should be interfertile to some extent where they co-occur (Stace 1980), so we would expect to find plants of intermediate morphology when two varieties of the same species are closely sympatric, as in our study area. However, these two putative varieties of *Lomatium triternatum* remain morphologically distinct in spite of occurring in close proximity. Mericarps of var. *anomalum* are larger than those of var. *triternatum* with little overlap, and leaflets of var. *anomalum* are wider than those of var. *triternatum* with no overlap. The two taxa differ in both fruit and leaf traits, which are unrelated characters likely coded for by different genetic pathways. For example, phenotypic differences in fruit and leaf traits have been shown to be attributed to different molecular traits or developmental pathways (Lippman and Tanksley 2001; Thul et al. 2009). Since traits among these two *Lomatium* taxa appear to be nearly discontinuous it suggests that they are genetically isolated in spite of occurring sympatrically.

Specific leaf area (SLA) for var. *triternatum* was nearly twice as great as for var. *anomalum*. Both infraspecific and interspecific differences in specific leaf area (SLA) have been linked to water stress (Fitter and Hay 2002; Hoffmann et al. 2005). Plants occurring in drought-prone areas tend to have lower SLA (thicker leaves) than those in more mesic environments (Reich et al. 1997; Cunningham et al. 1999; Wright et al. 2001; Hoffmann et al. 2005). Furthermore, plant species often express phenotypic plasticity in SLA—e.g., sun leaves have a lower SLA than shade leaves (Chazdon and Kaufmann 1993; Lichtenthaler et al. 2007). Thus, if the two forms of *Lomatium* were ecotypes of the same species, we would expect the swale var. *anomalum* to have a higher SLA than var. *triternatum,* which occurs in more xeric habitats. Instead, we found the opposite. Given the difference in SLA, it is unlikely that these forms are interbreeding and that morphological differences are simply a result of plasticity. In the case of these two taxa, the differences in SLA are more likely attributed to entirely different gene pools (White and Montes-R 2005), with SLA being a genetically determined morphological difference related to other traits such as water use (Nobel 1980), leaf temperature (Van Volkenberg and Davis 1977), or internal anatomical differences (Nobel 1991). SLA may not evolve independently of other morphological traits; var. *anomalum* may belong to a lineage with relatively low SLA that has been conserved along with other adaptations, such as large leaves, which correspond to its relatively mesic habitat. Our combined morphological results suggest that the two taxa are not exchanging

genes for SLA or other leaf and fruit traits and may not even belong to the same lineage within *Lomatium*. Indeed, recent molecular-based phylogenetic research indicates that the two taxa belong to separate clades (D. Mansfield, College of Idaho, personal communication).

Lomatium triternatum var. *anomalum* and *L. t.* var. *triternatum* occupy different habitats in northwest Montana and have different leaf and fruit morphologies with little or no overlap even when populations occur intermixed. In addition, differences in leaf anatomy between the two taxa are likely genetically determined. Taken together, our results from this site of sympatry support treatment of *Lomatium triternatum* var. *anomalum* as a separate species: *Lomatium anomalum* M. E. Jones ex J. M. Coult. & Rose.

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DATURA ARENICOLA (SOLANACEAE): A NEW SPECIES IN THE NEW SECTION DISCOLA FROM BAJA CALIFORNIA SUR, MEXICO

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Abstract

Datura arenicola, a new species originally collected and named by H. S. Gentry, is documented from Baja California Sur, Mexico. Following a study of *Datura* (Solanaceae) in western Mexico, the new species is placed in the new section **Discola**, with section *Dutra* emended and the revision of section *Ceratocaulis* proposed. **Datura arenicola** is found at elevations of 75–100 m on the eastern Vizcaíno Desert, and is characterized by a short basal stem, decumbent habit, pubescent lobulate leaf, prismatic calyx, violet flower, and pendant globose spiny fruit, dehiscent in four parts. The new species is known from a very limited geographical area, 12 km across the range. A description of the *Datura* on the southern Baja California peninsula and a key to the comparable species are provided.

Resumen

Datura arenicola, una nueva especie recogida y nombrada originalmente por H. S. Gentry, es documentada de Baja California Sur, México. Después de un estudio de la *Datura* (Solanaceae) en México occidental, la nueva especie se sitúa en la nueva sección **Discola**, con la sección *Dutra* enmendada y la revisión propuesta de la sección *Ceratocaulis*. **Datura arenicola** se encuentra en las elevaciones de 75–100 metros en el este del desierto de Vizcaíno, y se caracteriza por un tallo básico corto, un hábito recostado, una hoja lobulada pubescente, un cáliz prismático, una flor violeta, y una fruta espinosa globosa pendiente, dehiscente en cuatro porciones. La nueva especie se conoce en un área geográfica muy limitada de 12 kilómetros a través de la gama. Una descripción de la *Datura* en al sur de la península de Baja California y una clave de las especies comparables se proveen.

Key Words: Baja California Sur, Mexico, **Datura arenicola** sp. nov., section **Discola** sec. nov., Solanaceae, taxonomy.

The genus *Datura* L. (Solanaceae) consists of 14 annual and perennial herbs distributed nearly worldwide but originally native to the xeric, temperate, and subtropical environments of the southern United States, Mexico, and Central and South America. All are weedy or showy plants collectively known to produce psychoactive tropane alkaloids and have been employed in medicine and shamanism from prehistoric times (Gayton 1928; Kroeber 1976; Boyd 2003; Felger 2007; Moerman 2009). The succulent, semi-woody species of *Datura* are capable of autonomous selfing and have the basic chromosome number of n = 12 (Avery et al. 1959).

During the 1947 Allan Hancock Foundation expedition to Baja California, Mexico, Howard Scott Gentry discovered a new *Datura* species on the Vizcaíno Desert 30 miles south of El Arco. Gentry's specimen #7881, with the unpublished epithet "arenicola," was examined at the California Academy of Sciences (CAS/DS), the Rancho Santa Ana Botanic Garden (RSA/POM), the University of Arizona Herbarium (ARIZ), and University of California herbaria (UC), on loan to Herbario Nacional de México (MEXU). Although it was labeled by Gentry "sp. nov.," this *Datura* has not been treated in any floristic account of the Baja California region

(Martínez 1947; Shreve and Wiggins 1964; Coyle and Roberts 1975; Wiggins 1980; Roberts 1989; León de La Luz et al. 1991; SDNHM 2009). Live plants were examined in November of 1983 at El Vizcaíno Junction, near Gentry's original location. Requiring additional data, Dr. Robert Bye of the Jardín Botánico, Instituto de Biología, Universidad Nacional Autónoma de México (UNAM), directed the January 2010 field project: Diversidad de *Datura* (Solanaceae) en la Reserva de la Biosfera El Vizcaíno. The present work contributes to the morphology and ecology of **Datura arenicola**. The chemical, cladistic, cytologic, DNA, and phenetic analyses may be available in future publications through the Instituto de Biología, UNAM. A native of Baja California Sur, this new taxon in the genus *Datura* (Bye 2001) is affiliated with the newly defined section **Discola**. The new species is known from a very limited geographical range with only two colonies located 12 km apart.

Taxonomy

Datura arenicola Gentry ex D. R. A. Watson, sp. nov. (Figs. 1, 2B, 3A–D).—TYPE: MEXICO, Baja California Sur, eastern Vizcaíno Desert, 30 miles south of El Arco, 23 Nov 1947, *H. S.*
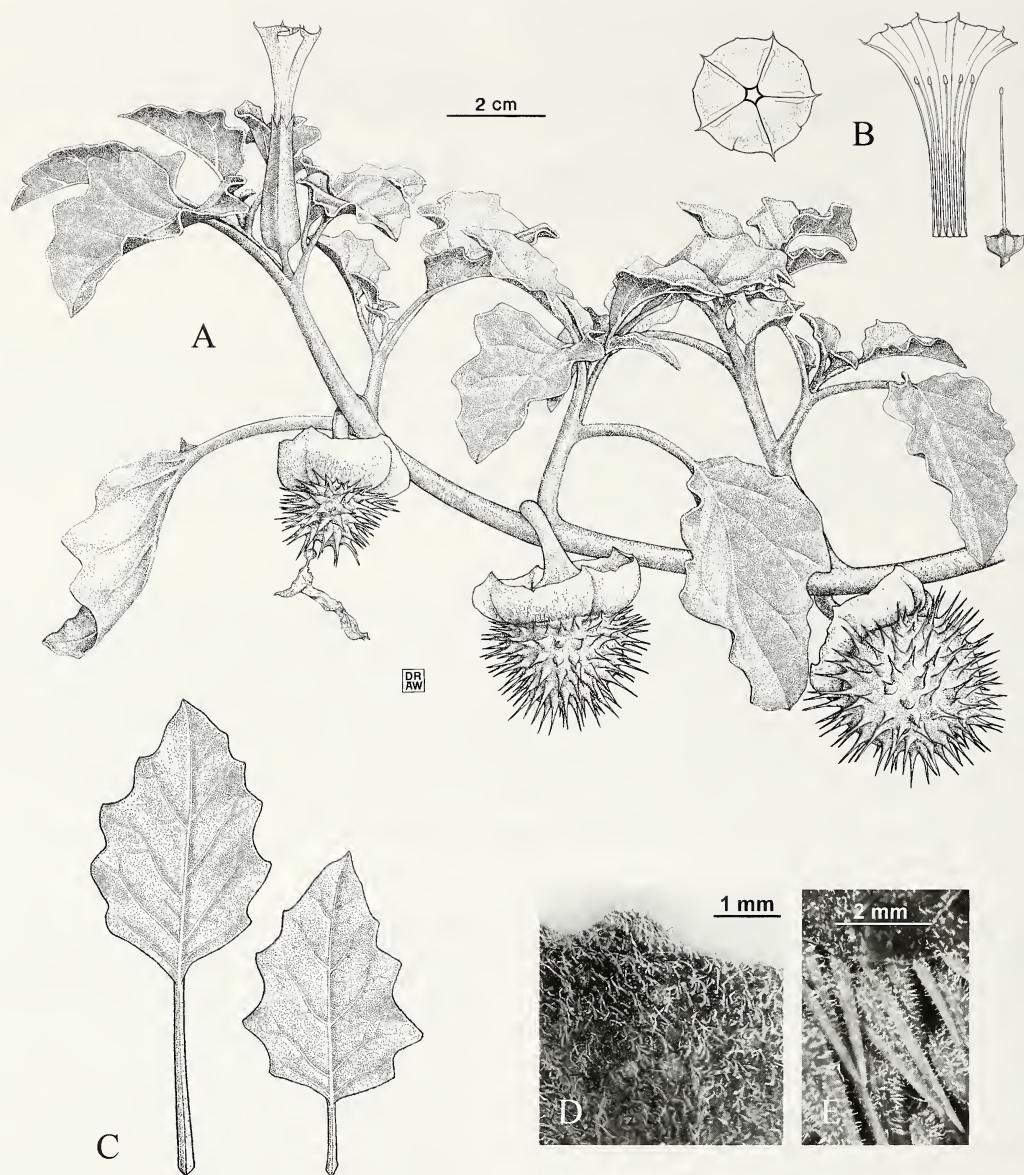
Fig. 1. *Datura arenicola*. **A.** primary branch. **B.** Corolla margin, with dissection showing anthers and stamen. **C.** Typical leaf types (*001 Watson* F). **D.** Non-glandular trichomes on desiccated leaf blade, and **E.** trichomes on spines of immature fruit. Illustration by Robert Watson.

Gentry 7881 (holotype: CAS; isotypes: ARIZ, RSA, SD, UC, UM, US).

Plantae annuae, altis 10–25 cm, diametris 32–140 cm, altitudinibus caulicium principalium comparate brevibus, ramis brevibus, erectis, foliis portatis singulariter, petiolis longis, villosis, laminis ± ovatis, marginibus sinuosis, apicibus obtusis-rotundatis, faciebus abaxialibus canescentibus, faciebus adaxialibus pubescentibus, floribus portatis singulariter, pedicellis erectis sub anthesi, reflexis ubi fructificantibus, calycibus oblongis-tubularibus, 5-costatis, in sectione transversali 5-angulatis, corollis violaceis, infundibulariformibus, limbis expansis vel ascendentibus, 2.8–4.5 cm longis, 5-lobatis, apicibus loborum subulatis, antheris dilutis luteis, fructibus pendulis, fere globosis, dehiscentibus in 4 partibus, seminibus nigris, compressis, testis laevibus, tumidis circa incisuram hili, marginibus externis subtiliter foveolatis, arillis elongatis.

Annual herbs 10–25 cm tall with decumbent branches spreading up to 1.4 m in diameter. Dichotomously branched, but appearing to divide by four stems from a basal stem 0.5–4.5 cm in height, the stems green speckled purple, glabrous. Leaves bluish-green, cinereous, pubescent above, canescent beneath, blades 4–9 cm long and 3.5–
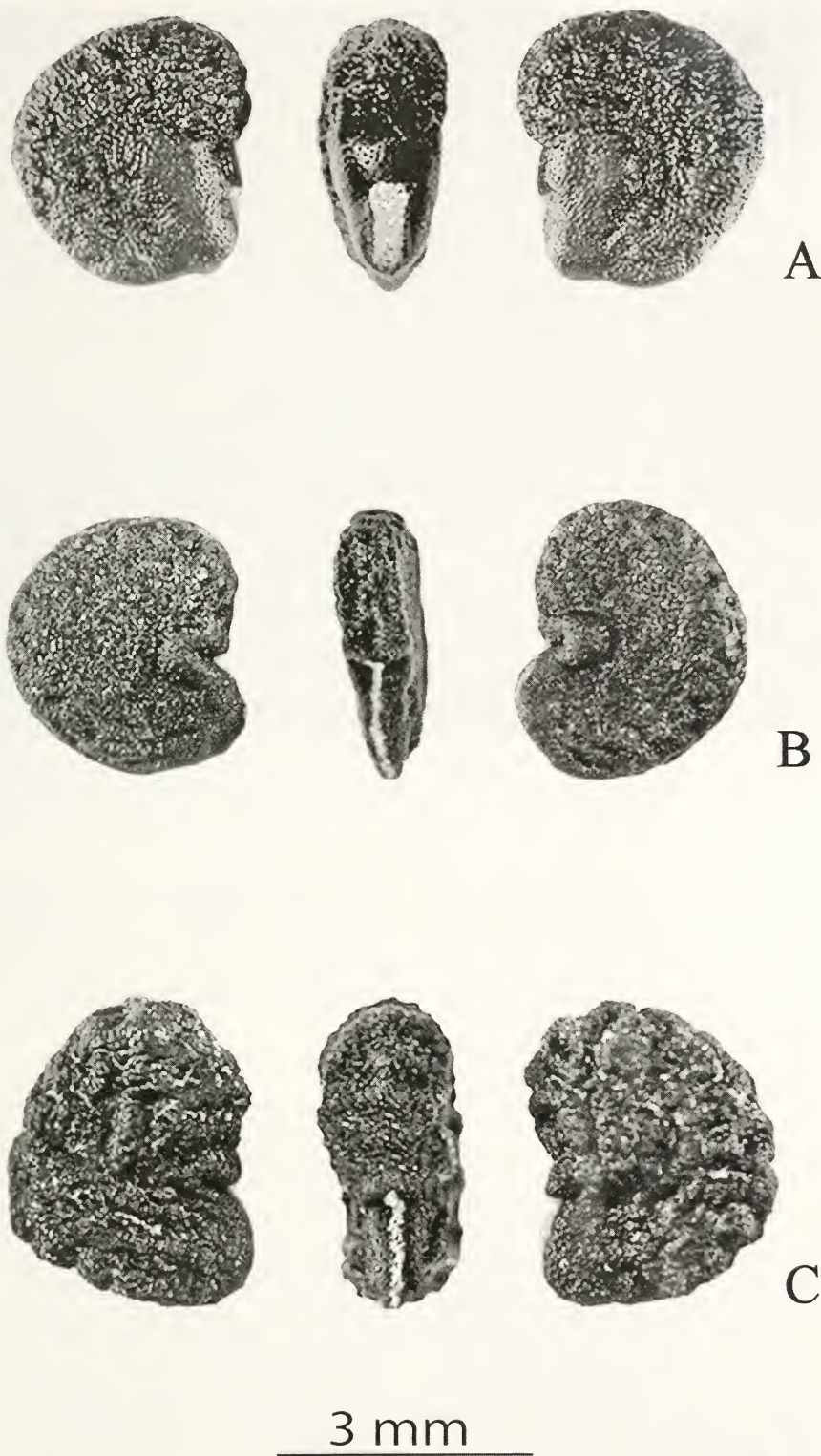
FIG. 2.   Seed-character transference is indicated by the testa foveae and inflation around the hilum of **A.** *Datura quercifolia* and **B.** *D. arenicola*, which displays the compressed D-shape with elongate aril common to section *Dutra* and the transversely notched hilum that is characteristic of **C.** *D. discolor*. Photographs by Robert Watson unless credited.
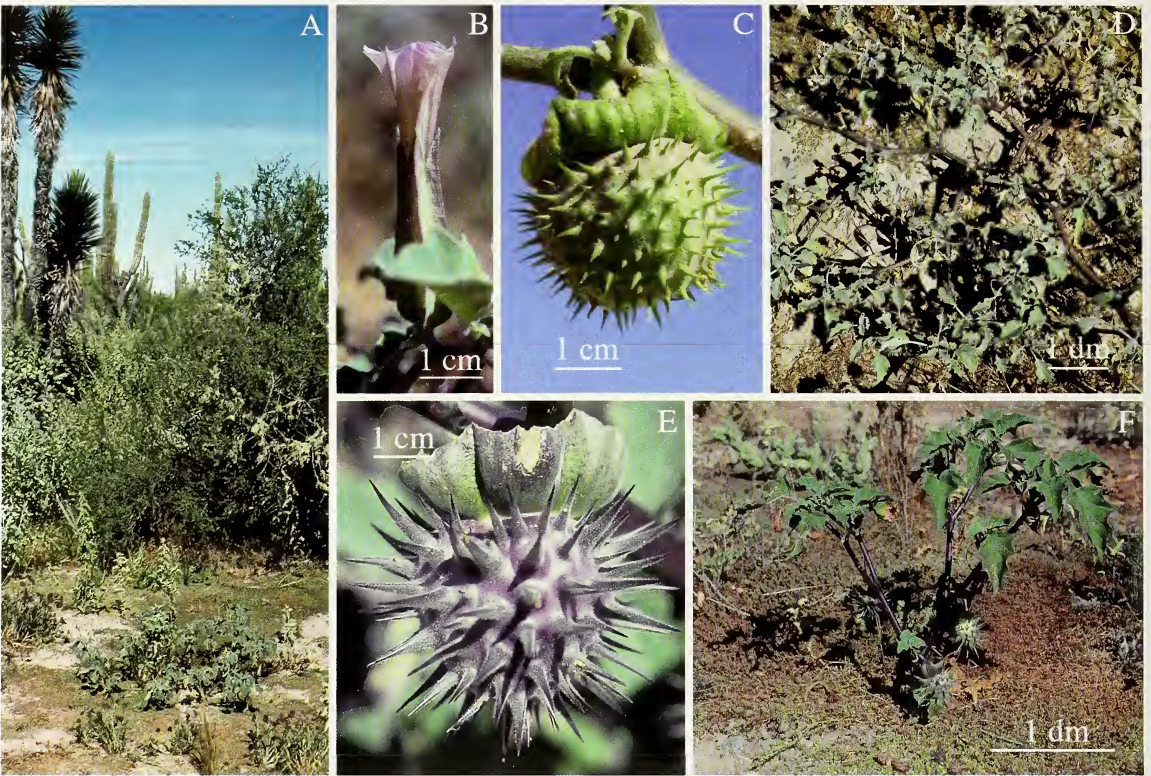
FIG. 3. *Datura arenicola*. **A.** Habitat. **B.** Flower in early anthesis. **C.** Capsule (photograph by Robert Bye). **D.** Specimen from El Vizcaíno Junction (*001 Watson* F). *Datura discolor* form *B* flower as in Figure 6F, **E.** capsule with spines suggesting *Ilex* aneuploidy, and **F.** dimorph with sinuate-dentate leaves from El Vizcaíno Junction (*002b Watson* F).

7.1 cm wide, acutely pointed ovoid, sinuous, with three to five obtusely dentate lobes along the undulating margins; petioles 1.5–6.8 cm long, villous, green with violet stripes, terete with a shallow groove on the upper side. Flowers tubular to funnel shaped, solitary, axillary, erect on 4–6 mm long pedicels; corollas deep purple to pale reddish violet becoming white toward the base, the tube 2.3–4.5 cm long, the flared lobes spreading 0.5–2.5 cm in diameter at the rim, crowned with five caudate lobes 1.7–2.6 mm long; stamens filiform, adnate one third the corolla tube length, anthers pale yellow 2.2–2.4 mm long and 1–1.3 mm wide; styles included, 2.1–2.9 cm long; calyces 1.6–3.6 cm long, one half to two thirds the length of the corollas, green with a purple tinge, oblong tubular, with five prismatic ribs, terminating in five acumina 2.5–7.8 mm long and 1.5–3 mm wide at their base, circumscissile, leaving a persistent rotate collar forming a membranous cap 2.2–4.1 cm in diameter above the mature fruits. Capsules globose, pale green, 2–3.4 cm long, 2.3–3.6 cm in diameter (excluding spines), dehiscing regularly by four valves, puberulent to pubescent, nodding on a recurved pedicel 1.8–2 cm in length; pericarp spinose, spines 0.4–1 cm long, sub-equal in length; ovary 2-locular. Seeds black,

compressed reniform, 3–3.4 mm long, 2.5–3.3 mm wide, 1 mm thick, the lateral surfaces of the testa smooth with minute foveae along the dorsal margins, inflated on both sides at the transverse notch of the hilum, aril elongated.

ASSOCIATIONS

The central Baja Californian province includes species from both tropical and temperate climates and is floristically distinguished by plants of southern Mediterranean-Tropical distribution (Peinado et al. 2009). According to Wiggins (1969), "Greater variety among the plant species is the rule along the eastern margin of the Vizcaíno Desert." He listed common plants in this area as: *Yucca valida* Brandegee, *Lycium californicum* (Nutt.) ex A. Gray, *L. berlandieri* Dunal, *Larrea tridentata* (Sessé & Moc. ex DC.) Coville, *Encelia farinosa* A. Gray ex Torr., *Cylindropuntia cholla* (F. A. C. Weber) F. M. Knuth, *C. calmalliana* (J. M. Coult.) F. M. Knuth, *Lophocereus schottii* (Englem.) Britton & Rose, *Stenocereus gummosus* (Englem.) A. C. Gibson & K. E. Horak, *Atriplex barclayana* (Benth.) D. Dietr., *A. canescens* (Pursh) Nutt., *Bahiopsis deltoidea* (A. Gray) E. E. Schill. & Panero, *Eriogonum scalare* S. Watson,

Euphorbia xanti Englem. ex Boiss., *Stillingia linearifolia* S. Watson, and *Pachycereus pringlei* (S. Watson) Britton & Rose. The common associates of *D. arenicola* are *Cenchrus palmeri* Vasey (desert sand burr) and *Datura discolor* Bernh. (desert thorn apple). The major herbivores include *Trichobaris compacta* (Curculionidae), *Lema daturaphila* (Coleoptera) and the "large moth larvae" listed on Gentry's label that was perhaps a species of *Manduca* (Sphingidae), the hawkmoths known to pollinate *Datura*.

Growing in sandy alluvium on the Pacific slope, *Datura arenicola* is a rare endemic native only to the Vizcaíno Region of the Sonoran Desert. The local campesinos call it *chamica*, as distinct from *tolguacha*, which in this area refers to the larger flowering *D. discolor*, also known as *toloache* elsewhere in Mexico. In allusion to *D. discolor*, Wiggins (1980) and Roberts (1989) mistakenly extend the range of *D. inoxia* Mill. throughout Baja California, the result of treatment by Barclay (1959) and Fosberg (1959) for the Sessé & Mociño plant previously known as *D. meteloides* DC. ex Dunal. This confusion was resolved on examination of BCMEX specimens which confirm that species to be *D. wrightii* Regel, a native of the coastal cismontane north of the 30th parallel, but also wrongly cited throughout the peninsula by Ewan (1944) and Wiggins (1980). Excluding *D. wrightii* cultigens, only *D. discolor* is found crossing the peninsula from 125 km north of the type locality, eastward in the watershed of the Sierra San Francisco and Sierra Guadalupe, to the south on the Pacific seaboard, along the Gulf coast and throughout the southern Cape region (Fig. 4). A description of this highly adaptable and widespread regional species is essential for taxonomic accuracy and in order to better understand relationships among the *Datura* on the Baja California peninsula.

Datura discolor Bernh. Über die Arten der Gattung *Datura*. Neues Journal der Pharmacie 26(1):149; 1833. Linnaea VIII. Litt. Ber.:138. (Figs. 5, 2C, 3E–F, 6A–I).—TYPE: DUTCH WEST INDIES [Netherlands Antilles], Curaçao (holotype: *Stramonia corassavica humilior*. Hermann, P. 1698. Paradisus Batavus. 1:233–234; lectotype: icon [Fig. 5]). In synonymy; *Datura thomasii* Torr. 1857 [1858]. Pacific Railroad Report. 5(2):362–363; 1857. United States and Mexican Boundary Survey 2(1):155. Commonly found on sandy flats, arroyos, margins of cienegas, playas, and roads throughout the Sonoran Desert and lower Baja California, sporadic on the Central Mesa, but largely native to tropical maritime Mexico and the West Indies.

Annual herbs, erect, 10–80 cm in height. Dichotomously branched, basal stem and branches green, or tinted violet to dark purple, glabrous with indumenta of simple and glandular hairs. Leaves green, glabrate to puberulent, sometimes cinereous,
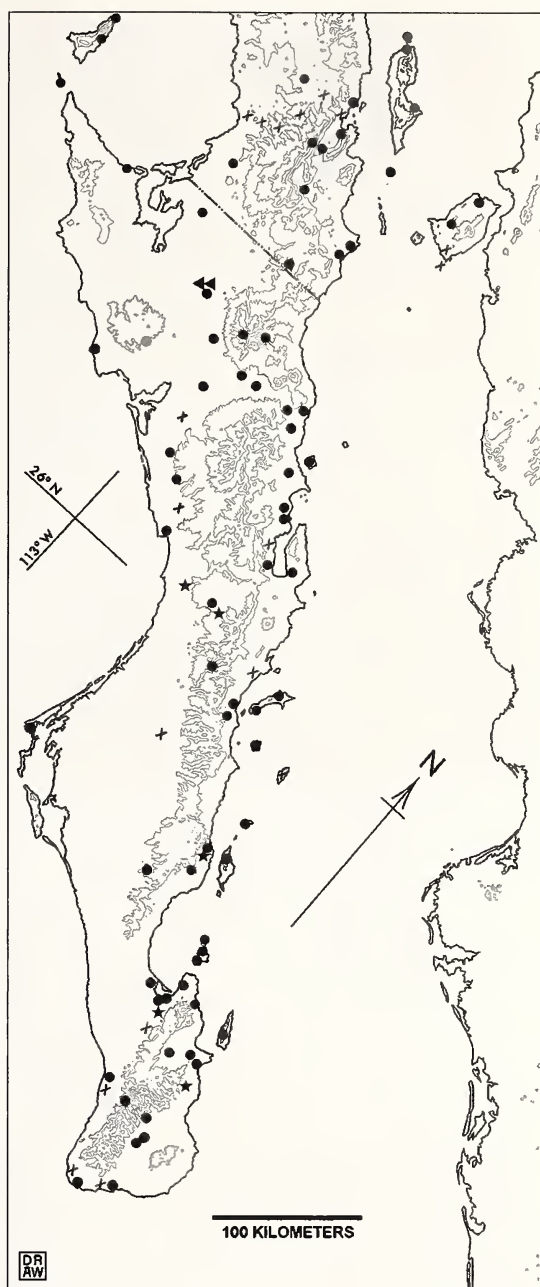
FIG. 4. Distribution of *Datura* species in Baja California Sur, Mexico; ▲ *D. arenicola*, ● *D. discolor* specimen vouchers, ✕ *D. discolor* field locations, and ★ *D. wrightii*. Map by Robert Watson, adapted from Landsat, contour elevations at 500 m. Biodiversity occurance data published by: Instituto de Biología, Universidad Nacional Autónoma de México (Accessed through GBIF Data Portal, data.gbiforg, 2013-08-12).

blades 3–15 cm long and 3–13 cm wide, acutely pointed ovoid to deltoid, entire to angular-sinuate but commonly bearing three to five acutely dentate lobes along each margin; petioles 1.5–8.8 cm long, green to purple, terate with a shallow groove on the

p.233.

STRAMONIA
Coraßavica humilior.

FIG. 5.   *Datura discolor* lectotype engraving of *Stramonia corassavica humilior*. Hermann, P. Paradisus Batavus. 1698:233–4 (seeds actual size). Courtesy of the Hunt Institute for Botanical Documentation, Carnegie Mellon University, Pittsburgh, PA.

FIG. 6. *Datura discolor*. **A.** Capsule, San Ignacio (*003d Watson* F). **B.** Corolla apex and **C.** side view of a Cabo San Lucas phenotype (*007 Watson* F). **D.** Heat reflectance defined by Kodak infrared film. **E.** The violet floral variant, Cedros Island (photograph by Jon Rebman). **F.** Form *A* flower, **G.** capsule, and **H.** dimorph with entire leaves from El Vizcaíno Junction (*002a Watson* F). **I.** Xerophyte flower at full anthesis, La Paz (*004 Watson* F).

upper side. Flowers tubular to trumpet shaped, solitary, axillary, erect on 4–6 mm long pedicels; corolla exterior greenish-yellow to yellowish, white, or violet becoming white toward the base, with five or more violet striae inside the throat, usually appearing as a ring, hence, the Latin epithet meaning "two colors," the tube 6–18 cm long with the flared limb spreading 1.2–8 cm in diameter, crowned with five subulate lobes 1.7–9.5 mm long, separated by angular interlobules giving the appearance of 10 acumina; stamens filiform, 6–14 cm long, adnate one third the corolla tube length, styles 6.4–10.4 cm long, anthers off-white, 3.7–9 mm long, and 1.5–2.8 mm wide; stigma below the anthers; calyces 3–9 cm long, two fifths to two thirds the length of the corolla, green or purple tinged, oblong tubular, with five prismatic ribs terminating in five acumina 4.5–15 mm long and 3.1–6 mm wide at their base, circumscissile, leaving a persistent rotate collar forming a membranous cup-shaped brim 1.5–5.8 cm in diameter above the mature fruit. Capsules ovoid, pale green to purple, 2.6–4.5 cm long, 1.5–3.8 cm in diameter (excluding spines), dehiscing regularly by four valves, sparsely puberulent to pubescent, nodding on a recurved pedicel 1.8–2 cm in length; pericarp spinose, spines 0.8–3.2 cm long, sub-equal

in length, a few occasionally missing; ovary two-locular. Seeds black, compressed reniform 3.1–4.2 mm long, 2.4–3.5 mm wide, 1.2–1.7 mm thick, lateral surfaces of the testa verrucose and rugulose, hilum transversely notched, aril elongated.

The phyletic plasticity observed in *D. discolor* requires further research. During the January 2010 central Gulf coast survey, individuals of *D. discolor* were observed with white or occasionally deep violet corollas (Fig. 6E). Thus *D. discolor* displays floral variants analogous to *D. stramonium* L., a genome that carries dominant violet (var. *tatula*) and recessive white (var. *stramonium*) alleles (Avery et al. 1959). During the Baja California survey in November of 1983, individuals of *D. discolor* were observed in warmer temperatures with yellowish to white corollas only, some of which were tinted violet at the rim but otherwise were identical to the whiter phenotypes (Fig. 6B, C). Bright sunlight and cool temperatures appear to trigger the violet floral variants, which produce an infrared reflective chromophore (Fig. 6D). Xerophytes occur along Gulf shorelines with 6 cm long, tubular, greenish-yellow corollas (Fig. 6I; *3226 Johnson* CAS), whereas the synonym *D. thomasii* (Torrey 1857) specified plants with dwarf corollas from

the extremely arid Colorado Desert (*015 D. R. A. Watson* F). Consistent with the leaf studies made by Ewan (1944), ancestral remnants of this widespread *Datura* may be preserved on the periphery of the range. For example, the West Indian *D. discolor* lectotype (Fig. 5), which Fosberg (1959) considered problematic, resembles in flower and fruit El Vizcaíno forms A and B (Fig. 6F, G). Forms A and B differ from peninsular *D. discolor* with over-sized calyces two thirds the length of the delicate corollas, dimorphic leaves either entire or dentate, and variation in fruits (Figs. 3E, 6G) suggesting some of the aneuploid forms described by Blakeslee in *D. stramonium* (Avery et al. 1959). *Datura discolor* is primarily identified by its uniquely wrinkled seed coat, associated with a prismatic calyx, violet striped corolla throat, and pendant spiny oval fruit.

Discussion

All species of *Datura* can be easily differentiated by variations in flower, fruit, and seed morphology. The seed of *D. arenicola* is clearly distinct from all other species in the genus (Fig. 2). However, seed character similarities can be observed in the testa foveae and inflation around the hilum in *D. arenicola* and *D. quercifolia* Kunth (1818). The compressed D-shape with elongate aril is common in seeds of section *Dutra*, but the transversely notched hilum is an attribute of *D. discolor*. The leaves and pendant capsules of *D. discolor* are very similar to *D. arenicola*, but in the latter the leaves are lighter bluish-green, undulate along the obtusely dentate margins, and the smaller globose fruits have relatively shorter spines (Fig. 3C, D). According to Felger (2000) *D. discolor* is one of the largest-flowered plants in the Sonoran Desert, however the flowers of some *D. discolor* xerophytes, as well as *D. quercifolia*, and *D. arenicola* are among the smallest in the genus *Datura*. The diminutive violet flower of *D. arenicola* strongly resembles that of *D. quercifolia*, along with a decumbent habit that is greater in width. Research into the legitimate priority of *D. gigantea* C. Huber (1867), also described as "low in height and very much wider in width," has confirmed the binomial to be a synonym of *D. quercifolia* from western Mexico (Watson 2012). The morphometric data provided in Table 1 display the character ranges and median (in parenthesis) of 24 *D. discolor* and 12 *D. arenicola* plants examined in herbaria and in the field November 1983 and January 2010.

Gentry noted *D. arenicola* grew on the lee side of dunes, but the typical disturbed areas in which the species prefers to grow today are found along graded roads. Such habitat disruptions have been correlated with germination in the genus *Datura*. The "sand dwelling" *Datura* exhibits adaptations

that may limit its dispersal to sandy habitats; *D. arenicola* has a short basal stem, decumbent posture, and more developed tap root system, while *D. discolor* rises on an elongate basal stem with a tap root typical of section *Datura*. Similarities to *D. quercifolia*, a representative of section *Datura*, may be the result of long-distance dispersal from an ancestral stock. The "oak leaf" *Datura* grows naturally in eastern Texas, southern New Mexico and Arizona, from the Colorado River in Baja California through the Sierra Madre Occidental, the Central Mesa, and the Sierra Madre Oriental (Luna-Cavazos and Bye 2011).

Within the genus *Datura*, three classical sections have been historically recognized. The widest-ranging section *Datura* L. (formerly section *Stramonium* [Tourn.] Bernh.), which includes *D. stramonium*, *D. ferox* L., and *D. quercifolia*, is distinguished by prismatic calyces, erect capsules dehiscing regularly by four valves, and black seeds. Section *Ceratocaulis* (Spach.) Bernh. is considered to be monospecific, including only the hydrophilic *D. ceratocaula* Ortega, which is characterized by tubular calyces, smooth pendant fruits dehiscing irregularly, and charcoal brown seeds. Section *Dutra* Bernh. with tubular calyces, pendant capsules dehiscing irregularly, and brown, reddish brown to buff-yellow seeds, has been divided into two sub-sections (Jiao et al. 2002; Luna-Cavazos et al. 2008): the tuberous-rooted perennials, *D. metel* L., *D. inoxia*, *D. velutinosa* V. Fuentes, *D. wrightii*, and *D. lanosa* Barclay ex Bye; and the tap-rooted annuals, *D. kymatocarpa* Barclay and *D. leichhardtii* F. Muell. ex Benth. (subsp. *pruinosa* [Greenm.] A. S. Barclay ex K. Hammer; in synonymy, *D. pruinosa* Greenm.). On occasion, *D. discolor* and *D. reburra* Barclay have been incongruously included in section *Dutra*.

Sectional Revisions

The 14 accepted species of the genus *Datura* may be separated into four sections (Table 2) as the result of several recent investigations. Based on the prismatic calyces and pendant capsules dehiscing regularly by four valves, *D. discolor* and *D. reburra* belong to an unnamed section proposed by Jiao et al. (2002), bridging sections *Datura* and *Dutra*. This new section was provisionally characterized by Mace et al. (1999) as section IV, *Discolor*. Cytology, phenetic and allozyme analyses (e.g., Palomino et al. 1988; Jaio et al. 2002; Luna-Cavazos et al. 2000), along with AFPL (Mace et al. 1999) and peroxidase isozyme studies (Conklin and Smith 1971; Fuentes 1983; Xiqués et al. 1986; Luna-Cavazos et al. 2008) establish the quantifiable validation for a new section diagnosis.

It is proposed that specific members of section *Dutra* be divided into two sections: *Datura* L.

TABLE 1.   MORPHOMETRIC COMPARISON OF DATURA DISCOLOR AND D. ARENICOLA.

Character	*D. discolor* (median)	*D. arenicola* (median)
Root length	14.0–23.0 cm (18.5 cm)	19.0–35.0 cm (30.0 cm)
Plant height	20.0–80.0 cm (30.0 cm)	10.0–25.0 cm (21.0 cm)
Plant width	17.0–67.0 cm (29.5 cm)	32.0–140.0 cm (60.0 cm)
Caulis height	4.0–45.0 cm (18.0 cm)	0.5–3.5 cm (1.3 cm)
Caulis width	0.7–1.7 cm (1.2 cm)	0.5–1.5 cm (0.9 cm)
Petiole length	1.5–8.8 cm (4.7 cm)	1.5–6.8 cm (5.2 cm)
Petiole width	0.3–0.5 cm (0.3cm)	0.3–0.4 cm (0.3 cm)
Leaf-5th node length	4.0–14.2 cm (7.1 cm)	4.0–9.0 cm (7.3 cm)
Leaf-5th node width	4.0–13.0 cm (5.3 cm)	3.5–7.1 cm (5.9cm)
Corolla length	6.0–18.0 cm (10.2 cm)	2.3–4.5 cm (3.6 cm)
Corolla width	2.0–7.8 cm (5.2 cm)	0.5–2.5 cm (1.4 cm)
Corrola acumen length	3.1–9.5 mm (4.0 mm)	1.7–2.6 mm (1.8 mm)
Style length	6.4–10.4 cm (9.3 cm)	2.1–2.9 cm (2.6 cm)
Anther length	3.7–8.6 mm (6.2 mm)	2.2–2.4 mm (2.5 mm)
Anther width	1.5–2.8 mm (1.8 mm)	1.0–1.3 mm (1.1 mm)
Calyx length	3.4–9.0 cm (6.3 cm)	1.6–3.6 cm (2.6 cm)
Calyx width	0.8–1.7 cm (1.6 cm)	0.7–1.0 cm (0.79 cm)
Calyx acumen length	4.5–12.9 mm (8.4 mm)	2.5–7.8 mm (4.1 mm)
Calyx acumen width	3.1–4.0 mm (3.2 mm)	1.5–3.0 mm (2.4 mm)
Calyx rotate collar height	0.7–1.5 cm (1.3 cm)	0.5–1.2 cm (0.7 cm)
Calyx rotate collar width	2.6–5.8 cm (4.3 cm)	2.2–4.1 cm (2.5 cm)
Capsule height	2.6–4.3 cm (2.9 cm)	2.0–3.4 cm (2.2 cm)
Capsule width	2.2–3.8 cm (2.7 cm)	2.3–3.6 cm (2.5 cm)
Spine length longer	12.5–25.2 mm (16.0 mm)	3.9–10.0 mm (5.5 mm)
Spine length shorter	10.3–20.0 mm (11.3 mm)	2.9–7.3 mm (4.9 mm)
Seed length	3.2–3.8 mm (3.5 mm)	3.0–4.0 mm (3.5 mm)
Seed width	2.7–3.4 mm (2.8 mm)	2.5–3.3 mm (3.2 mm)
Seed thickness	1.2–1.7 mm (1.5 mm)	1.0 mm (1.0 mm)

sect. *Dutra* (Bernh.) emend. D. R. A. Watson *sensu stricto*, with *D. metel*, *D. inoxia*, *D. velutinosa*, *D. wrightii*, and *D. lanosa*, and a new section established for *Datura*.

Datura L. sect. **Discola** D. R. A. Watson, sect. nov.—TYPE: *Datura discolor* Bernh.

Plantae annuae, calycibus in sectione transversali 5-angulatis, fructibus pendulis dehiscentibus in 4 partibus.

Morphology determines that section *Discola* includes *D. discolor*, *D. reburra*, and *D. arenicola*, based on prismatic calyces, pendant capsules dehiscing regularly by four valves, and black to brown seeds. The analogous etymology is Latin for "of another habitat," distinguishing the coastal shelf distribution of *Datura* annuals with prismatic calyces and pendant seed capsules.

KEY TO DATURA ARENICOLA AND COMPARABLE SPECIES WITH PRISMATIC CALYCES

1. Fruit erect: Section *Datura* L. (following Hammer et al. 1983) . . . . *D. quercifolia*
1' Fruit pendant: Section *Discola* D. R. A. Watson (following Mace et al. 1999; Jiao et al. 2002)
   2. Corolla 6–18 cm; capsule ovoid; seeds rugulose; leaves glabrate to puberulent, entire to angular-sinuate, or bearing acutely dentate lobules . . . . *D. discolor*
   2' Corolla 2.3–4.5 cm; capsule globose; seeds smooth; leaves pubescent to shortly vil-

lous, bearing obtusely dentate lobules . . .
. . . . *D. arenicola*

It seems plausible that the four sections in the genus *Datura* correlate to geological epochs, orogenic influences, and climatic changes. At one time considered a section of the genus *Datura* (Bernhardi 1833), the tree daturas of the genus *Brugmansia* Pers. diverged during the Andean uplift in the late Tertiary (Lockwood 1973). This implies an earlier ancestral lineage that in all probability has evolved into the widest-ranging section *Datura*. Apparently the widespread *D. discolor* of section *Discola* populated the Sonoran Desert following increasing aridity in the late Tertiary (Axelrod 1950). As indicated by Dr. Robert Bye (UNAM, personal communication), the spineless *D. ceratocaula* emerged with central Mexico's Neovolcanic orogeny, which closed off the Balsas depression, inundating the Central Mesa during the Pliocene-Pleistocene. Thus species in section *Dutra* most likely evolved tubular calyces and irregularly dehiscent fruits during the Pleistocene pluvial period; when the epicarp ceased to dry and shrink, the spines no longer functioned to open the capsule valves. Considering the Neovolcanic influence and climate change over the biogeographic provinces, it is proposed that section *Ceratocaulis* be revised to include the Balsas basin species *D. kymatocarpa* and *D. leichhardtii*. This sectional emendment for *Datura* defines the

TABLE 2. GENUS *DATURA* SECTION REVISIONS.

Section *Datura*

Wide-ranging annuals with prismatic calyx; erect capsule with spiny or smooth pericarp dehiscing regularly by four valves; seed black.

Included species: *D. stramonium, D. ferox, D. quercifolia*

Section *Discola* [Sect. nov.]

Coastal annuals with prismatic calyx; pendant capsule with spiny pericarp dehiscing regularly by four valves; seed black or brown.

Included species: *D. discolor, D. reburra, D. arenicola*

Section *Ceratocaulis* [Sect. rev.]

Inland annuals with tubular calyx, spathe-like or 5-acumina; pendant capsule with spiny, semi-capillaceous or smooth pericarp dehiscing irregularly; seed charcoal-brown, brown, red-brown or buff-yellow.

Included species: *D. ceratocaula, D. leichhardtii, D. kymatocarpa*

Section *Dutra* [Sect. emend.]

Tuberous rooted perennials with tubular calyx; pendant capsule with spiny, tubericate or smooth pericarp dehiscing irregularly; seed brown, reddish-brown, reddish-yellow or buff-yellow.

Included species: *D. wrightii, D. inoxia, D. metel, D. lanosa, D. velutinosa*

evolution of all inland annual species with tubular calyces and irregularly dehiscent fruits (Table 2).

CONCLUSION

The new species was appropriately named the "sand dweller" by H. S. Gentry, who discovered it in the late 1940's during extensive botanizing in western Mexico. Very few botanical surveys have been carried out in the northern part of Baja California Sur, an area in which Dr. Jon Rebman predicts that many new species will be found. The Sierra San Francisco and Sierra Guadalupe may have provided the only corridor for plant dispersal in the late Pliocene, when sea levels were higher and the lower deserts were under water (Rebman 1997). The extensive distribution of *D. discolor* corresponds with the uplifting of the Lower Peninsula, where the small number of *D. wrightii* implicates anthropogenic origin. West of the Sierra San Francisco, the endemic *D. arenicola* inhabits the lower San Pablo watershed, which flows toward Laguna San Ignacio. In danger of extinction by human development, this species may be a candidate for the IUCN Red List of Threatened Species. For that reason it is not precisely located, although it is legally protected in La Reserva de la Biósfera El Vizcaíno. Additional field work is needed to establish the extent of distribution, as only 12 occurrences of *D. arenicola* are known to date.

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APPENDIX 1

SPECIMENS EXAMINED

Datura arenicola; MEXICO, BAJA CALIFORNIA SUR: Topotype: El Vizcaíno Junction, alt. ±90 m. *001 D. R. A. Watson*, 27 Nov 1983 [F]; El Vizcaíno Junction, alt. 90 m, *045 R. A. Bye & D. R. A. Watson*, 23 Jan 2010 [MEXU]; El Vizcaíno Junction, *046 R. A. Bye & D. R. A. Watson*, 23 Jan 2010 [BCMEX]; El Vizcaíno Junction, *052 R. A. Bye & E. Linares*, 24 Jan 2010 [MEXU]; El Vizcaíno Junction, *050 D. R. A. Watson*, 25 Jan 2010 [MEXU]; El Vizcaíno Junction, *051 D. R. A. Watson*, 25 Jan 2010 [MEXU]; San Pablo arroyo, *053 D. R. A. Watson*, 25 Jan 2010 [MEXU]; San Pablo arroyo, *054 D. R. A. Watson*, 25 Jan 2010 [MEXU].

Datura discolor; MEXICO, SONORA: Freshwater, Tiburon Island, *1010 Y. E. Dawson*, Jan 1925 [RSA]; Tiburon Island, 28°57′N, 112°27′W, *12322 R. Felger*, 2 Jan 1965 [MEXU]. BAJA CALIFORNIA (norte) & ISLAS FEDERAL: Bahía de Los Angeles, *251a J. Rempel* May 1920 [USC]; South Bahía de Los Angeles, 28°53′N, 113°31′W, *32,698 F. R. Thorne & J. Henrickson*, 26 Feb 1963 [RSA]; North Isla Partida, 28°52′N, 113°2′W, *3226 I. M. Johnston*, 22 Apr 1921 [CAS, DS, GH]; Near Bahía Santa Teresa, alt. 50 m ca. 28°24′N, 112°53′W, *5732 P. Tenorio & C. R. Tenorio*, 7 Apr 1987 [BCMEX]; 2 mi S of lighthouse, E Cedros Island, 28°22′N, 115°13′W, *5509 C. Davidson*, 23, Feb 1977 [RSA]; Santa Gertrudis Mission, 28°03.577′N, 113°06.277′W, *037 D. R. A. Watson & J. Johnson*, 19 Jan 2010 [MEXU]; In vado W of Santa Gertrudis Mission, 28°02.146′N, 113°11.245′W, *038, 039 D. R. A. Watson & J. Johnson*, 20 Jan 2010 [MEXU]. BAJA CALIFORNIA SUR & ISLAS FEDERAL: El Vizcaíno Junction, *002a, b D. R. A. Watson*, 27 Nov 1983 [F]; El Vizcaíno Junction, alt. 90 m, *047 R. Bye & D. R. A. Watson*, 23 Jan 2010 [MEXU]; Road to Sierra de San Francisco, 27°26.857′N, 113°14.857′W, alt. 100 m, *049 D. R. A. Watson*, 24 Jan 2010 [MEXU]; Mezquitalito Rancho, Sierra de San Francisco, 28°22′N, 115°13′W, *048 D. R. A. Watson*, 24 Jan 2010 [MEXU]; Sierra San Francisco & Sierra Guadalupe, San Gregorio Cañón, 27°40′N, 112°59′W, *9303, 11,111 J. Rebman*, 18 Oct 1997 [BCMEX, SD, HCIB]; Desviación a los Picachos, Desierto Vizcaíno, km 45 to Punta Abreojos, B. C. S. 26°59′N, 113°22′W, *2416 J. L. León de la Luz*, 29 May 1990 [HCIB]; Arroyo San Pedro near La Bocana B. C. S, *12,513 R. Moran* 1966 [RSA]; San Ignacio, *003a–d D. R. A. Watson*, Nov 26 1983 [F]; San Ignacio, SW of the plaza, *044 D. R. A. Watson*, 23 Jan 2010 [MEXU]; Tata Viejo vado, S of San Ignacio, *042, 043 D. R. A. Watson & M. Somers*, 22 Jan 2010 [MEXU]; 5.6 mi N of Santa Rosalia, *11,057 J. M. Porter*, 1995 [RSA]; Arroyo San Bruno, SE of Santa Rosalia, 4.8 mi off Mexico 1 toward San Jose de Magdalena, *5852 R. F. Thorne & S. Boyd*, 1991 [RSA]; NW Isla San Marcos, 27°14′N, 112°06′W, *11,835 J. L.* León de la Luz, 12 Oct 1996 [HCIB]; Between Santa Rosalia and Mulegé, boca de Magdalena Arroyo, ca. 27°04′18″N, 112°06′45″W. *13,101 J. M. Porter & L. E. Machen*, 28 Dec. 2003 [BCMEX]; Below the bridge at Mulegé, corollas violet & white; *040, 041 D. R. A. Watson*, 22 Jan 2010 [MEXU]; SW Bahía Concepcion peninsula, *7515 A. C. Sanders* [RSA]; Isla Carmen, Puerto Balandra, 26.083°N, 111.318°W, *3737 A. Carter*, 11 Mar 1960 [UC]; Arroyo de Sierra la Giganta, 24°41′N, 111°11′W, *7865 J. L. León de la Luz*, 12 Oct 1996 [HCIB]; At foot of eastern hill, Cabo San Lazaro, Isla Magdalena, *2017 C. Davidson*, Apr 1973 [RSA]; Cañada del faro, S Isla Santa Cruz, 25°17′N, 110°44′W, *8533 & 8536 J. L. León de la Luz*, 11 Mar 1997 [HCIB]; NE Isla San Jose, *430 G. Flores*, 1987 [RSA]; Rancho Monte Alto, N of Mesa San Alejo, Sierra la Giganta, 25°55′N, 111°37′W, *17,503 J. J. Perez Navarro*, 13 Dec 2000 [HCIB]; El Embudo, Isla Partida, 24°26′N, 110°22′W, *12,982 J. L. León de la Luz*, 16 Oct 1998 [HCIB]; Bahía San Gabriel, SE Isla Espíritu Santo, 24°25′N, 110°21′W, *7639 M. D. Leon*, 26 Sep 1996 [HCIB]; El Comitán, 17 km NE La Paz, 24°13′N, 110°20′W, *5278 J. L. León de la Luz*, 1 Nov 1986 [HCIB]; La Paz, to San Juan de la Costa, 24°07′N, 110°24′W, *7549 J. L. Leon de la Luz*, 6 Nov 1996 [HCIB]; La Paz, 24°4′N, 110°24′W, *24,399 M. E. Jones*, 9 Feb 1928 [POM]; On the beach at the marina, La Paz, *004 D. R. A. Watson*, 10 Nov 1983 [F]; Arroyo Paredones Blancos, Isla Ceralvo, 24°15′N, 109°52′W, *6860 M. D. Leon*, 26 Nov 1994 [HCIB]; Boca del Alamo, enter los Barriles y los Planes, 23°55′N, 109°50′W, *3594 J. L. León de la Luz*, 15 Jan 1991 [HCIB]; Sierra la Laguna, Agua del El Palmillar, 33°31′N, 110°01′W, *5352 J. L. León de la Luz*, 12 Nov 1986 [HCIB]; Sierra la Laguna, Cañón de la Zorra, W of Santiago, 23°30′N, 109°52′W, *2417 & 5340 J. L. León de la Luz*, 1 Nov 1986 [HCIB]; Miraflores, *005 D. R. A. Watson*, 10 Nov 1983 [F]; San Jose del Cabo, 23°3′N, 109°42′W, *24,396 M. E. Jones*, 18 Jun 1928 [POM]; Cabo San Lucas, *006–8 D. R. A. Watson*, 11 Nov 1983 [F].

A NEW SUBSPECIES OF *LIMNANTHES* (LIMNANTHACEAE) FROM SAN MATEO COUNTY, CALIFORNIA

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Abstract

Limnanthes douglasii R. Br. subsp. **ornduffii** E. G. Buxton (Limnanthaceae), a narrowly endemic meadowfoam from Moss Beach (Half Moon Bay) in San Mateo County, California, is described. Though it shares the morphological trait of being tetramerous with *Limnanthes macounii* Trel., an endemic species in British Columbia, Canada, it is not a sister taxon to *L. macounii* based on molecular sequence evidence. *L. douglasii* subsp. *ornduffii* appears in an unresolved group with other *L. douglasii* populations/subspecies. Molecular data coupled with morphological distinctiveness and geographical endemism provide a credible basis for recognizing the Moss Beach population as a *L. douglasii* subspecies. Data suggest that tetramerism in the genus has arisen more than once.

Key Words: Endemic, *Limnanthes douglasii*, *L. macounii*, Moss Beach, sister taxon, tetramerous.

In March 1998, I observed a large population of an unknown, tetramerous meadowfoam (*Limnanthes* sp.) while conducting fieldwork in a fallow agricultural field in Moss Beach, San Mateo Co., CA. The Moss Beach population, belonging in sect. *Limnanthes* based on petals reflexing as the fruits mature, was the first one with a tetramerous flower recorded in the USA. I contacted Dr. Robert Ornduff, University of California Berkeley (UCB), the authority on Limnanthaceae and the author of this family in *The Jepson Manual* (Ornduff 1993). After examining a specimen I sent to him, he contacted Adolf Ceska, a botanist familiar with the tetramerous *Limnanthes macounii* Trel.in British Columbia, Canada. Ceska found some morphological differences but suggested that it could be *L. macounii*, previously thought to be an endemic species of about 50 populations on Vancouver Island and a few adjacent islands in and near Victoria, British Columbia. Dr. Ornduff suggested that the *Limnanthes* population in Moss Beach could be the result of an accidental introduction from the Vancouver area (personal communication); like several of the members of the genus, including *L. douglasii* R. Br. (Kesseli and Jain 1985), this species is autogamous, therefore a single nutlet could theoretically have established the population. However, it seemed unlikely that human activity had moved the plant from Canada to California; and if dispersal had occurred via bird vectors, there should have been other known, disjunct populations between British Columbia and Moss Beach. Dr. Ornduff found it best that we co-publish a note in the "Noteworthy Collections" section of *Madroño* (Buxton and Ornduff 1998) to alert people to the possibility that the plant at Moss Beach may be *L. macounii* and that it may occur elsewhere in coastal Central California.

After growing plants from seed from the Moss Beach and British Columbia populations in a common garden, Dr. Ornduff stated "your plants are definitely not stray *L. macounii*" (personal communication). Similarly, after observing garden-grown plants, Ceska did not think that the Moss Beach plants "fit exactly anything known in British Columbia." (personal communication). Based on the traditional morphological species concept, the plant occurring in Moss Beach would warrant recognition at species rank, perhaps even genus rank based on its tetramerism. After careful observations and measurements of the two entities grown in large numbers in the garden as well as indoors, where fruits developed in the absence of pollinators, and taking into consideration the results of a phylogenetic molecular study (Meyers et al. 2010), I am circumscribing the Moss Beach population as a subspecies of *L. douglasii*. To honor Dr. Ornduff, who called the plant at Moss Beach "a very interesting find" and asked me "to stay on it" shortly before his death (personal communication), I take pleasure in naming it **Limnanthes douglasii** subsp. **ornduffii** (Ornduff's meadowfoam).

Taxonomic Treatment

Limnanthes douglasii R. Br. subsp. **ornduffii** E. G. Buxton, subsp. nov. (Figs. 1 and 2).—TYPE: USA, California, San Mateo Co., Moss Beach, east side of California State Route 1, opposite Half Moon Bay airport, 0.6 km S of its junction with Etheldore St., in wet portions of seasonally fallow agricultural field, elev. 18 m, 24 March 1998, *E. Buxton s.n.* (holotype: JEPS; isotypes: UC, CAS, DAV, UBC, DAO; paratype: *R. Ornduff 10168,* 12 April 1998 [JEPS 95209]).
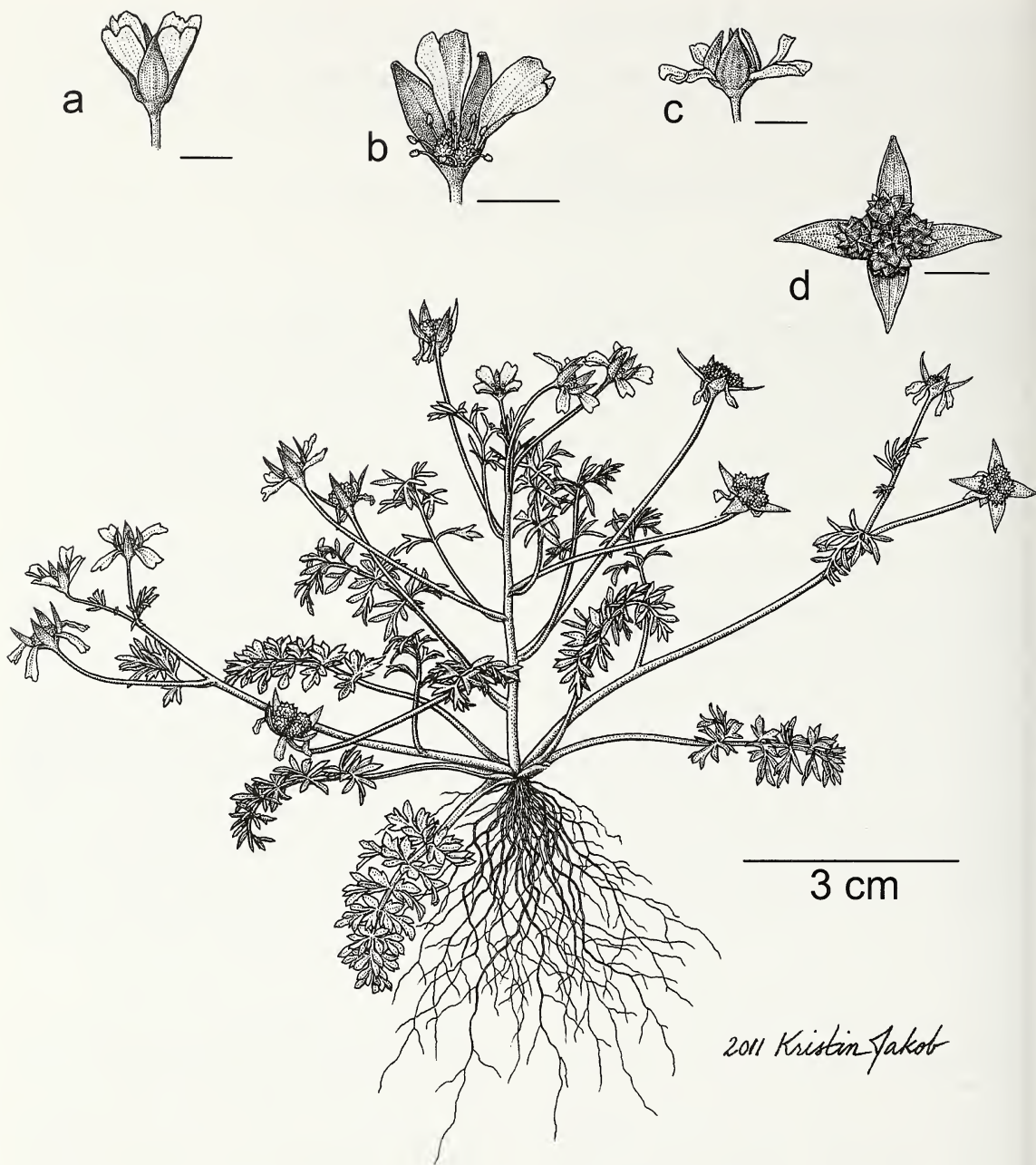
FIG. 1. *Limnanthes douglasii* subsp. *ornduffii*. a. Young flower. b. Dissected flower with stamens and style. c. Senescing flower. d. Calyx with mature nutlets. Bars for a–d are 5 mm.

Plants annual, glabrous, yellowish-green, sparingly to much branched at base. **Stems** 6–20 cm long, erect or ascending. **Cotyledons** erect. **First foliage leaves** erect, with narrowly oval distant leaflets. **Mature leaves** 3–13(16) cm long, alternate, basal leaves lanceolate to triangular, exstipulate, bipinnately divided (odd-pinnate) or incised to axis, leaflets opposite (rarely alternate) on leaf axis, petiole equaling or longer than blade; first division 3–8 pairs, 4–10(13) mm long,

second division 2–3 pairs, some lobed or toothed, 2–6 mm long; petioles of basal leaves with membranous wings, 2–3 mm wide. **Flowers** tetramerous, perfect, bowl-shaped to campanulate, at ends of bractless, axillary peduncles, peduncles somewhat compacted at distal end of stems, elongating in fruit at a ca. 90-degree angle to stem, surpassing in length axillary leaf; **sepals** lanceolate, 5–6(8) mm long, 2–3 mm wide, acuminate, elongating in fruit; **petals** cuneate,

FIG. 2. *Limnanthes douglasii* subsp. *ornduffii* in flower and fruit.

FIG. 3. Habitat of *Limnanthes douglasii* subsp. *ornduffii*.

6–7 mm long, 2.5–3 mm wide, white, faintly yellow near base, veins hyaline, tip truncate, mostly notched, erose, reflexed in fruit, claw with a few long hairs; **stamens** 8, filaments flat, ca. 2 mm long, anther ca. 0.5 mm long, yellow; **style** ca. 2 mm long, stigma 4-lobed, lobes ca. 0.5 mm long. **Nutlets** 4, ovoid, 3.5–4 mm long, 2.5–3.5 mm wide, dark reddish brown, walls strongly wrinkled, sharp-edged tubercles covering upper 3/4 of nutlet.

Phenology

Limnanthes douglasii subsp. *ornduffii* is a winter annual, germinating soon after the first rains in the fall. The blooming period lasts from (November) December until April (May). Flowering and fruiting occur simultaneously after initial growth.

Habitat

Limnanthes douglasii subsp. *ornduffii* grows in low-lying portions of an agricultural field when it is fallow (Fig. 3), as well as in drainage ditches and ruts within and adjacent to the field, in soils that are saturated to the surface for an extended period of time. In garden experiments, plants co-occurring with *L. vinculans,* a vernal pool species, survived four months of inundation. However, plants also grew to maturity in dryer conditions. The field has been planted in artichokes, fava beans, and brassicaceous plants for at least 15 yr, and is plowed at least once a year.

Distribution

Limnanthes douglasii subsp. *ornduffii* is known from a single population just south of Moss Beach, San Mateo Co. (Fig. 4). In 1998, the meadowfoam was estimated to provide a nearly complete absolute cover on ca. 18 acres; however,

its spatial distribution in the field has diminished somewhat (now ca. 90 percent), apparently due to greater competition from *Stellaria media* (L.) Vill., *Fumaria officinalis* L., *Veronica chamaedrys* L., *Lythrum hyssopifolia* L., and *Poa annua* L., and perhaps untimely plowing. In 2008, a disjunct colony of three individuals grew in a field that appeared to have been cultivated in the past, west of the Half Moon Bay airport, approximately 2.4 km from the fallow field, but this stand was not found in 2009, 2010, or 2011 (personal observation).

Table 1 presents a comparison of morphological, phenological, and ecological features of *Limnanthes douglasii* subsp. *ornduffii* and *L. macounii*. *Limnanthes d.* subsp. *ornduffii* is morphologically distinct from all other entities in the *L. douglasii* complex in the USA based on its tetramerism and much smaller flowers, and is distinct from the only other tetramerous *Limnanthes* taxon, which occurs in British Columbia. In addition to a 1400 km (860 mi) geographical disjunction, floral size, nutlet differences, and leaf

FIG. 4. Approximately 90% absolute cover of *Limnanthes douglasii* subsp. *ornduffii* on Moss Beach site.

TABLE 1. MORPHOLOGICAL, PHENOLOGICAL, ECOLOGICAL, AND DISTRIBUTIONAL DIFFERENCES BETWEEN *LIMNANTHES DOUGLASII* SUBSP. *ORNDUFFII* AND *L. MACOUNII*. Measurements and observations were made on fresh, garden-grown material of *L. d.* subsp. *ornduffii*. Data for *L. macounii* were obtained from fresh material and the Morin (2012). A. Ceska provided phenological and ecological information from British Columbia (BC).

Character	*Limnanthes douglasii* subsp. *ornduffii*	*Limnanthes macounii*
Plant	5–15(20) cm, erect or ascending; mostly branching with axillary peduncles at ca. 90° angle to stem	2–7(15) cm, decumbent (sometimes upcurved apically); mostly unbranched
Cotyledon/first leaf	erect	prostrate
Cotyledon color	yellowish green	grayish green
Cotyledon shape	oval	round
First leaf distant leaflets	narrowly oval	roundish
Mature leaf structure	bipinnate; 2° pinnae lobed or toothed	pinnate; pinnae toothed
Mature leaf length	3–13(16) cm	1–7 cm
Mature leaf, number of 1° leaflets	7–17	3–15
Sepal	5–6 mm, elongating in fruit	3–4 mm
Petal	6–7 mm	4–5 mm
Stamen/petal relationship	¼ to 1/3	½ to 2/3
Nutlet size	3.5–4 mm	3 mm
Nutlet ornamentation	sharp-edged tubercles covering top ¾ of fruit; walls strongly wrinkled	rounded tubercles, some sharp-edged on top portion; some wrinkles on walls
Nutlet color	dark reddish brown	light brown
Nutlet/sepal relationship	sepals extending beyond nutlets	sepals not extending beyond nutlets
Blooming period	(November)December–April (May) in CA.	March–early May in BC.
Start of flowering in garden-grown plants in 2004 in Marin Co., CA	January 16	February 22
Survival in sub-0°C temperature in BC.	poor to none	normal (can be imbedded in ice)
Distribution	Moss Beach, San Mateo Co., CA	Vancouver Island and vicinity, BC.

characters are distinctly dissimilar in the two taxa; the leaves in *L. d.* subsp. *ornduffii* are bipinnate to incised to the rachis, whereas those in *L. macounii* are pinnate. Foliar characters have been used in the past to distinguish species within the genus; for example, these characters "serve readily to distinguish *Limnanthes vinculans* Ornduff from all other members of the genus" (Ornduff 1969).

DISCUSSION

Molecular Analysis and Taxonomic Relationships

Plotkin (1998) conducted the first molecular phylogenetic study of Limnanthaceae using DNA sequence data, concluding that *Limnanthes striata* Jeps. may be treated as a subspecies of *L. douglasii*. *Limnanthes macounii* was also nested within the *L. douglasii* clade. Subsequently, Morin (2007) demoted *L. striata* to a subspecies of *L. douglasii*, but she left *L. macounii*, making *L. douglasii* paraphyletic. Four species and five subspecies in sect. *Limnanthes* are recognized in the Flora of North America (FNA) (Morin 2010): *Limnanthes macounii*; *L. douglasii* subsp. *douglasii*, *L. d.* subsp. *sulphurea* (C. T. Mason) C. T. Mason, *L. d.* subsp. *nivea* (C. T. Mason) C. T. Mason, *L. d.* subsp. *rosea* (Benth.) C. T. Mason,

L. d. subsp. *striata* (Jeps.) Morin; *L. bakeri* J. T. Howell; and, *L. vinculans*. *Limnanthes macounii* was maintained as a species because of its highly disjunct distribution and unique characteristics, including nutlet sculpturing and the presence of alleles at three loci found in no other taxa of the genus (Morin 2010). Ornduff and Morin (2012) include the same species as those listed in the FNA, except for *L. macounii*, which occurs only in British Columbia.

Meyers et al. (2010) conducted a phylogenetic study to resolve relationships within the genus *Limnanthes* by using one nuclear (nrITS) and two chloroplast (*trnL* intron and *trnS*-*trnG* intergenic spacer) genes. They included the meadowfoam population from Moss Beach in their survey to attempt to explain its taxonomic status and biogeographic origin. The study confirmed the monophyly of two sections within *Limnanthes*: *Limnanthes* (=*Reflexae*) and *Inflexae*. They concluded that the results of the molecular study, as well as crossing experiments, did not support taxonomic recognition of the Moss Beach (Half Moon Bay) population, rather it is "part of a highly polymorphic *Limnanthes douglasii sensu lato*" and is an ecologically interesting and morphologically divergent population within this polymorphic species. They further suggest that the divergence of extant taxa may have been a

recent and rapid event and too few mutations have accumulated in the genes or were detected in the markers tested. This supports the notion that non-resolution in cladograms is not uncommon with closely related taxa, i.e., purported subspecies.

Locating Populations

Repeated attempts to locate additional populations of a tetramerous meadowfoam along the coasts of Washington, Oregon, and California have failed. Ceska (Ceska and Ceska 1999) suggested that the present range of *Limnanthes macounii* in British Columbia is a northern extension of an originally more southerly distribution of this species, which together with various other southern floristic species spread during the Hypsithermal period; *L. macounii* either became extinct or has been overlooked. Consequently, at his suggestion, concentrated efforts to locate this species in California were made in 1977 by Ph.D. students at UCB and UC Davis (UCD). No populations were found, and they concluded that this species could not have been overlooked, if, in fact, it grew in California (Ceska and Ceska 1999). I have searched wet portions of the hills to the east of the agricultural field, wetlands south of Montara and to the north of the site, and some areas between Moss Beach and Santa Cruz, but have found only the small stand on the west side of the Half Moon Bay airport in 2008. Meyers et al. (2010) unsuccessfully attempted to locate tetramerous plants in California and Oregon during four field seasons. No such meadowfoam populations were found during thorough field surveys between Devil's Slide and Pescadero (San Mateo Co.), including agricultural fields and marshes on the east side of State Route 1, conducted in preparation for *Plants and Plant Communities of the San Mateo Coast* published by San Mateo Coast Natural History Association in 2009. Dr. Dean W. Taylor (independent botanist) has done floristic surveys in Santa Cruz and San Mateo counties, and has searched agricultural settings along the coast from Santa Cruz toward Moss Beach without finding any meadowfoam populations (personal communication). The closest documented *L. douglasii* subsp. *douglasii* populations historically occurred ca. 10 km to the east (San Andreas Lake, San Mateo Co.) and ca. 55 km to the north of Moss Beach (San Rafael, Marin Co.) (CCH 2010). *Limnanthes d.* subsp. *sulphurea* (JEPS 19572) grows in a marshy area near the town of Pescadero, 40 km to the south (N. Kramer, Kramer Botanical, personal communication).

Human History of Site

The natural environment in parts of the San Mateo coast has experienced great transformation over the past centuries and many native plant communities were likely changed or eradicated in the early to mid-1800's. In 2010, a historic research study document was prepared in connection with the acquisition of the *Rancho Corral de Tierra* (*Rancho*), which included the agricultural field now supporting the meadowfoam, by the Golden Gate National Recreation Area (GGNRA) (NPS 2010). The field is presently owned by the Peninsula Open Space Trust (POST) and leased to Cabrillo Farms. The document traces the human history of the *Rancho* area, revealing how land usage has changed from the Ohlone Indians burning the landscape for centuries to improve grazing for large game, to the raising of cattle and sheep by the Mission fathers in the late 1700's. In the 1800's, the land was mainly used for dairy farming and production of hay, grains, and potatoes. In April of 1860, the *San Mateo Gazette* declared the *Rancho* as "one of the most productive ranchos of its kind mainly for grain and stock grazing in California" (NPS 2010). This gave way to a floriculture and modern agriculture growing vegetables, including Brussels sprouts and artichokes in the late 1900's and early 2000's. The Half Moon Bay Airport, located directly west of the field, was constructed in 1942 for the U.S. Army.

Conclusions

I propose that *Limnanthes douglasii* subsp. *ornduffii* is a relic taxon that arose independently and is persisting in wet depressions, fed by seeps and small streams still in existence in the hills directly east of the agricultural field. In the past, the Moss Beach area was likely a marine terrace/coastal prairie with various types of wetlands forming during the wet season. The taxon may have been more widespread before its habitat was altered or destroyed by cattle grazing, agriculture, and urban development during past centuries; thus, extirpated populations could have flourished in areas of similar soils and hydrology. Non-native species have invaded many plant communities in California, including wetlands, where they have outcompeted native species. The Moss Beach taxon is likely persisting in the agricultural field due to the continual disturbance and removal of competing plants during the plowing of the field every year. This view has also been put forth by Plotkin (unpublished), who stated in regards to the Moss Beach taxon that "it is certainly not impossible that it is a remnant population that persists here."

Limnanthes douglasii subsp. *ornduffii* is morphologically distinct from all other sect. *Limnanthes* taxa based on its tetramerism and smaller flowers and is also distinct from *L. macounii*, the only other tetramerous taxon. *Limnanthes douglasii* subsp. *ornduffii* groups with some *L.*

douglasii populations/subspecies and not with *L. macounii* in Meyers' et al. (2010) cladogram. This clustering suggests that tetramerism has evolved more than once in the genus, thus tetramerous floral morphology is homoplastic within *Limnanthes*. The Moss Beach taxon is described at the rank of subspecies on the basis of its alignment with *L. douglasii* in the cladogram. Until additional data on the taxonomic, evolutionary, and biogeographic relationships of the Moss Beach plants are obtained that present greater resolution within sect. *Limnanthes*, this population warrants taxonomic recognition at the subspecific level.

Conservation Consequences

Not recognizing the various morphological entities, including *Limnanthes douglasii* subsp. *ornduffii*, would be a deterrent to the legal protection of disjunct, rare populations in the *L. d.* complex. Meyers et al. (2010) suggest that it might be a benefit to conservation work to merge the various *L. douglasii* taxa, as that would result in a greater amount of genetic diversity available for restoration. That would, however, result in no protection for rare taxa within the *L. douglasii* group. For example, it would be possible to mitigate for *L. d.* subsp. *sulphurea* (state-listed as endangered and occurring in a few colonies on the Point Reyes peninsula in Marin Co. and near Pescadero in San Mateo Co.), and *L. vinculans* (federally- and state-listed as endangered and endemic to a few vernal pools in Sonoma Co.), by using *L. d.* subsp. *douglasii*, a very common wetland plant throughout most of California. (The California Environmental Quality Act [CEQA] mandates mitigation for impacts to listed and other rare or endangered species.) By considering *L. douglasii* a polymorphic species, protection of morphological distinctiveness and geographical endemism would be lost.

Based on NatureServe criteria (Faber-Langendoen et al. 2012), *L. douglasii* subsp. *ornduffii* is eligible for a G1 designation, indicating that the taxon is *critically imperiled* across its entire range due to only one known occurrence. Based on IUCN (2010) criteria, the taxon may qualify for Red List Category *Vulnerable*—high risk of endangerment in the wild—because of its only known occurrence in an agricultural field. However, as repeated disturbance of the habitat of *L. douglasii* subsp. *ornduffii* appears to be the reason for the plants' persistence in the agricultural field, no protective measures relating to this subspecies and its habitat should be necessary. Seeds should be collected and deposited in a botanic institution that is a participating member in the Center for Plant Conservation's network to serve as a resource in reintroduction projects should a devastating event eradicate the only known occurrence.

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THE FERN-LEAVED MONKEYFLOWER (PHRYMACEAE), A NEW SPECIES FROM THE NORTHERN SIERRA NEVADA OF CALIFORNIA

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Abstract

The fern-leaved monkeyflower, **Mimulus filicifolius** (Phrymaceae, Section *Simiolus*), is a new species described from the northwestern corner of the Sierra Nevada of California. The new taxon is differentiated from close relatives of *Mimulus* L. (*M. laciniatus* Gray and *M. guttatus* DC.) mostly by having many finely divided, bi-pinnately compound leaves. **Mimulus filicifolius** occurs mainly within ephemeral seeps of rock outcrops, where it occupies similar habitats to *M. laciniatus*, which occurs farther south in the Sierra Nevada. **Mimulus filicifolius** appears to be highly geographically restricted, and is currently known only from Butte and Plumas Counties within the Plumas National Forest. It therefore merits strong conservation consideration.

Key Words: California, compound leaves, fern-leaved monkeyflower, *Mimulus*, *Mimulus guttatus*, *Mimulus laciniatus*, Plumas National Forest.

The genus *Mimulus* L. (Phrymaceae) is a diverse plant group that has its center of diversity in western North America (Grant 1924). Within this group, section *Simiolus* contains a variety of species that inhabit a wide array of habitats, from coastal areas to high mountains, and has become a focal group of interest in ecological and evolutionary studies (Wu et al. 2007). Within section *Simiolus*, the *Mimulus guttatus* DC. species complex comprises a group of morphologically differentiated, yet often interfertile species (Vickery 1964). Here we describe a new species that is distinguished within section *Simiolus* mainly by having finely divided leaves, specimens of which were previously determined as *Mimulus laciniatus* A. Gray.

Species having divided leaves and leaf margins are rare within the genus *Mimulus*. *Mimulus guttatus* can have toothed margins, especially near the leaf base (Grant 1924), yet leaves of *M. guttatus* are mostly entire. Section *Simiolus* specimens having very finely divided leaves have been collected in and near Plumas National Forest since 1974 (CA S871913). *Mimulus laciniatus* was previously the only known member of *Mimulus* to have strongly dissected leaf margins (Grant 1924; Thompson 2012). *Mimulus laciniatus* is an annual plant endemic to the central

western slope of the California Sierra Nevada where it primarily occupies ephemeral granite seeps at elevations generally >900 m (Sexton et al. 2011). *Mimulus laciniatus* leaf divisions extend throughout the leaf, forming a laciniate or pinnately compound shape. The *M. laciniatus* species range is found between Tulare and Amador counties from south to north, respectively, but the morphologically distinct taxon described here (previously described as *M. laciniatus*) occurs approximately 150 kilometers north of the nearest known populations of *M. laciniatus* (Fig. 1).

Butte and Plumas County specimens, previously determined as *M. laciniatus*, differ morphologically from *M. laciniatus* mainly by having leaves that are finely twice-pinnately compound and having more primary leaf divisions, giving the leaves a delicate, fern-like appearance. Molecular genetic analyses indicate that the Butte Co. subpopulation from which the type specimen described here originates is genetically distinct from the *M. laciniatus* clade, and reproductive barriers in the form of hybrid sterility exist between this subpopulation and *M. laciniatus* and *M. guttatus* populations (Ferris et al., unpublished data). First-generation hybrids between individuals from this new taxon and *M. guttatus* and *M. laciniatus* individuals exhibited hybrid sterility, whereas there is no comparable barrier between the same *M. laciniatus* and *M. guttatus* individuals. The above evidence of

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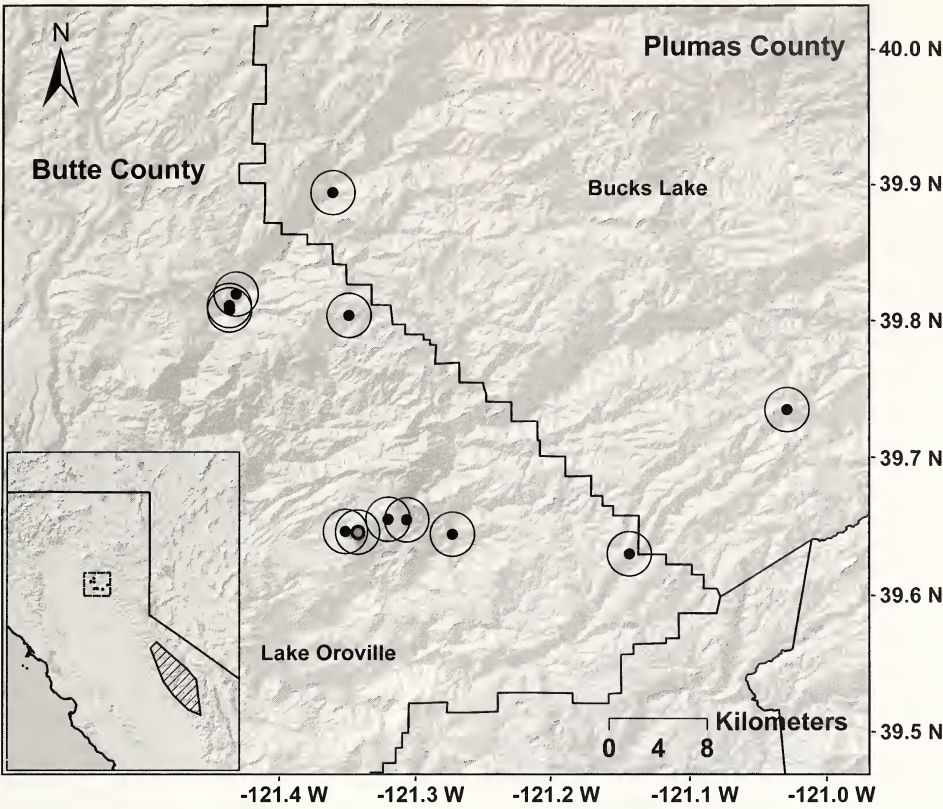
Fig. 1.   Species distribution of known *Mimulus filicifolius* locales within Butte and Plumas Counties (dashed-line box within map inset), of the northwestern Sierra Nevada of California. The open circle represents the location of the *M. filicifolius* type specimen at Big Bald Rock (39°38′39″N, 121°20′36″W). The species range of the morphologically similar *Mimulus laciniatus* in the central Sierra Nevada is shown as the polygon with diagonal lines in the map inset.

strongly differing morphological characters, reproductive barriers, and evidence of divergent evolution leads us to conclude that the northern Sierran plants previously identified as *M. laciniatus* should be treated as a distinct species.

TAXONOMIC TREATMENT

Mimulus filicifolius J. P. Sexton, K. G. Ferris & S. E. Schoenig, sp. nov.—TYPE: USA, California: Butte County, granite seeps of easterly area of Big Bald Rock, 39°38′39″N, 121°20′36″W, ca. 930 m elev., 22 May 2010, *J. P. Sexton 1* (holotype, DAV). Figures 2 and 3.

Herbaceous annual, 3–38 cm, glabrous throughout. **Leaf petioles** 0–32 mm, **leaf blade** 3–68 mm, oblanceolate to ± ovate, bi-pinnately, narrowly to finely lobed (linear) or dissected, often having >8 primary pinnae divisions on a side. **Inflorescence** a raceme, generally >5-fld; bracts clasping at base, entire, ovate. **Flowers** open, occasionally cleistogamous; **pedicel** 2.5–14 mm; **calyx** 2–11 mm, strongly curved (rounded), asymmetrically swollen in fruiting, ± glabrous, lobes unequal, lowest 2 upcurved in fruiting; **corolla** pale yellow, tube-

throat 4–8 mm; **placentas** axile. **Fruit** 3–8 mm, ovoid to fusiform, loculicidal (indehiscent), chambers 1–2; **seeds** many, generally <1 mm, ovoid, ± yellow to dark brown.

Mimulus filicifolius is distinguished from *M. laciniatus* by having strongly bi-pinnately and finely divided—often linear—leaf margins in larger plants, and more primary leaf divisions (often having 8 or more primary leaf divisions on one leaf side) (Figs. 4, 5), as opposed to having mostly laciniate to occasionally bi-pinnate leaf shapes (with 7 or less primary leaf divisions on one leaf side, often 3 or less) with oblanceolate lobes; having clasping, entire, ovate floral node bracts, as opposed to having bract bases long-tapered to petioled, and bracts narrowly lanceolate to pinnately lobed; and having pedicels less than 2 times the calyx length, as opposed to often having pedicels equal to 2 times the calyx length or longer (Table 1, Fig. 5).

Paratypes

We examined all of the known herbarium specimens of *M. filicifolius*, including paratypes

FIG. 2. *Mimulus filicifolius* prior to flowering, growing near Feather Falls, Butte Co., California, 12 May 2012. Photo by S. Schoenig.

(Table 2). The following paratypes (herbarium and specimen codes are given in parentheses) are from the *M. filicifolius* geographic range and were previously identified as *M. laciniatus*: USA. CALIFORNIA. **Butte Co.:** South of Lumpkin Ridge, 12 May 1987, *L. Ahart 5634* (CAS 916469,

FIG. 3. *Mimulus filicifolius* flowering at basalt site south of Lumpkin Ridge, Butte Co., California. Photo by Robert Schlising.

FIG. 4. *Mimulus filicifolius* leaves from plants growing at Big Bald Rock, Butte Co., California. Photograph by S. Schoenig. Scale bar = 5 mm.

CHSC 42866); Fall River at the head of Feather Falls, 30 April 1990, *V. Oswald 4175* (CHSC 50115); along Bean Creek Rd near Little Bald Rock, 22 May 1985, *L. Ahart 5027* (CHSC 40889), 7 June 2009, *D. Grossenbacher and M. James 1032-a* (DAV 189651); Big Bald Rock, 14 June 1980, *R. Banchero 220* (CAS 871914, CHSC 33342); Bald Rock Dome, 15 May 1983, *R. Schlising 4414* (CHSC 39058); between Pulga and Poe Dam near the North Fork of the Feather River, 11 September 2006, *L. Ahart 13,293* (CHSC 94564); Poe Dam area, 26 April 1986, *V. Oswald 1981* (CHSC 49002). **Plumas Co.:** North Fork Feather River 1/2 mile below the mouth of Rock Creek, between Storrie and Elephant Butte Tunnels, 28 April 1974, *W. Dakan* (CAS 871913).

Additionally, three locales of *M. filicifolius* that are awaiting accession or have not yet been collected include the following: **Butte Co.:** Poe Dam area, along Camp Creek Road at crossing of Dogwood Creek, 21 May 2013, *L. Janeway 11,114* (awaiting accession); Rody Creek, 4 October 2012, *T. Hanson and M. Williams* (not collected). **Plumas Co.:** Northeast end of Lumpkin Ridge, 21 May 2013, *T. Hanson* (awaiting accession).

Morphological Analysis

We quantified differences in leaf shape and pedicel length between *M. filicifolius* and *M. laciniatus* from herbarium specimens. Analyses included nine locales (of 12 known) of *M. filicifolius* from Butte and Plumas counties, and
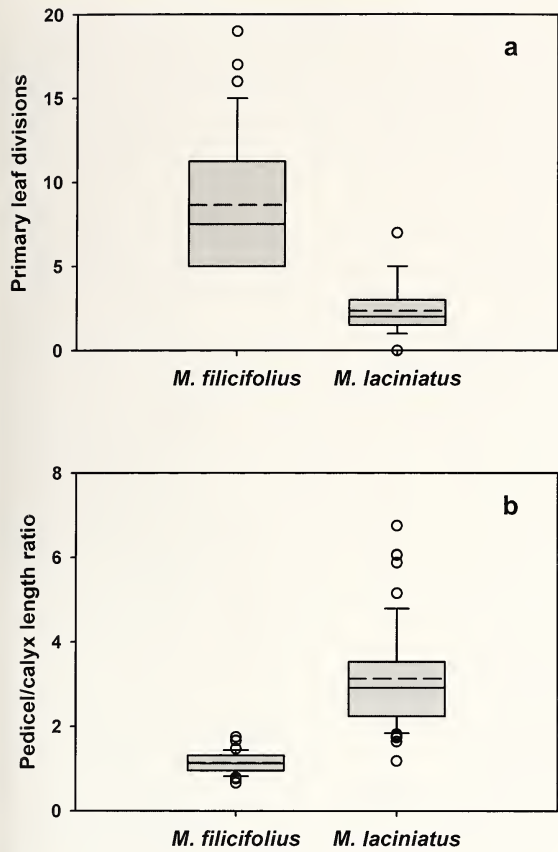
FIG. 5. Box plots of morphological data of distinguishing characters between *Mimulus filicifolius* and *Mimulus laciniatus*. (a) Number of primary leaf divisions (range = 5–19 and 0–7 for *M. filicifolius* and *M. laciniatus*, respectively). (b) Pedicel/calyx length ratio (range = 0.667–1.75 and 1.19–6.75 for *M. filicifolius* and *M. laciniatus*, respectively). Box boundaries are 25th and 75th percentiles. Dashed centerline is the mean; unbroken centerline is the median. Whiskers are 90th and 10th percentiles. Unfilled circles are points outlying.

12 locales from four counties representing much of the species range of *M. laciniatus* (Table 2). We recorded data from each plant having clearly observable traits on a herbarium collection sheet (Table 2). Only complete individuals (i.e., having attached roots or being the only specimen on a sheet) were counted. For leaf shape, we recorded the greatest number of primary divisions on one side of the longest leaf on a plant. Leaf margin lobes near the leaf tip were included in counts since it was difficult to distinguish primary and secondary pinnae there. A total of 34 and 57 individuals were measured for leaf shape in *M. filicifolius* and *M. laciniatus*, respectively. For pedicel length, we measured the longest pedicel and its associated calyx on a given plant and recorded the pedicel/calyx length ratio. We measured a total of 36 and 73 individuals for pedicel/calyx length ratios for *M. filicifolius* and *M. laciniatus*, respectively.

Morphological data were analyzed using REML (JMP, version Pro 10). The effect of species was considered a fixed factor, whereas population (locale) was considered a random factor nested within species since we were primarily interested in species differences. Species differences were highly significant for both leaf and pedicel traits. For leaf shape, *M. filicifolius* and *M. laciniatus* had least square means of 8.23 ($\pm$0.78 SE) and 2.52 ($\pm$0.65 SE) primary pinnae, respectively (df = 1; error df = 17.29; F = 31.75; P < 0.0001; Fig. 5a). For pedicel length, *M. filicifolius* and *M. laciniatus* had least square means of 1.15 ($\pm$0.32 SE) and 3.23 ($\pm$0.24 SE) pedicel/calyx length ratios, respectively (df = 1; error df = 16.89; F = 26.91; P < 0.0001; Fig. 5).

Distribution and Habitat

The epithet ('fern-leaved' in Latin) for the new species refers to its strong and finely compound leaf structure (Figs. 2–4). *Mimulus filicifolius* is known between 430–1280 m within the Feather River watershed of the northern California Sierra Nevada (Fig. 1) and most specimens are known from slow-draining, ephemeral seeps of the Bald Rock Pluton in Butte County (e.g., Big Bald Rock, Little Bald Rock, and Bald Rock Dome), with noted exceptions (e.g., localities on Lovejoy basalt at Lumpkin Ridge). These habitats are mainly comprised of exfoliating granite slabs on which mosses and club mosses grow and occur within a mixture of chaparral and yellow pine forest, dominated by *Arctostaphylos viscida* Parry, *Quercus chrysolepis* Liebm., *Quercus kelloggii* Newb., *Pinus ponderosa* ex Lawson and C. Lawson, and *Pseudotsuga menziesii* (Mirb.) Franco. Noted native plant associates of *M.*

TABLE 1. DIAGNOSTIC MORPHOLOGICAL CHARACTERS BETWEEN *MIMULUS FILICIFOLIUS* AND *M. LACINIATUS*.

Trait	*M. filicifolius*	*M. laciniatus*
Leaf shape	pinnate to strongly bi-pinnate, having fine, linear lobes; often having 8 or more primary pinnae on a side	laciniate to bi-pinnate, lobes oblanceolate, ≤7 primary pinnae on a side and often having 3 or less.
Floral bracts	clasping, ovate, entire	base long-tapered to petioled, lanceolate to pinnately lobed
Pedicels	relatively short, <2 times calyx length	relatively long, often ≥2 times calyx length

TABLE 2. SUMMARY INFORMATION FOR THE 12 KNOWN LOCALES OF *MIMULUS FILICIFOLIUS* AND 12 LOCALES OF *MIMULUS LACINIATUS* TO WHICH MORPHOLOGICAL CHARACTERS WERE COMPARED. Leaf shape and pedicel/calyx length ratio data were recorded from herbarium sheets. Herbarium code and specimen number are given in the Specimen ID column and the number of individual plants examined from each herbarium sheet for each trait is given in subsequent columns. CAS = California Academy of Sciences; CHSC = Chico State Herbarium, California State University, Chico; DAV = University of California, Davis Center for Plant Diversity; JEPS = Jepson Herbarium. Additionally, three records of *M. filicifolius* that have not yet been accessioned or collected are listed (NA).

Specimen ID	Species	Locale	N (leaf)	N (pedicel)	Lat.	Long.
CHSC 39058	*M. filicifolius*	Bald Rock Dome, Butte Co., CA, USA	6	9	39.6536	−121.3067
CHSC 40889, DAV 189651	*M. filicifolius*	Bean Creek Road, near Little Bald Rock, Butte Co., CA, USA	4	4	39.6539	−121.3203
CAS 871914, CHSC 33342	*M. filicifolius*	Big Bald Rock, Butte Co., CA, USA	2	2	39.6450	−121.3517
DAV 190412, DAV 190658, DAV 190659	*M. filicifolius*	Big Bald Rock, Butte Co., CA, USA	4	5	39.6445	−121.3427
CHSC 50115	*M. filicifolius*	Feather Falls Trail, Butte Co., CA, USA	4	3	39.6431	−121.2731
CA S916469, CHSC 42866	*M. filicifolius*	Lumpkin Ridge, Butte Co., CA, USA	9	8	39.6286	−121.1436
CHSC 94564	*M. filicifolius*	Poe Dam area, Feather River, Butte Co., CA, USA	1	1	39.8072	−121.4367
CHSC 49002	*M. filicifolius*	Western Pacific Railroad between Pulga and Poe Dam, Butte Co., CA, USA	2	2	39.8106	−121.4369
NA	*M. filicifolius*	Poe Dam area, along Camp Creek Road at crossing of Dogwood Creek, Butte Co., CA, USA	NA	NA	39.8189	−121.4319
NA	*M. filicifolius*	Rody Creek, Butte Co., CA, USA	NA	NA	39.8032	−121.3490
CAS 871913	*M. filicifolius*	North Fork Feather River, Plumas Co., CA, USA	2	2	39.8933	−121.3610
NA	*M. filicifolius*	Northeast end of Lumpkin Ridge, Plumas Co., CA, USA	NA	NA	39.7342	−121.0278
JEPS 10456	*M. laciniatus*	Yosemite National Park, Mariposa Co., CA, USA	—	4	—	—
JEPS 10937	*M. laciniatus*	Hog Ranch, Tuolumne Co., CA, USA	6	7	37.8822	−119.8547
JEPS 10938	*M. laciniatus*	Dardanelle, Tuolumne Co., CA, USA	5	7	38.3411	−119.8328
JEPS 11022	*M. laciniatus*	Yosemite Falls, Mariposa Co., CA, USA	1	7	—	—
JEPS 11025	*M. laciniatus*	Strawberry Lake, Tuolumne Co., CA, USA	4	6	38.1954	−119.9808
JEPS 11026	*M. laciniatus*	Marble Fork, Sequoia NP, Tulare Co., CA, USA	1	2	36.5534	−118.8102
JEPS 23793	*M. laciniatus*	Jose Basin, Fresno Co., CA, USA	9	9	37.1014	−119.3738
JEPS 33899	*M. laciniatus*	Mono Hot Springs Campground, Fresno Co., CA, USA	8	9	37.3267	−119.0167
JEPS 53950	*M. laciniatus*	Vermillion Valley, Fresno Co., CA, USA	9	7	37.4081	−118.9383
JEPS 55430	*M. laciniatus*	Miramonte, Fresno Co., CA, USA	3	3	36.6925	−119.0514
JEPS 6975	*M. laciniatus*	Mills Creek, Fresno Co., CA, USA	7	8	37.4244	−118.8578
JEPS 82859	*M. laciniatus*	Clover Creek, Tulare Co., CA, USA	4	4	36.6019	−118.7428

filicifolius at Big Bald Rock include species of *Bryum* Sendtn. ex C. Müll., *Cheilanthes gracillima* D. C. Eaton, *Heterocodon rariflorum* Nutt., *Penstemon newberryi* A. Gray, and *Selaginella wallacei* Hieron. Flowering specimens of *Mimulus filicifolius* have mostly been collected or observed from April to June, with one specimen collected in September (L. Ahart 13293, CHSC 94564).

Conservation Considerations

Mimulus filicifolius is endemic to the northwestern corner of the California Sierra Nevada and is known from only 12 locales on or adjacent to the Plumas National Forest, several of which are closely spaced (Fig. 1). We did not perform extensive searches to locate new populations

within suitable habitat. Besides Big Bald Rock, the type specimen locale, we visited several other locales from 2006 to 2012 to observe habitats and the range of phenotypes from several sites across the species range. The locale visited at Big Bald Rock appeared to be healthy (containing thousands of individuals). Nevertheless, we were unable to locate plants at the paratype locales near Pulga and Poe Dam near the North Fork of the Feather River from which specimens had been collected by *L. Ahart 13,293* (CHSC 94564) and *V. Oswald 1981* (CHSC 49002). L. Ahart described the population at this locality as "uncommon, only one plant seen." However, a new locale nearby was recorded by Lawrence Janeway (collection number 11114) in 2013, confirming that plants still occur in this area. Additionally, at the paratype collection site near Little Bald Rock, *M. filicifolius* was described as "uncommon," although we did not visit this locale. The population that we observed at Feather Falls Trail was fairly small, consisting of perhaps a few dozen individuals adjacent to a scenic overlook. Since there are few known populations, some of which are small and occur close to each other, we recommend that conservation managers include this species in monitoring programs to limit future risks to existing populations (e.g., species invasions, land clearing, livestock introductions). Additionally, suitable habitats within the region should be searched in case other populations exist.

Discussion

We find no evidence that *Mimulus laciniatus* occurs within the species range of *M. filicifolius*. All specimens known from Butte and Plumas counties are consistent with the *M. filicifolius* phenotype and it appears from our analysis that these two taxa are strongly diverged geographically and evolutionarily.

Mimulus filicifolius has a lobed leaf shape similar to, but more finely dissected than, *M. laciniatus. Mimulus filicifolius* and *M. laciniatus* also occupy similar habitats—seeps in rocky outcrops. *M. laciniatus* has been shown to be adapted to these habitats compared to its close relative, *M. guttatus* (Peterson et al. 2013). Since *M. filicifolius* is genetically distinct from *M. laciniatus* (Ferris et al., unpublished data) its leaf shape may be an independent derivation of lobed leaves in the genus *Mimulus*, which would represent parallel phenotypic evolution in parallel environmental conditions and thus be strong evidence of adaptation.

A lobed leaf shape may be adaptive in exposed, outcrop environments because it may help reduce heat stress and water loss in the daytime and/or reduce cold stress at night. Rock outcrops are drier, more light-intensive and have more extreme ground temperatures than the longer-lasting seep and stream habitats of nearby Simiolus species such as *M. guttatus* or *M. nasutus* (K. Ferris unpublished data). Lobed leaves have thinner boundary layers than round leaves, which increases the efficiency of convective heat transfer. Heat loss through convection can reduce the amount of water lost to evaporative cooling in hot, dry environments like rocky outcrops (Givnish 1978; Schuepp 1993; Nobel 2005; Nicotra et al. 2011).

Lobed leaves may also contribute to freeze tolerance early in the growing season when nights are still cold. On clear nights, leaves in exposed, open areas like *M. filicifolius* and *M. laciniatus* habitats radiate heat to the cold sky. This radiation can cause leaf temperatures to fall below air temperature by several degrees and thus leaves can freeze when air temperatures are near, but still above 0°C (Darwin and Darwin 1880; Nobel 2005). Because of their reduced boundary layer lobed leaves should stay closer to air temperature than round leaves and thus warmer at night. Because of the above physiological effects lobed leaves in *M. filicifolius* and *M. laciniatus* could be a key adaptive trait in the rocky outcrop environments they occupy, although we acknowledge that these hypotheses remain to be rigorously tested.

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REVISIONS IN *POLEMONIUM* (POLEMONIACEAE): A NEW SPECIES AND A NEW VARIETY FROM CALIFORNIA

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Abstract

Polemonium eddyense Stubbs, sp. nov. (Polemoniaceae) is a localized endemic from Mt. Eddy in the Klamath Ranges of northern California. The new species resembles *P. chartaceum* H. Mason from the White and Sweetwater mountains. It is distinct from *P. chartaceum* in having round, rather than acuminate calyx lobes, heavier seeds, longer styles, and greater stigma exsertion. **Polemonium pulcherrimum** Hooker var. **shastense** (Eastw.) Stubbs, is a new combination from Mt. Shasta and Mt. Lassen. It differs from other varieties of *P. pulcherrimum* in corolla color, as well as geography, elevation, stature, and pubescence.

Key Words: Alpine flora, Mt. Eddy, Mt. Shasta, phylogeny, Polemoniaceae, *Polemonium*, *Polemonium chartaceum*, *Polemonium pulcherrimum*.

Over the past several decades there has been an ongoing series of systematic relationships proposed within *Polemonium* (Polemoniaceae). Pritchett (1993) and Pritchett and Patterson (1998) first undertook a morphometric analysis of relationships of alpine species in western North America. De Geofroy (1998) followed with a survey of western North American species using molecular sequence data. Timme (2001) expanded on de Geofroy's molecular research by examining relationships across the entire genus. Finally, Worley et al. (2009) published a phylogeny of the genus using AFLPs. These efforts have resulted in a substantial understanding of the taxonomy of the genus in California and western North America. *The Jepson Manual: Vascular Plants of California, 2nd ed.* (Timme and Wilken 2012) recognizes seven species of *Polemonium* in California.

In the most recent study, Stubbs (2012) undertook a thorough examination of remote populations in the field and used both morphological data and an updated molecular phylogeny of the genus, including taxa heretofore unsampled, to address three taxonomic problems that had not been resolved during earlier studies: 1) the issue of whether *P. carneum* A. Gray still occurred in California; 2) the status of the Mt. Eddy sky pilot; and 3) whether or not there are previously recognized infraspecific taxa within *P. pulcherrimum* Hook. worthy of recognition. As to the first issue, Stubbs and Fallscheer (2011) reported the occurrence of several healthy populations of *P. carneum* in northern California. Results of the rest of Stubbs' phylogenetic study have been published elsewhere (Irwin et al. 2012); here we propose new names so that they can be included in the forthcoming *Flora of North America North of Mexico, vol. 15* (FNANM).

Taxonomy

New Species

Polemonium eddyense Stubbs, sp. nov.—TYPE: USA, California, Siskiyou Co., Klamath Mountains, summit of Mt. Eddy; 2750 m; 15 July 2010, *Rebecca Stubbs 015* (holotype CAS; isotype MO).

Cespitose perennials 6.5–11 cm tall, densely viscid hairy; peduncles simple, not branching, glandular-pubescent throughout. Most leaves in basal rosettes, 14–46 mm long, 3–6 mm wide; petioles 5–10 mm, sheathing at base; leaflets 16–26, 1–6 mm long, 0.5–5 mm wide, 1–3 at point of attachment to rachis, lobes entire and obtuse or spatulate, terminal leaflet free but deeply lobed. Inflorescences capitiform, pedicels 3–6 mm. Perianth and androecium 5-merous, gynoecium 3-merous. Calyx 4.5–7.5 mm long, lobes lanceolate to obtuse, rounded, circumference 7–10 mm, hairy; corolla funnelform, petals 5, lobes violet, throat yellow, corolla circumference 7.8–11.3 mm, tube 5.9–11 mm long, lobes 3.5–6 mm long, 3–4.7 mm wide; stamens 5, exserted, anthers yellow, filaments glabrous, 3.4–8.1 mm long, attached 2.8–7.1 mm above corolla tube base; style exserted, 5.6–11.7 mm long, stigma 3-parted, 1.3–2 mm long. Seeds not mucilaginous when wet, lenticular, 2–3 mm long, 0.5–1.0 mm wide, dark brown.

Mt. Eddy, in the Klamath Range, is the only known location of *P. eddyense*. Historically, this population was referred to as *P. chartaceum* H. Mason, a species also found in the Sweetwater and White mountains, approximately 500 km to the south (Fig. 1). Pritchett (1993) and Pritchett and Patterson (1998) noted differences in average calyx lobe shape, seed weight, style length, and stigma exsertion in the Mt. Eddy population
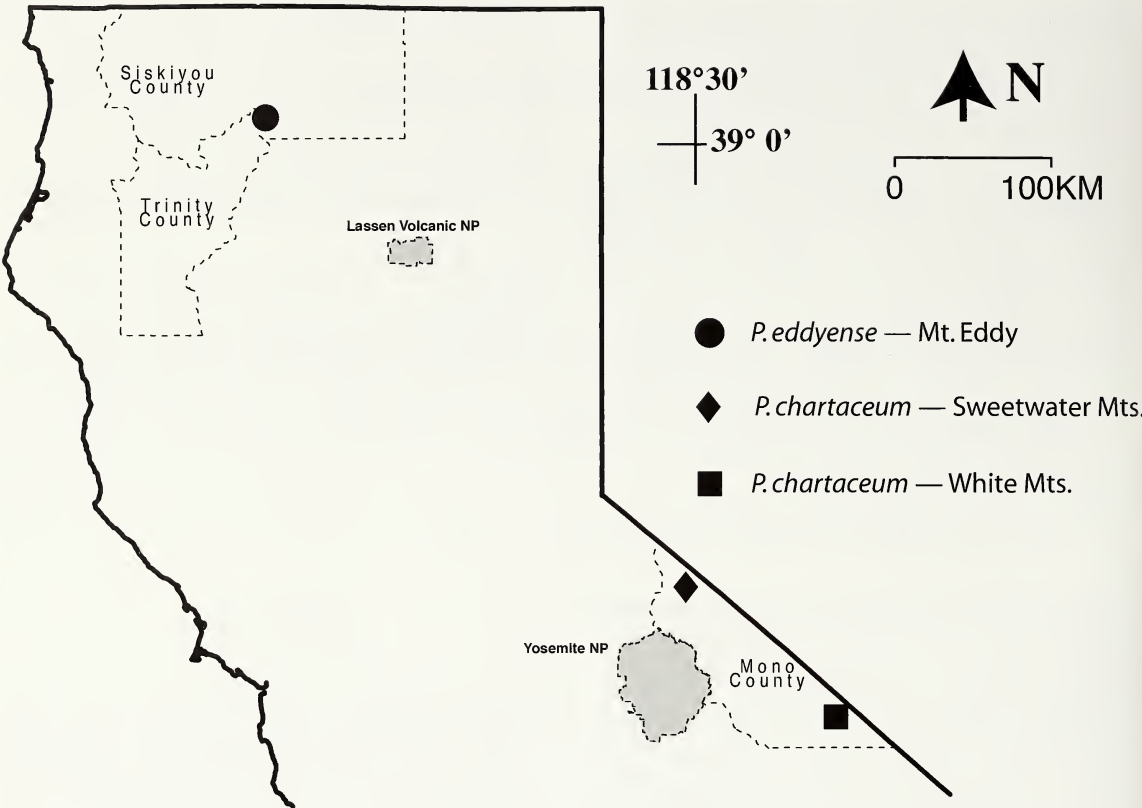
Fig. 1. Locations of *Polemonium eddyense* (Mt. Eddy) and *P. chartaceum* (Sweetwater and White mountains).

(Table 1). The most notable characteristic in the field is the long style and strongly exserted stigma in *P. eddyense* (Fig. 2A). In contrast, in *P. chartaceum* the style and stigma do not usually exceed the corolla orifice (Fig. 2B). Additionally, molecular sequence data from the ITS region (Irwin et al. 2012; Table 2) supports that the Klamath population is not phylogenetically close to the Sweetwater and White mountains populations of *P. chartaceum* (Fig. 3). Based on morphology, molecular research, and biogeography, it is clear that the Mt. Eddy population warrants taxonomic recognition as a new species.

Paratypes: USA. CALIFORNIA. Siskiyou Co.: Klamath Mtns., T40N R5W S18 NE¼, 0.8 km E of Mt. Eddy; 2707 m, 23 June 1990, *Daniel W. Pritchett 100*. Trinity Co.: T40N R6W S13 NE¼, unnamed peak 1.6 km NW of Mt. Eddy, on summit and down SW slope, 24 June 1990, *Daniel W. Pritchett 101*.

Mt. Eddy is the highest and most northerly peak in the Klamath Province and is composed predominantly of serpentinized peridotite. Mt. Eddy contains twenty-one species that have California Rare Plant Ranks (CNPS 2012), many of which, like *P. eddyense*, are endemic to serpentine soils (Cheng 1996; DellaSala et al. 1999). Recognition of *P. eddyense* as being distinct from *P. chartaceum* has significant implications for conservation due to this being the only known location of this species.

New Combination

Polemonium pulcherrimum Hook. var. **shastense** (Eastw.) Stubbs, stat et comb. nov. *Polemonium shastense* Eastw. Bull. Torrey Bot. Club 32:205–206. 1905. *Polemonium pulcherrimum* subvar. *shastense* (Eastw.) Brand. Das Pflanzenreich 250:34–36. 1907. *Polemonium shas-*

TABLE 1. MORPHOLOGICAL DIFFERENCES BETWEEN *POLEMONIUM EDDYENSE* AND TWO *P. CHARTACEUM* POPULATIONS (PRITCHETT 1993).

	Calyx apices	Seed weight	Style length	Stigma exsertion
P. eddyense Klamath Mtns.	rounded	9.62 mg	9.63 mm	2.91 mm
P. chartaceum Sweetwater Mtns.	acuminate	N/A	6.71 mm	0.29 mm
P. chartaceum White Mtns.	acuminate	3.92 mg	7.81 mm	1.59 mm

FIG. 2. Detailed photos of *Polemonium* subsp. A. *P. eddyense* showing strongly exserted stigma. B. *P. chartaceum* with stigma not exceeding corolla orifice. C. *P. pulcherrimum* var. *shastense* with pink venation radiating from corolla tube.

TABLE 2. COLLECTION NUMBER FOR VOUCHER SPECIMEN AND GENBANK ACCESSION NUMBER FOR ITS SEQUENCE (IRWIN ET AL. 2012).

Taxon	Collection number	GenBank ITS
P. acutiflorum	*de Nevers 2073*	DQ320767
P. boreale	*Cody 26927*	DQ320769
P. brandegeei	*Worley 006*	DQ320771
P. caeruleum	*McNeal 3530* (BRY)	EU628253
P. californicum	*Stubbs 12* (SFSU)	JX879092
P. californicum	*Stubbs 18* (SFSU)	JX879107
P. carneum	*Stubbs 07* (SFSU)	JX879106
P. carneum	*Stubbs 10* (SFSU)	JX879108
P. carneum	*Stubbs 11* (SFSU)	JX879104
P. chartaceum	*Stubbs 24* (SFSU)	JX879095
P. chartaceum	*Stubbs 23* (SFSU)	JX879102
P. chinense	*Ting-nong 1543*	DQ32078
P. eddyense	*Stubbs 15* (SFSU)	JX879096
P. elegans	*Worley 18*	DQ320783
P. elusum	*Irwin 5038* (RM)	JX879101
P. elusum	*Irwin 5039* (RM)	JX879111
P. elusum	*Irwin 5148* (RM)	JX879089
P. elusum	*Irwin 5496* (RM)	JX879099
P. eximium	*Stubbs 14* (SFSU)	JX879094
P. eximium	*Stubbs 21* (SFSU)	JX879109
P. eximium	*Stubbs 22* (SFSU)	JX879100
P. foliosissimum	*Halse 4261*	DQ320787
P. grandiflorum	*Zamudio 7469*	DQ320788
P. mexicanum	*Koch 75399*	DQ320789
P. micranthum	*Stubbs 04* (SFSU)	JX879093
P. micranthum	*Stubbs 05* (SFSU)	JX879113
P. micranthum	*Taylor 12548*	DQ320791
P. occidentale	*Stubbs 17* (SFSU)	JX879110
P. occidentale	*Timme 015*	DQ320793
P. occidentale	*Stubbs 13* (SFSU)	JX879112
P. pauciflorum	*LeBuhn s.n.*	DQ320794
P. pectinatum	*Worley 001*	DQ320796
P. pulcherrimum var. *delicatum*	*de Geofroy 127*	DQ320797
P. pulcherrimum var. *lindleyi*	*Grimes 2159*	DQ320801
P. pulcherrimum var. *pulcherrimum*	*Stubbs 19* (SFSU)	JX879091
P. pulcherrimum var. *pulcherrimum*	*Stubbs 20* (SFSU)	JX879103
P. pulcherrimum var. *pulcherrimum*	*Stubbs 33* (SFSU)	JX879097
P. pulcherrimum var. *shastense*	*Stubbs 16* (SFSU)	JX879105
P. pulcherrimum var. *shastense*	*Stubbs 26* (SFSU)	JX879098
P. reptans	*Keil 6266*	DQ320805
P. viscosum	*Worley 004*	DQ320806
Leptosiphon croceus	*Hankamp 043* (SFSU)	JX879090
Linanthus caespitosus	*Wilken 13982* (SFSU)	AF119443
Linanthus jonesii	*Owings 047* (SFSU)	AF119430
Phlox diffusa	*Peterson 97–110* (SFSU)	AF119444
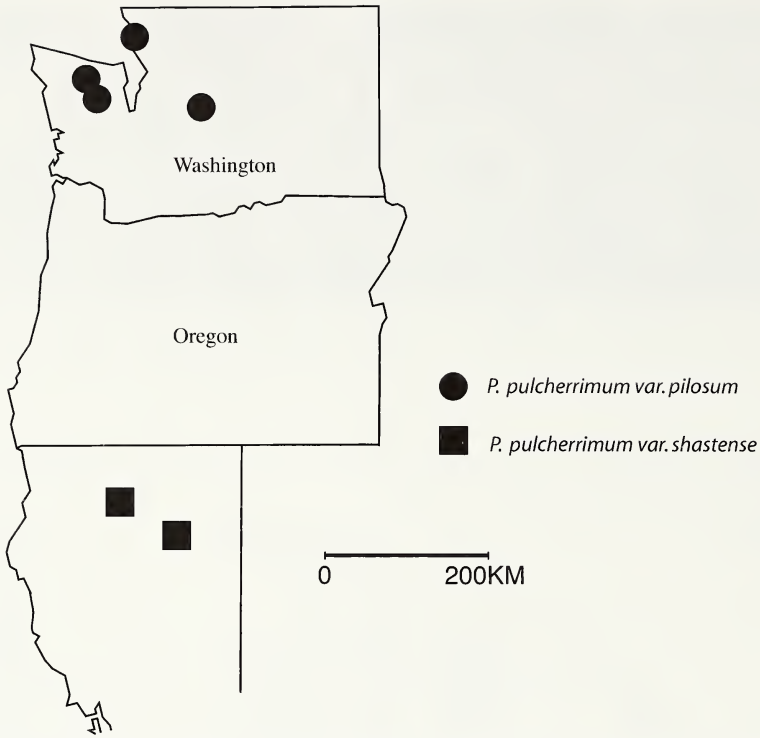
Fig. 3. Locations of *Polemonium pulcherrimum* var. *pilosum* in Washington and *P. p.* var. *shastense* in California.

tense f. *shastense* (Eastw.) Wherry Amer. Midl. Naturalist 27:753. 1942.—Type: USA, California, Siskiyou Co., Mt. Shasta, 10,400 ft, 16 July 1903, *Copeland s.n.* distributed as *Baker's 3515* (holotype: CAS!)

Polemonium pulcherrimum is a primarily subalpine and montane species and is widespread throughout western North America. Based on the amount of morphological variation in this species, there have been up to 35 intraspecific names and synonyms described (Brand 1907; Wherry 1942; Davidson 1950; Grant 1989). Many of the varieties and subspecies for *P. pulcherrimum* are readily discounted based on an acceptable spectrum of phenotypic variation expected for a species with an extensive range. Out of the plethora of proposed names published over the past century, five varieties appear distinct: *P. p.* var. *delicatum* (Rydb.) Cronquist, *P. p.* var. *lindleyi* (Wherry) J. P. Anderson, *P. p.* var. *pilosum* (Greenm.) Brand, *P. p.* var. *pulcherrimum*, and *P. p.* var. *shastense*.

Historically, two varieties have been recognized in California: *P. p.* var. *pulcherrimum* and *P. p.* var. *pilosum*. Very few collections have been made of *P. p.* var. *pilosum*, the only white-flowered morph of *P. pulcherrimum*, and it has not been sampled to be included in molecular-based phylogenetic analyses. In California, what formerly passed as *P. p.* var. *pilosum* occurs only on Mt. Shasta and Mt. Lassen. Populations from

these locations differ from populations in Washington in size, petiole length, pubescence type, corolla color, and elevational range. Additionally, we have examined two specimens from California labeled as *P. pulcherrimum* var. *pilosum* (*Taylor 4690* JEPS, *Barbe 325* RSA) that might be *P. p.* var. *shastense*, but this is difficult to confirm without seeing live material.

Similar to the nomenclatural confusion surrounding the varieties of *P. pulcherrimum*, the specific epithets "*shastense*" and "*pilosum*" have a convoluted history. It began in 1898 when Greenman first recognized *P. viscosum* Nutt. var. *pilosum* Greenm. from Goat Mountain in Washington, noting the pilose pubescence and white corolla with a yellow throat. He pointed out that "somewhat intermediate between the above variety and the species proper are specimens from Lassen's Peak, California." The use of the name *P. viscosum* for this plant produced confusion. *Polemonium viscosum* is a sky pilot from the Rocky Mountains and north into Canada and differs substantially from *P. pulcherrimum* in leaf attachment, leaflet shape, and inflorescence shape. This mistake can be attributed to an error on the herbarium sheet in the Gray Herbarium that was mentioned in the new species description (Rydberg 1897; Wherry 1942). The sheet, labeled *Polemonium viscosum*, inexplicably included two plants ("Evidently an accident occurred in the mounting room" cf. Wherry

TABLE 3. DIFFERENCES BETWEEN *POLEMONIUM PULCHERRIMUM* VAR. *PILOSUM* AND *P. P.* VAR. *SHASTENSE*.

	P. p. var. *pilosum*	*P. p.* var. *shastense*
General location	Washington	California
Elevation	1524–1828 m	2590–3900 m
Plant size	6–13 cm	7–18 cm
Petiole length	8–10 mm	10–33 mm
Pubescence	viscid glandular	densely woolly
Corolla color	white	white with pink

1942), one fitting Nuttall's original description of *P. viscosum* and the other fitting *P. pulcherrimum* var. *shastense* (Wherry 1942).

In 1905, Eastwood described *P. shastense* Eastw. from Mt. Shasta, California, distinguishing it as having glandular pubescence with a white corolla "often tinged with pink." Two years later Brand (1907) recognized *P. pulcherrimum* subvar. *shastense* Brand, addressing for the first time the distinction between what is now being recognized as *P. p.* var. *shastense* and *P. p.* var. *pilosum,* the former densely woolly with white flowers and the latter viscid glandular.

Jones (1936) elevated the Washington populations to species level, *P. pilosum* (Greenm.) G. N. Jones, but less than a decade later Wherry (1942) used Eastwood's *P. shastense* and applied this name to not only the plants in California but also to those in the Cascade Mountains. Like Brand, he recognized that the populations from the two states differed and distinguished the Washington material as *P. shastense* f. *pilosum* and the California material as *P. shastense* f. *shastense,* with taxon *pilosum* having leaflets more acute than those of taxon *shastense.*

Davidson (1950), in his monograph of the genus, included 16 synonyms under *P. pulcherrimum,* recognizing only *P. delicatum* Rydb.as a distinct taxon. Grant's (1989) study of the alpine polemoniums mentioned *P. pulcherrimum* var. *pilosum* "from the Cascade region of Washington and northeastern California," but only to say that it was being placed into synonymy and was a good candidate for taxonomic recognition.

Upon thorough reexamination of these taxa, particularly of extant populations in the field, it is apparent that varieties *pilosum* and *shastense* are distinct based on an array of features. The Californian entities are larger, both in habit and in size of organs (Table 3). *Polemonium pulcherrimum* var. *shastense* grows to 18 cm tall, while *P. p.* var. *pilosum* grows to 13 cm. Longer petioles, from 10–33 mm, occur in var. *shastense,* while in var. *pilosum* the petioles range from 8–10 mm. There is also a difference in the pubescence between the two varieties: var. *pilosum* is densely woolly and var. *shastense* is viscid glandular.

The most noticeable difference is corolla color. The description of the type specimen of *P. p.* var. *pilosum* describes the corolla as white with a yellow throat (Greenman 1898). Eastwood (1904) described the corolla of the California species as white with pink veins or tinges of pink. The Washington material never has pink in its corollas, while the California material generally has shades of pink (Brand 1907; Jones 1936). The bright pink venation (Fig. 2C) or pink tinge in the corolla of *P. p.* var. *shastense* is present in every population, though not in every individual flower. On Mt. Shasta, the corollas are white with bright pink striations along the veins, while on Mt. Lassen the corollas are often tinged with pink but never with a distinct separation between the pink and white parts of the corolla. Additionally, these two taxa are also separated by over 800 km, and there are no white-flowered *P. pulcherrimum* populations in Oregon (Fig. 3). Overall, the differences between these taxa are of similar scope with differences that distinguish other varieties of *P. pulcherrimum.* To conform to the FNANM policy that all infraspecific taxa within a genus be at the same rank, recognition of a new combination is warranted.

Due to its small population sizes and its distribution restricted to two heavily used alpine areas, Mt. Lassen and Mt. Shasta, *Polemonium pulcherrimum* var. *shastense* warrants conservation status.

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LAGOPHYLLA DIABOLENSIS (COMPOSITAE–MADIINAE), A NEW HARE-LEAF FROM THE SOUTHERN DIABLO RANGE, CALIFORNIA

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Abstract

Lagophylla diabolensis is a new hare-leaf from the southern Diablo Range of Fresno, Monterey, and San Benito counties, California. Plants of the Diablo Range hare-leaf were previously included within *L. dichotoma*, which is treated here in a restricted sense to comprise plants from the Sierra Nevada foothills and eastern Great Central Valley. Lagophylla diabolensis differs morphologically from *L. dichotoma* by having consistently glandular distal foliage (glands clear to dark-purple), narrower cauline leaves, generally uniformly tawny stems, and smaller heads. The taxonomic significance of those morphological differences is corroborated by other evidence that L. diabolensis is more closely related to the widespread *L. ramosissima* than to *L. dichotoma sensu stricto*. The Diablo Range hare-leaf occurs as scattered colonies, often in clayey soils of grassy openings in oak-pine woodland below 1100 m elevation. Extreme rarity and paucity of recent collections of L. diabolensis and *L. dichotoma* in the current sense indicates that both species warrant conservation concern.

Key Words: Asteraceae, California flora, Lagophylla diabolensis, *Lagophylla dichotoma*, Madieae, Madiinae, new species, tarweed.

Lagophylla Nutt. (Compositae–Madiinae) is a tarweed genus of spring- and summer–fall-flowering annuals commonly called hare-leaves, for the soft-hairy (hare's fur-textured) leaves of the type species, *L. ramosissima* Nutt. Hare-leaves represent a well-supported, diploid ($x = 7$) clade of the "Layia lineage" (Baldwin 2003) and share with *Layia* the characteristic of obcompressed ray cypselae that are each completely enwrapped by a phyllary. Thompson (1983), who conducted biosystematic and cytogenetic studies of *Lagophylla*, and most subsequent authors (e.g., Keil 1993; Baldwin 2012) have recognized four species of hare-leaves, one of which (*L. ramosissima*, including *L. congesta* Greene) is self-compatible and widespread from western and northeastern California to central Washington, western Idaho, and northern Nevada. The other three species [*L. dichotoma* Benth., *L. glandulosa* A. Gray, and *L. minor* (D. D. Keck) D. D. Keck] are relatively showy, self-incompatible or pseudo-self-compatible taxa that are endemic to California and the California Floristic Province, with distributions that are non-overlapping or nearly so (Thompson 1983).

Taxonomic and floristic accounts of *Lagophylla* reflect long-standing confusion about the relationships and distributions of the showy, strongly self-incompatible, and spring–early-summer-flowering members of the genus, which were initially all treated as *L. dichotoma*. Bentham (1849) described *L. dichotoma* from an 1847 collection by Hartweg, reportedly from pastureland in the Sacramento Valley. Based on collections by Hartweg, Bigelow, and Fitch, Gray (1880) indicated the distribution of *L. dichotoma* as being from "(p)lains of the Sacramento and Feather Rivers," in the Sacramento Valley. Jepson (1925) noted a broader distribution of *L. dichotoma* from "(s)lopes of mtns. bordering or near the Sacramento Valley," in the northern Sierra Nevada foothills and the Inner North Coast Ranges. Keck (1935) recognized that the showy, spring-flowering, serpentine-dwelling populations of the northern Sierra Nevada foothills and Inner North Coast Ranges, included in Jepson's circumscription of *L. dichotoma*, warranted recognition as a distinct taxon, *L. dichotoma* subsp. *minor* D. D. Keck, which he later elevated to species rank (Keck 1958) as *L. minor*. Keck's (1959) revised concept of *L. dichotoma* (=*L. dichotoma* subsp. *dichotoma* [Keck 1935]) included spring–early-summer-flowering, mostly non-serpentine populations with broader and duller ray cypselae, shorter-haired phyllaries, and stricter habits, with a less open branching pattern. *Lagophylla dichotoma sensu* Keck (1959) comprised a set of populations from the Great Central Valley and adjacent Sierra Nevada foothills and a disjunct, western set of populations in the southern Diablo Range, of the Inner South Coast Ranges. Keck's (1959) circumscription of *L. dichotoma* was adopted by authors of subsequent floristic treatments (e.g., Keil 1993; Baldwin 2012) and by Thompson (1983), who was able to include only one population (from the Diablo Range) in his biosystematic and cytogenetic study of *Lagophylla*.

Morphological differences between populations of *L. dichotoma sensu* Keck (1959) in the

Diablo Range and those to the east, in the Great Central Valley and Sierran foothills, have been intimated previously. Robert F. Hoover, who collected *L. dichotoma* in the Great Central Valley and Sierran foothills in 1937, 1938, and 1939, identified his 1946 collection of *L. dichotoma sensu* Keck (1959) from the Diablo Range (*Hoover 6098*, CAS 457623, UC 285370, UC 771656) to genus only, with the following parenthetical note added in his hand to CAS 457623 and UC 285370: "referred to *L. dichotoma* by Keck—needs more study." Rimo Bacigalupi called attention to the glandulosity of plants from the Diablo Range in an annotation (11 Mar 1958) of Hoover's collection (UC 771656). Baldwin and Strother (2006) noted that plants of *L. dichotoma* from the Inner South Coast Ranges "... are notably stipitate-glandular, unlike most Sierran and San Joaquin Valley collections." (Note: Their reference to the San Joaquin Valley rather than the Great Central Valley in general reflects the absence of any known collections of *L. dichotoma sensu* Keck [1959] from the Sacramento Valley [or anywhere north of Knights Ferry, Stanislaus Co.] since the 19th Century).

Morphological comparisons of additional specimens, including field collections from 2010 and 2011, have demonstrated that plants of *L. dichotoma sensu* Keck (1959) from the Diablo Range differ from plants elsewhere in the range of the species in vegetative and reproductive characters (see below). Phylogenetic analyses of nuclear ribosomal DNA and chloroplast DNA sequences of *Lagophylla*, including representatives of populations sampled across the distribution of each currently recognized species, have provided two lines of molecular evidence for a closer relationship of *L. dichotoma sensu* Keck (1959) from the Diablo Range to *L. ramosissima* than to *L. dichotoma sensu* Keck (1959) from the San Joaquin Valley and Sierran foothills (B. G. Baldwin unpublished). Examination of a probable isotype (fragmentary) of *L. dichotoma* (*Hartweg 1793*, GH 9562) and a photograph (UC 202612) of the holotype at Kew indicate that the species recognized here for the Great Central Valley and Sierra Nevada foothill populations should bear that name. A new name is needed for the species recognized here for plants of the southern Diablo Range, described below.

Taxonomy

Lagophylla diabolensis B. G. Baldwin, sp. nov. (Fig. 1).—TYPE: USA, California, San Benito Co., 4.1 mi SE of junction with State Highway 25 along Coalinga Road, in foothill woodland, 21 May 1988, *B. G. Baldwin 701* (holotype: JEPS; isotypes: CAS, DAV).

Annuals, to 1 m high, foliage pale-green, aromatic; **stems** usually uniformly tawny (rarely distally purplish), sparsely strigose to hirsute, also sparsely stalked-glandular distally, glands clear to dark purple; **cauline leaves** mostly alternate (proximally opposite), sessile, 1–5 cm long, 1–5 mm wide, linear to lance-linear or oblance-linear, entire, sparsely long-ciliate proximally, faces strigose-hirsute, hairs shorter abaxially; **basal leaves** withered at flowering; **capitulescence** paniculiform, to 40 cm wide, with dominant central stem slightly zig-zag, branches ascending, ultimate branchlets filiform; **calycular-like bracts** 2–3, elliptic to elliptic-oblanceolate, each 5–6 (–11) mm long, overtopping body of involucre, exceeded by phyllary tips or not, coarsely ciliate (hairs to 1.5 mm long), hirsutulous and abaxially stalked-glandular, glands clear to dark purple; **heads** radiate; **involucre** obconic-hemispheric, ca. 5 mm diam; **phyllaries** 5, each completely enfolding a ray ovary (margins of phyllary body connivent, minutely ciliate) and falling with fruit, 4–5 mm long (body usually 2.5–3 mm long; free tip 1.5–2 mm long), lance-linear, body ca. 1.5 mm side-to-side, 1 mm front-to-back, hirsute (hairs ascending), at least near folded edge, to hirsutulous, and stalked-glandular (glands clear to dark-purple), tip straight; **receptacles** bristly at center, paleae in 1 peripheral series, usually 5, 3.5–5 mm long, alternating with phyllaries, free, each partially clasping a disk corolla, herbaceous except for hyaline margins of clasping portion, puberulent, tip ± erect, ca. 1 mm; **ray florets** 5, pistillate, corolla bristly-hirsute in proximal third abaxially and proximal to lobes adaxially, tube 0.5–1 mm long, laminae 4–9 mm long, broadly obovate-obdeltate, light yellow except for purplish main veins abaxially on lobes, at least distally, lobes 3, 1/3–1/2 length of laminae, creased (and folding inwardly, especially under heat or drought stress) along main veins, lateral lobes 1.5–3 mm wide, central lobe 0.5–1.5 mm wide; **disc florets** 6 (5 peripheral, alternating with ray florets, and 1 central, 1 mm longer than others), functionally staminate (ovary sterile), corollas yellow, 2.5–3 mm long, narrowly funnelform, tube/throat 2–2.5 mm long, sparsely bristly near base, lobes 5, spreading to reflexed, 0.5–0.75 mm long, ovate-deltate, adaxially papillate; anthers dark purple, appendages ovate-deltate; ovaries 0.5–1.75 mm (ovary of central disk floret 1 mm longer than ovaries of peripheral disk florets), glabrous, style branches erect, fused throughout length, densely bristly-puberulent, pappus absent; (ray) **cypselae** 2.3–3 mm long, oblanceolate to obovate in outline, obcompressed (1.0–1.7 mm side-to-side; 0.6–1 mm front-to-back), slightly arched outwardly, black with irregular brown mottling or crust, finely striate, glabrous, pappus 0. Chromosome number $2n = 7_{II}$ (Johansen 1933; Thompson 1983).
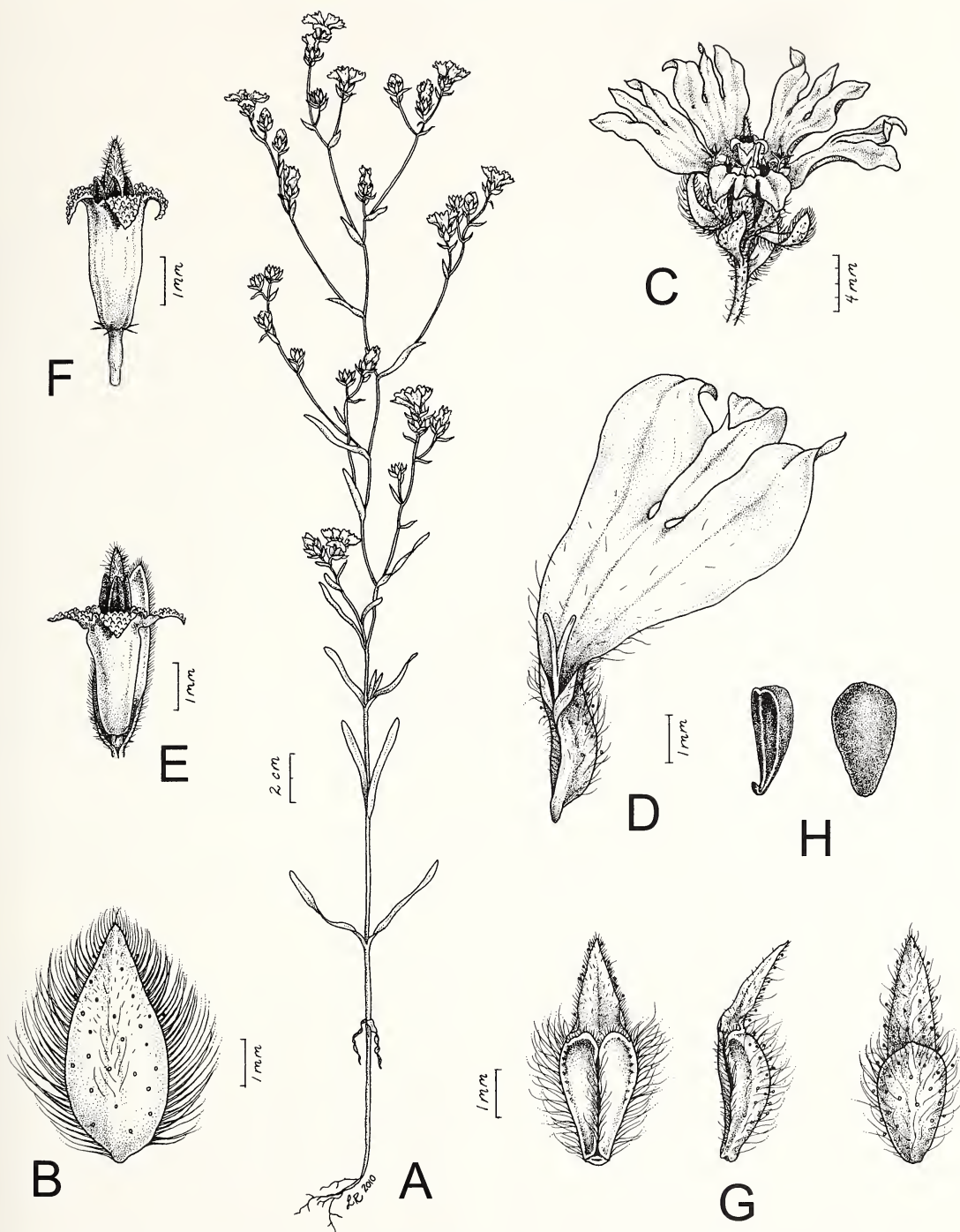
Fig. 1.   *Lagophylla diabolensis.* A. Habit. B. Calycular-like bract. C. Head. D. Ray floret and associated (clasping) phyllary. E. Disc floret and associated palea. F. Disc floret. G. Phyllary clasping cypsela in (left-to-right) adaxial, obliquely lateral, and abaxial views. H. Cypsela in (left-to-right) obliquely lateral and abaxial views.

Paratypes

USA, California: Fresno Co., near eastern base of Coalinga-Parkfield grade, 12 Jun 1915, *H. M. Hall 10028* (DS 635069, DS 188348, GH).

Monterey Co., 15 mi N of San Miguel, in Indian Valley, 1200 ft elev., 27 Apr 1934, *D. D. Keck 2844* (CAS, DS 635073, DS 328347, GH, UC); between Black Mountain and Mustang Peak, 3500 ft, 26 Jun 1964, *C. B. Hardham 18,142*
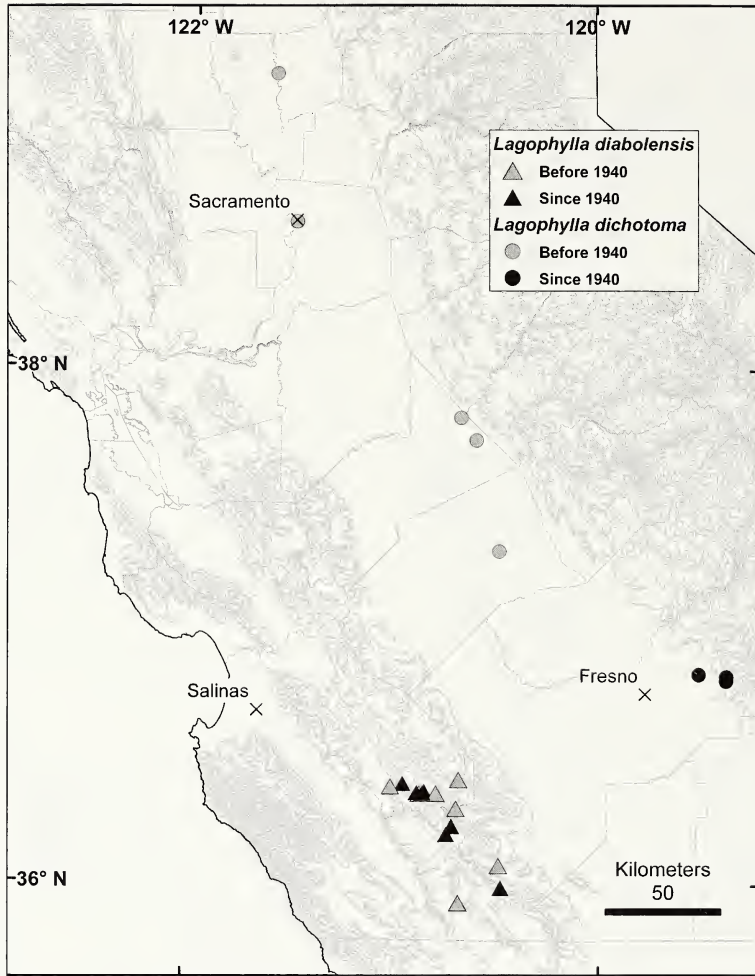
Fig. 2. Geographic distribution of *Lagophylla diabolensis* and *L. dichotoma* based on herbarium records. Note the paucity of occurrences for both species, especially based on documented collections since 1940 (see text).

(CAS); Mustang Grade, 12 Jun 1938, *A. East-wood and J. T. Howell 5821* (CAS, DS); Hwy 198, ½ mi W of mile marker #22, 31 May 1982, *V. Yadon H-2214* (PGM). San Benito Co., North Fork Road, near Le Neve Ranch, 3.5 mi N of Priest Valley School, 1 Jul 1982, *V. Yadon H-2491* (PGM); 1.5 mi from junction of San Benito-Hernandez road on cross-road to Bitterwater Valley, 2000 ft elev., 1 May 1933, *D. D. Keck 2052* (DS); San Benito Valley, 19.6 mi from King City (in pencil), 10 Jun 1931, *H. M. Hall 13158* (DS); Lorenzo Creek, 2400 ft elev., 2 Jun 1927, *W. L. Jepson 12,221* (JEPS); Coalinga Road, about 4 mi N of Clear Creek Road, 4 Jun 1962, *V. F. Hesse 3146* (JEPS, UC); same locality as holotype (*BGB 701*), 36.39896°N, 120.94571°W, 1850 ft elev., 27 Jun 2010, *B. G. Baldwin 1543* (JEPS); Coalinga Road, 9.45 mi SE of California State Highway 25, 36.36368°N, 120.87760°W, 2200 ft elev., 27 Jun 2010, *B. G. Baldwin 1542* (JEPS); first ridge on Hernandez road after

leaving Hollister-King City road, 31 May 1946, *R. F. Hoover 6098* (CAS, UC 285370, UC 771656); Coalinga Road, at summit 11.4 mi SE of junction with California State Highway 25, 21 May 1988, *B. G. Baldwin 702* (CAS, DAV); same locality as *BGB 702*, 36.35965°N, 120.84891°W, 2900 ft elev., 26 Apr 2011, *B. G. Baldwin 1566* (JEPS); Hernandez, 17 May 1893, *A. Eastwood s.n.* (UC 89193) [note: label indicates Warthen, 11 May 1893; annotation by A. Eastwood indicates locality and date given here]; near Hernandez, San Benito Co., 17 Aug 1933, *J. T. Howell 11545* (CAS, DS); near Harrisons, Hernandez, San Benito Co., 1 Jun 1899, *W. R. Dudley s.n.* (DS 3514); upper San Benito River, 2900 ft elev., 1 Jun 1927, *W. L. Jepson 12,203* (JEPS); above New Idria, San Benito Co., 31 May 1899, *W. R. Dudley s.n.* (DS3365).

Lagophylla diabolensis differs from *L. dichotoma* in the narrow sense by its consistently stalked-glandular (versus often eglandular) distal

foliage, linear to lance- or oblance-linear (versus oblanceolate to spatulate) and entire (versus entire to toothed) leaves, generally uniformly tawny (versus tawny to dark purplish) stems; and smaller heads, with phyllaries 4–5 mm (versus 6–6.5 mm) long, ray laminae 4–9 mm (versus 4–13 mm) long, and disc corollas 2.5–3 mm (versus 4 mm) long.

Lagophylla diabolensis is known from southwestern Fresno, southeastern Monterey, and southern San Benito counties, generally in dense clay soils of grassy openings in foothill woodland, from about 350 to 1070 m elev. (Fig. 2). One collection with minimal and uncertain label information (Tulare County, Apr 1900, *D. G. B. [?] s.n.* [DS 3366]) is a geographic outlier of doubtful provenance. Flowering is mainly from late April to early July, with last heads sometimes produced as late as August (in contrast to documented flowering of *L. dichotoma sensu stricto (s.s.)* from early April to mid May). Woody associates include *Pinus sabiniana* D. Don, *Quercus douglasii* Hook. & Arn., *Q. lobata* Née, and *Toxicodendron diversilobum* (Torr. & A. Gray) Greene. Associated native forbs and grasses include taxa of *Achillea* L., *Achyrachaena* Schauer, *Agoseris* Raf., *Corethrogyne* DC., *Clarkia* Pursh, *Delphinium* L., *Lupinus* L., *Madia* Molina, and *Poa* L. Non-native associates include species of *Avena* L., *Bromus* L., *Centaurea* L., *Elymus* L. (*Taeniatherum* Nevski), and *Lactuca* L.

Etymology

Apparent restriction of *L. diabolensis* to the Diablo Range is the basis for the species epithet.

Conservation Status

Keck (1935), in reference to the taxon he then treated as *L. dichotoma* subsp. *dichotoma* (=*L. dichotoma sensu* Keck [1959]), which comprised plants treated here as *L. diabolensis* and *L. dichotoma*, noted that "(t)his is one of the very rare tarweeds." Persistent paucity of herbarium collections and known localities for plants belonging to *L. diabolensis* and *L. dichotoma s.s.* is consistent with the extreme rarity of both species (Fig. 2). Lack of collections of *L. diabolensis* (and *L. dichotoma s.s.*) may in part reflect year-to-year variation in emergence of plants, inconspicuousness of plants when heads are closed in the afternoon in response to heat or drought stress (Thompson 1983), and inaccessibility of extensive private land near known collection areas, where undocumented populations may occur.

Lagophylla dichotoma, already listed by the California Native Plant Society (2012) as rare, threatened, and endangered in California and elsewhere (California Rare Plant Rank 1B.1), is here recognized as a much rarer species, with only five general occurrences known to me outside the Sacramento Valley, where evidently no collection of *L. dichotoma* has been made since the 19th Century (Fig. 2). Early, Sacramento Valley records are vague or general as to locality: "along the Feather River north to Chico (?) or beyond" (13– ? 16 Apr 1847) for a large set of specimens including Hartweg's type collection (fide McVaugh 1970); "plains of Feather River near Marysville" (May, no year given; *Bigelow s.n.*, GH 9563); and "Sacramento" for an undated, fragmentary collection (*Fitch s.n.*, GH) in a packet on the same sheet as the putative isotype and Bigelow specimens. For three of the five general occurrences for *L. dichotoma s.s.* south of the Sacramento Valley, I know only of collections made from 1915 to 1939, from Merced (23 Apr 1915, *Eastwood 4431*, CAS, UC), in Merced Co., and from Knights Ferry (4 May 1937, *Hoover 2040*, DS, JEPS, UC; 9 May 1938, *Hoover 3377*, JEPS, UC) and Warnerville (4 May 1937, *Hoover 2050*, CAS, DS 318633, DS 635059, DS 253131, JEPS, UC), in Stanislaus Co. The other two general localities, where plants were documented historically and recently, are both in Fresno Co., at Round Mountain (31 May 1946, *Carter 89*, DS, UC; 24 Apr 2010, *Baldwin et al. 1539*, JEPS) and Tivy Mountain (10 Apr 1939 ["Piedra"], *Hoover 3982*, CAS, DS 318632, DS 635068, DS 266092, JEPS, UC; 21 Apr 2001, *Greenhouse and Greenhouse 5015*, JEPS; 24 Apr 2010, *Baldwin et al. 1533, 1536*, JEPS), where the Sierra Foothill Conservancy's Tivy Mountain Preserve and any conservation efforts directed toward the population on Round Mountain may be key to survival of *L. dichotoma*.

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REVIEW

Woody Plants of Utah

A Field Guide with Identification Keys to Native and Naturalized Trees, Shrubs, Vines, and Cacti

Renée Van Buren, Janet G. Cooper,
Leila M. Shultz, and Kimball T. Harper

Photographs by R. Van Buren et al.; Plant Diagrams by J. G. Cooper

Woody Plants of Utah: A Field Guide with Identification Keys to Native and Naturalized Trees, Shrubs, Cacti, and Vines. By RENÉE VAN BUREN, JANET G. COOPER, LEILA M. SHULTZ, AND KIMBALL T. HARPER. 2011. Utah State University Press, Logan, UT. 513 pp. ISBN 978-0-87421-824-4 (paperback); ISBN 978-0-87421-825-1 (e-book). Price $34.26.

This is a handsome volume with dichotomous keys, up-to-date taxonomy, many excellent photographs, semitechnical descriptions, habitat and range statements, specimen-based range maps, and anecdotal information including derivations of scientific names. "Woody" is defined broadly for this work, including not just the trees, shrubs, and woody vines that traditionally would be so treated, but also various subshrubs, more or less suffrutescent herbs, and succulents. Utah's cacti, including small, spherical taxa only a few cm tall, are all included. The result is a treatment of 152 genera, 385 species, and 446 taxa assigned to 51 families.

Chapter 1, Introduction to the Woody Flora, provides summary information of various types, including several tables. Because of difficulties associated with identification of mistletoes (Viscaceae) to the species level, the authors chose to leave them out of keys and descriptions, and instead listed them in a table in the Introduction; users are referred to more technical references for species identification. The omission of the two mistletoe genera, *Arceuthobium* and *Phoradendron*, from both keys and descriptions bothers me; for completeness I think it would have been much more useful to have the mistletoes keyed to the genus level with disclaimers in the generic treatments about the difficulty of species determination and references to technical sources. A user who encounters a mistletoe may be puzzled by its apparent non-inclusion and not know to seek it out in the Introduction.

Chapter 2, Major Utah Plant Communities, includes a short discussion of plant community concepts and characteristics followed by brief descriptions and photographs of 20 major Utah plant communities. A discussion of anthropogenic impacts on Utah communities is accompanied by a discussion of management and restoration of woody plant communities. The community chapter concludes with a bracket-format dichotomous key to the 20 communities. The authors acknowledge that there are other communities of lesser areal extent in the state that are not discussed. Some of these are referred to in the habitat and range statements in chapters 4 and 5.

Chapter 3 is a bracket-format dichotomous key to the woody plants of Utah. The Major Group Key separates out Key I: Gymnosperms; Key II: Monocot Trees and Shrubs; Key III: Dicot Trees; Key IV: Cactus Family; Key V: Vines; and Key VI: Shrubs. The keyer will discover 20 pages later that Key VI is subdivided into four groups based on combinations of vegetative features. A more straightforward approach would have been to ditch the Roman numerals and include these four groups in the Major Group Key. Key VI, Group 4 (shrubs; leaves simple, alternate, basal or in loose rosettes; stems and leaves lacking spines) is by far the longest of the keys with 288 couplets. That's a lot of slogging. This key could probably have been broken up into smaller, more manageable subgroups. Couplet 1b in the Major Group Key includes a misleading statement: "some leaves modified as spines," which one must get past to key out all of the non-spiny plants in subsequent groups. The authors undoubtedly intended this to mean "leaves in some taxa modified as spines," but that's not the way it reads. I ran a few plants through the keys and encountered no other major problems, though I stumbled over a few awkward wordings. Vegetative features predominate in the keys, a boon to those encountering the plants out of the often-brief flowering season. A color-coded running header helps the keyer to keep track of the contents of the key he or she is using. I don't particularly like bracket keys—the key provides no structural cues to the keyer's position, but they are more economical of space than indented keys.

Chapter 4, Gymnosperm Descriptions, and Chapter 5, Angiosperm Descriptions, form the main body of the book, with information provided about each taxon. Taxa are arranged alphabetically within the two major groups, from family down. Family names are in the running header. Descriptions are included for each taxonomic level. Here and there I encountered descriptions of species in the same genus that are difficult to compare because different features or descriptors are included for one taxon or the other. The family description of the Rhamnaceae is garbled. Standard botanical descriptions generally leave out most or all articles; they are included here, probably to make the text seem

less foreign to non-specialists. Users will have to deal with technical terminology. A glossary, which follows the taxonomic treatments, includes the majority of the terms used in the keys and descriptions. The omitted terms probably will have little impact on the more proficient of these users, but may occasionally deter or confuse those with less botanical expertise.

Some of Utah's woody plants are armed with stiff, sharp-pointed structures of various derivations. Unfortunately, the authors frequently misinterpret these features or misuse the terminology that should be applied to them, occasionally treating them differently in the keys and the descriptions. The glossary definition of spine is both inaccurate and incomplete: "a rigid, sharp-pointed outgrowth of the stem, without conducting tissue; a modified leaf or stipule." The first portion of this definition is inaccurate—spines are modified leaves or leaf parts and generally do contain conducting tissue, and the second is incomplete—other leaf parts may be modified as spines—for instance the hard, stiff tip of an *Agave* leaf. A more accurate description would be "a rigid, sharp-pointed leaf or leaf part." The glossary definitions of prickle and thorn are accurate, but these terms are sometimes misapplied, with spine used where prickle or thorn should have been applied. *Rosa nutkana*, for instance, is described as armed with spines below the stipules, and the branches of *R. woodsii* are described as armed with prickles and spines; actually, all of the sharp structures of both species are prickles. *Acacia greggii* stems are said to be armed with spines (Key III, leads 8a, 9b) and with thorns (species description), but the sharp structures are actually prickles. Various *Atriplex* species are described as spiny, but more properly are thorny since sharp stem tips are thorns, not spines; likewise *Pleiacanthus* stems are thorn-tipped, not spine-tipped. Stems of *Psorothamnus polydenius* are described as having straight spines between the nodes, but these too are thorns. *Menodora spinescens* and *Grayia spinosa* are thorny, not spiny, despite their names. Leaves of *Linanthus pungens* key as prickly (Key 6, Group A, 8b), but in the description are more accurately treated as spinulose (minutely spiny).

Derivations of scientific names are given for generic names and for specific and infraspecific epithets. This is a desirable feature for a book of this nature except in that in various cases the etymology given is incorrect. Examples: *contorta* (*Pinus contorta*) refers not to "the twisted needles" [they are not] but to the bent and twisted growth forms of the coastal race of the species; *schidigera* (*Yucca schidigera*), is derived from *schidax*, Greek for splinter, describing the marginal fibers, and does not mean "spine bearing"; *plummeri* (*Zuckia brandegei* var. *plummeri*) honors A. Perry Plummer (1911–1991), Utah teacher, naturalist, range scientist, not Sarah Allen Plummer, 19th-century botanist; *puberulus* (*Chrysothamnus viscidiflorus* var. *puberulus*) means minutely pubescent, not "somewhat pubescent" [the glossary correctly defines the English equivalent, puberulent]; *petradoria* (*Gutierrezia petradoria*) means rock goldenrod (*petra* [Greek] means rock; *Doria* is a 16th century generic name for a goldenrod), not "petro suggests 'among the rocks' and dorii means 'gift'"; *polydenius* (*Psorothamnus polydenius*) means many glands, not "many teeth"; *columbiana* (*Clematis columbiana*, *Crataegus columbiana*) refers to the Columbia River valley where the species were discovered, not to British Columbia [the former species does not occur there]; *tremuloides* (*Populus tremuloides*) refers to the resemblance of the American quaking aspen to *Populus tremula* L., its Eurasian counterpart, rather than to the "trembling or quaking leaves" [which both species share]. My list of inaccurate etymologies includes quite a few more.

For the most part, Woody Plants of Utah is up to date with the many changes in taxonomy and names that have resulted from recent phylogenetic studies. An exception is the inclusion of *Nolina* in Agavaceae. Monocot family taxonomy remains in flux, but the resemblance of *Nolina* to *Yucca* and *Agave* is apparently a result of evolutionary convergence and not close relationship.

An appendix contains a list of the accepted scientific names arranged by families in parallel with chapters 4 and 5 along with common names and lists of synonyms. The synonymies are eclectic, and some lists include names long out of use. Having the synonyms segregated as an appendix declutters the taxonomic treatments, but the synonyms are not indexed. Consequently users seeking the disposition of a name used in another reference may have difficulty finding the accepted taxon to which it applies.

Notwithstanding my various quibbles, I think Woody Plants of Utah is a valuable resource. It's full of useful information. The book is aimed at "professionals, students of botany, naturalists, and curious wanderers," and I think all of these users will find it to be a handy field guide.

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REVIEW
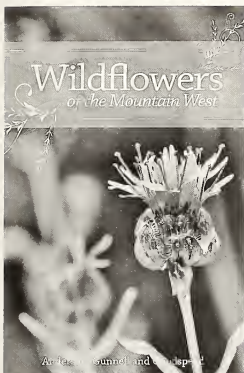
Wildflowers of the Mountain West. By RICHARD M. ANDERSON, JAYDEE GUNNELL, AND JERRY L. GOODSPEED. 2012. Utah State University Press, an imprint of University Press of Colorado, Boulder, CO. 300 pp. ISBN 978-0-87421-895-4 (spiral bound) $24.95; ISBN: 978-0-87421-896-1 (e-book) $20.00.

When I arrived in Utah as an assistant professor three years ago, I was given Field Botany to teach. For me, this assignment was a bit intimidating since my formal botanical training was limited. As a developmental geneticist, I am much more comfortable dealing with genes than with genera. Always an enthusiastic amateur botanist (emphasis on amateur), I eagerly embarked on a crash course to learn the 200 trees and shrubs that we require our students to recognize in the field and on campus. I quickly caught the bug, and lately have been exploring my local herbaceous flora as well. So I was delighted to see that a new field guide, *Wildflowers of the Mountain West*, is now available. In many ways this book is exactly what I needed.

The first thing I did when my copy arrived was to find the new acquaintances from the canyon close to my home that I had met and keyed out last summer. I would expect any decent field guide to include the most common flowers, and this one delivered. Like searching for friends in my high school year book, my botanical compatriots were all there. Each species is given two pages, with taxonomy, description, habitat and county-level distribution map on the first page, and high-resolution photos on the second page. Each species has a close-up of the flower as well as the whole plant in situ. These photos are likely the most useful part of the book, and the authors clearly took care to deliver a quality product. The species are grouped first by flower color and then by family, which I found to be helpful. With a little knowledge of families, zeroing in on, for example, the possible purple-flowered, pea-family contenders, is very quick. The species descriptions (130 in total) comprise the majority of the book, with some introductory material on the mountain west and simple illustrations of floral and leaf morphology terms to round it out.

The authors readily admit that using the most current taxonomy is not one of their concerns. Nevertheless, keeping *Penstemon* (Plantaginaceae), *Castilleja* (Orobanchaceae), *Mimulus* (Phrymaceae), and others as members of the old polyphyletic Scrophulariaceae seems unnecessarily old-fashioned, even to me. Using the current taxonomy would not have been that onerous (at least at the family level). Another concern is that the book completely ignores exotics. I understand the desire to tout our native flora, however, the most obvious and showy flowers a naïve botanist is likely to encounter on his or her first foray are the non-native dalmatian toadflax (*Linaria vulgaris*) and whitetop (*Lepidium draba*). Providing pages for common weeds would have provided important information to budding flower enthusiasts. Once you know that the attractive flower you just found is actually crowding out other native beauties, it is suddenly illuminated by an entirely different light. But these concerns are really trifles, and don't substantially take away from an otherwise excellent field guide. I am happy to have *Wildflowers of the Mountain West* on my book shelf, and expect it will come into the field with me as a handy first reference as soon as spring arrives.

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NOTEWORTHY COLLECTION

CALIFORNIA

Sphaeropteris cooperi (Hook. ex F. Muell.) R. M. Tryon (synonym *Cyathea cooperi* (Hook. ex F. Muell.) Domin (CYATHEACEAE) (Australian tree fern, Cooper's tree fern).—Los Angeles Co., Santa Catalina Island, Twin Rocks, channel-side coastal bluff, uncommon but widespread along open, rocky cliff faces, characterized by exposed, granitic and sedimentary sandstone soils, and very little annual rainfall, 33°24′50″N, 118°22′26″W, elev. 218 m (715 ft), 23 June 2011, *J. R. Clark 1020 with T. Dvorak, C. de la Rosa, S. Ratay, and T. M. Sunmers* (CATA, RSA, SBBG, UC).

Collection notes. Associated species include *Dudleya virens* (Rose) Moran subsp. *hassei* (Rose) Moran, *Mimulus aurantiacus* Curtis var. *parviflorus* (Greene) D. M. Thomps., *Opuntia littoralis* (Engelm.) Cockerell, and *Rhus integrifolia* (Nutt.) Benth. & Hook. f. ex Rothr. A stand of *Lyonothamnus floribundus* A. Gray subsp. *floribundus* (the endemic Catalina ironwood) is also present near the site, although no *S. cooperi* are immediately adjacent to this stand. Only two other fern species were documented in the vicinity, a single individual of *Woodwardia fimbriata* Sm. growing in a damp seep along the south side of the bluff and scattered individuals of *Polypodium californicum* Kaulf. growing mostly in shaded areas.

A general survey of the locality was undertaken and at least 20 individuals of *S. cooperi* were observed growing in and among the cracks and hangs of the bluffs. Some of these individuals were growing in areas that were accumulating and storing water while others appeared to be growing directly from the dry, barren rock faces. Aspect did not appear to have bearing on plant establishment; all slopes of the formation had *S. cooperi* individuals growing on them. Species directly associated with individual *S. cooperi* plants were few, and of these *Mimulus aurantiacus* was most commonly seen in physical proximity to the ferns.

Individual plants of *S. cooperi* ranged in size from less than one meter in height, including fronds, to approximately 1.5 meters total height. The largest trunk observed measured approximately one meter tall with a diameter of approximately 10–15 cm. Fronds were on average one meter in length, although smaller on some individuals growing in particularly exposed areas. All plants that were physically accessible were observed to have fertile fronds and were actively releasing spores via sori near the distal ends of the fronds. Older, dead fronds did not appear to be dehiscing from the trunk as is thought common for the species (Medeiros et al. 1992); instead, on all observed specimens, trunks were routinely covered in dead fronds. Age could not be assessed, but previously unidentified photographs of the naturalized tree ferns from 2007 were recently discovered and reviewed in preparation for this paper (Catalina Island Conservancy private photograph collection; images not shown). Based on this finding, the population is at least 6 years old and most likely older, considering the size of specimens in the photographs.

Previous knowledge. *Sphaeropteris cooperi* is a commonly planted ornamental tree fern species native to the subtropical rainforest of eastern Queensland and eastern New South Wales, Australia. Cultivated widely in much of the temperate, subtropical, and tropical world, the species exhibits considerable ecological tolerance, being capable of survival in a variety of conditions from periodic cold and freezing to extreme heat – so long as ample water is available. The species has long been used ornamentally, particularly in Hawaii and other tropical Pacific islands (Medeiros et al. 1992; Wagner 1995). In North America, *S. cooperi* has been widely cultivated and is commonly seen in managed landscapes throughout California and as far north as British Colombia, as well as in the American Southwest where irrigation is regular, and into the Southeast as far South as Florida and the Caribbean (Wood 2008).

Significance. First report of the species being naturalized in California. The potential for invasiveness by *S. cooperi* is thought to be high in the wet tropics and the species is considered a noxious weed in all of Hawaii (Medeiros et al. 1992) as well as other tropical regions including Mauritius and Madagascar. Moist subtropical and even temperate areas have also been invaded by *S. cooperi* including southern regions of Eastern and Western Australia and, most recently documented, a restricted coastal region of the temperate rainforests of Oregon, USA (Wood 2008). The discovery of a naturalized population in southern California represents the first-ever report of the species being naturalized in a markedly dry, Mediterranean-type climate.

Recent research in modeling natural and escaped ranges for potentially invasive species suggests that native ranges and ecologies might under-predict the diversity of habitats available to a particular species for invasion (Fitzpatrick et al. 2007; Pearman et al. 2007; Rödder and Lödders 2009; Mandle et al. 2010). The discovery of a naturalized population of *S. cooperi* on Catalina Island in an area of relatively high exposure and very little apparent moisture supports this prevailing notion. However, habitats such as the California Channel Islands that at first appear unsuitable for wet-loving species such as *S. cooperi* should be reconsidered in light of phenomena such as a persistent marine layer and fog drip that can dramatically increase available moisture (Fischer et al. 2009). These and other environmental variables, if modeled, might accurately reflect true invasible ranges for the species (Peterson and Nakazawa 2008; Mandle et al. 2010).

Within species variation and local adaptation must also be considered in explaining the apparent range expansion for *S. cooperi* (Broennimann et al. 2007; Mandle et al. 2010; Wang and Guan 2011). Ferns in general are ecologically plastic and both the gametophytic and sporophytic generations exhibit the propensity to tolerate and adapt to harsh environments (Watkins et al. 2007), including those created following disturbance and/or dispersal to new and different environments (Page 2002; Saldaña et al. 2007). Many ferns including *S. cooperi* exhibit high reproductive output via spores that are highly dispersible, factors that might be contributing to dispersal to, and increased odds for, establishment in drier and presumably less-typical environments for the species (Durand and Goldstein 2001; Page 2002; see also Lavergne and Molofsky 2007).

Regardless of cause, the potential for additional naturalized populations of *S. cooperi* along the California coast and other coastal Mediterranean environments worldwide is expected. Research into modeling and identifying these expected ranges and localities is therefore justified. On-the-ground surveys are also needed to locate and manage naturalized populations, if and where they exist. The novelty of this recent discovery of naturalization and potential ecological range expansion warrants additional field observation and study as well as population genetics research. As of this publication, the Catalina Island population of *S. cooperi* is being closely monitored but not eradicated to facilitate current and future study.

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NOTEWORTHY COLLECTION

CALIFORNIA

Trifolium suffocatum L. (FABACEAE) (suffocated clover).—Monterey Co., along 180 m of incompletely vegetated use trail on old sand dunes of former Fort Ord, in chaparral, with *Matricaria discoidea* DC, *Lepidium strictum* (S. Watson) Rattan, *Triphysaria pusilla* (Benth.) T. I. Chuang & Heckard, *Hypochaeris glabra* L., *Trifolium angustifolium* L., *Spergula arvensis* L., *Cardionema ramosissimum* (Weinm.) A. Nelson & J. F. Macbr., *Plantago coronopus* L., *Silene gallica* L., *Logfia gallica* Coss. & Germ., *Aira caryophyllea* L., *Bromus diandrus* Roth, and *B. hordeaceus* L., UTM: 10S 0606738E, 4055848N, elev. 82 m, 3 May 2010, *Styer 37318* (CDA), identified by Randall Morgan and confirmed by Michael Vincent; Monterey Pines Golf Course, UTM: 10S 0601813E, 4050118N, elev. 34 m, 28 June 2012, and UTM: 10S 0601573E, 4050001N, with 40–50 plants, all past bloom and withered, in incompletely vegetated, unplanted "lawn" on old sand dunes, with *Aira caryophyllea, Plantago coronopus, Lasthenia minor* (DC.) Ornduff, *Medicago polymorpha* L., *Trifolium tomentosum* L., *Cotula australis* (Sreng.) Hook. f., *Silene gallica, Piperia yadonii* Rand. Morgan & Ackerman, *Festuca bromoides* L., *Bromus diandrus, B. hordeaceus, Hypochaeris glabra,* and *H. radicata* L., elev. 36 m, 5 July 2012, *D. & J. Styer 37467* (CDA).

Collection notes. Plant densely cespitose, apparently without stems, ca. 5–10 cm diameter; inflorescence without peduncle, of many minute green calyces clustered in center of plant; and flowers cleistogamous. With respect to the key in Vincent and Isley (2012), this could be placed at the beginning of Group 2, and it would separate *T. suffocatum* from all others in the group. It is the only CA clover with neither stem nor peduncle.

A population of apparently several hundred plants of this species was first noted by Morgan at the Monterey Pines Golf Course on 17 April 1999, with *Lasthenia minor*, growing as a weed on irrigated, mowed lawn just inside the golf course. The clover was in vegetative condition at the time, but he removed a small clump of turf containing several plants, grew them out to maturity, and identified them as *T. suffocatum* from Zohary and Heller (1984). It is worth noting that 13 years later the population is still extant on the golf course grounds.

Significance. This is the first report of *T. suffocatum* for North America. According to Zohary and Heller (1984), this native of Europe and the Mediterranean grows in "grazed places and roadsides." An account of *T. suffocatum* in the British Isles may be found in the Online Atlas of the British & Irish Flora (2012). It is naturalized in the golf course, and it is likely naturalized on the former Fort Ord. During the late 1800's, the golf course was a resort. The gardener, Rudolf Ulrich, brought plants from all over the world. Even after the Navy acquired the property, it was never used for military purposes. Both areas have been subject to much human traffic from local areas and abroad. *T. suffocatum* has not been noted in the local horticultural trade.

We wish to thank Fred Hrusa and Michael Vincent for their assistance.

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NOTEWORTHY COLLECTION

CALIFORNIA

ERIOGONUM HERACLEOIDES Nutt. var. *HERACLEOIDES* (POLYGONACEAE).—El Dorado Co., the intersection of North Upper Truckee Rd and Shoshone Rd, South Lake Tahoe, CA, 1.9 mi N of U.S. Hwy 50, 38.87152°N, −120.03767°W, 6473 ft, July 28, 2012; same site different occurrence at the intersection of U.S. Hwy 50 and Pioneer Trail, SE corner about 50 ft from the roadside, 38.859059°N, −120.011704°W, 28 July 2012, *Hoyer 2* (BH, JEPS, RENO, SD). Identification confirmed by Dr. James L. Reveal (Cornell Univ.).

Observed at two locations alongside the road within 1.5 mi of each other, one with approximately 50 plants and the other with hundreds of plants. Plants were growing in partial shade to full sun. Associated species include: *Pinus contorta* Douglas ex Loudon, *P. jeffreyi* Balf., and *Eriogonum umbellatum* Torr.

NEVADA

ERIOGONUM HERACLEOIDES Nutt. var. *HERACLEOIDES* (POLYGONACEAE).—Douglas Co., Stateline, NV, at the intersection of Kingsbury Grade Rd (Nevada Hwy 207) and Kahle Dr, 0.2 mi E of U.S. Hwy 50, 38.96860°N, −119.93191°W, 6335 ft, 28 July 2012, *Hoyer 1* (BH, JEPS, RENO, SD, US). Identification confirmed by Dr. James L. Reveal (Cornell Univ.).

Observed at one location, with slightly less than 100 plants. Plants appeared to be planted as part of a restoration project and were growing in full sun. Associated species: *Pinus jeffreyi* Balf.

Previous knowledge. Eriogonum heracleoides var. *heracleoides* is a perennial herb that forms a spreading mat. It has a distinctive whorl of foliacious bracts about midway up the flowering stem. The previously known distribution spanned from southern British Columbia, Canada, S through Washington and Oregon to northeastern California (Modoc Co.), and E across Idaho, portions of Nevada (Elko, Eureka, Humboldt, Washoe, and White Pine cos.), and northern Utah to western Montana, western Wyoming, and northwestern Colorado (Baldwin et al. 2012; J. L. Reveal, Cornell Univ., personal communication), and is absent from the Tahoe Basin (Smith 1984).

Significance. This site represents the southernmost occurrence in California and the first within the Tahoe Basin. Both locations abut roadsides suggesting the taxon was introduced by restoration efforts mitigating roadwork impacts. Natural resource management agencies should be aware of this possible introduction pathway and avoid introducing this species outside its native range. (Special thanks to my father, Dr. William F. Hoyer Jr., for bringing this population to my attention).

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NOTEWORTHY COLLECTION

MONTANA

BERGIA TEXANA (Hook.) Seub. (ELATINACEAE).— Carter Co., ca. 3 km W of Albion, T7S R60E S24, common in drying mud on the shore of a stock pond with *Eleocharis palustris* (L.) Roem. & Schult. and *Hordeum jubatum* L., 1005 m, 14 September 2010, *P. Lesica 10,497* (MONTU). Photograph determined by G. Yatskievych (MO).

Previous knowledge. Previously known from southern South Dakota to California, Nevada, Utah, New Mexico, Texas, and Louisiana, disjunct along the Columbia River in Oregon and Washington.

Significance. First report for Montana (Dorn 1984), a range extension of ca. 350 km northwest from southern South Dakota.

CENTAUREA MACROCEPHALA Muss. Puschk. ex Willd. (ASTERACEAE).—Pondera Co., ca. 19 km E of Conrad adjacent to a two-track access road, T28N R5W S27-28 line, native range drainage area, 1065 m, 28 October 2011, *B. Birch s.n.* (MONTU).

Previous knowledge. An ornamental native to Eurasia and sporadically escaped in northern U.S., adjacent Canada, and Colorado (Keil and Ochsmann 2006).

Significance. First report for Montana.

LACTUCA MURALIS (L.) Gaertn. (=*Mycelis muralis* (L.) Dumort) (ASTERACEAE).—Sanders Co., Cabinet Mts., ca. 4 km E of Hwy 200 along the Rock Creek Rd, T26N R32W S22 SW1/4 of SE1/4, one plant along the road in undisturbed western redcedar forest, 755 m, 11 October 2011, *L. Larsen s.n.* (MONTU).

Previous knowledge. Introduced from Europe to NE and NW North America (Strother 2006).

Significance. First report for Montana.

LIMONIUM VULGARE Mill. (PLUMBAGINACEAE).— Pondera Co., along Cathedral Rd. ca. 1.5 km N of Trunk Butte and 9 km from Hwy 44, T36N R3W S17, dry pasture land with alkaline soil, 1065 m, 5 August 2010, *B. Christiaens s.n.* (MONTU, UC). Determined by A. Smith (UC).

Previous knowledge. An ornamental native to Europe and reported escaped in Ontario, Saskatchewan, and California.

Significance. First report for Montana.

PSILOCARPHUS TENELLUS Nutt. (ASTERACEAE).— Sanders Co., E side of Donlan Flats ca. 0.2 km S of Hwy 135, T18N R26W S9 SW1/4, in muddy tire tracks of a lightly used two-track road with *Centaurea stoebe* L., *Gnaphalium palustre* Nutt., *Heterocodon rariflorum* Nutt., *Juncus bufonius* L., *Pinus ponderosa* P. Lawson & C. Lawson, *Plagiobothrys scouleri* (Hook. & Arn.) I. M. Johnst., and *Potentilla recta* L., 800 m, 23 June 2009, *C. Odegard 43* (MONTU), photograph verified by L. Morefield (RENO); Clear Cr valley floor, on Forest Rd 153 ca. 7.2 km from Prospect Cr Rd, T21N R30W S4 SW1/4, in compacted silt loam at a roadside campsite with *J. bufonius*, *Matricaria discoidea* DC., *P. ponderosa*, *Potentilla argentea* L., *P. gracilis* Douglas ex Hook., *Pseudotsuga menziesii* (Mirb.) Franco, and

Veronica verna L., 865 m, 16 July 2010, *C. Odegard 45* (MONTU).

Previous knowledge. Distributed from extreme SW British Columbia to Baja California, east to northern Idaho (Morefield 2006). Ranked S2 (imperiled) in Idaho and considered sensitive by the Idaho Native Plant Society (Anonymous 2011).

Significance. First report for Montana and a range extension of ca. 115 km E from Kootenai Co., Idaho. In Montana *P. tenellus* has been observed only in road corridors, suggesting its presence in the state could be human-mediated.

RANUNCULUS SULPHUREUS Sol. (RANUNCULACEAE).—Carbon Co., Beartooth Mts., Silver Run Plateau, T8S R18E S20, common in wet turf along a small stream on a gentle south-facing slope with *Caltha leptosepala* DC and *Carex scopulorum* Holm, 3475 m, 29 August 2011, *P. Lesica 10,742 with D. Hanna* (MONTU, MONT, ALA). Verified by D. Murray (ALA).

Previous knowledge. A circumpolar plant previously known from as far south in western North America as northern British Columbia and central Northwest Territories (Whittemore 1997).

Significance. First report for Montana and the contiguous U.S., a range extension of 1950 km southeast from northern British Columbia and 2200 km from Northwest Territories.

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NOTEWORTHY COLLECTION

OREGON

CLAYTONIA SAXOSA Brandegee (MONTIACEAE).— Jackson Co., Cascade-Siskiyou National Monument, ca. 50 m NW of BLM Rd 40-3E-30.0, ca.1.5 km W of junction with BLM Rd 40-3E-5 (site sometimes known as Quarry Hill), 42°03.11′N, 122°30.90′W, elev. 1684 m, population of ca. 100 plants in coarse gravel of diabasic, possibly gabbroic, origin, on barren, SE-facing slope adjacent to a large borrow pit, associated species include *Claytonia rubra* (Howell) Tidestr., *Lomatium macrocarpum* (Torr. & A. Gray) J. M. Coult. & Rose, *Chaenactis douglasii* Hook. & Arn., *Penstemon deustus* Douglas ex Lindl., *Minuartia nuttallii* (Pax) Briq., *Cercocarpus ledifolius* Nutt., *Juniperus occidentalis* Hook., and *Fritillaria glauca* Greene, photographed and collected 6 June 2010, *J. T. Duncan s.n.* (OSC) with Belinda Vos and Bob Vos, verified by K. L. Chambers; Grizzly Peak, NE of Ashland across Bear Creek Valley, along Grizzly Peak trail down slope from the far SW point of Grizzly Peak plateau, 42°15.60′N, 122°37.69′W, elev. 1714 m, flat, open area, in fine gravelly, basaltic soil, associated species include *Juniperus occidentalis, Balsamorhiza deltoidea* Nutt., *Amsinckia menziesii* A. Nelson & J. F. Macbr., *Phacelia hastata* Lehm., *Clarkia rhomboidea* Douglas, *Gilia capitata* Sims, *Castilleja pruinosa* Fernald, and *Calochortus tolmiei* Hook. & Arn., discovered and photographed 12 June 2010 (not collected) by Dominique Guillet, confirmed by J. T. Duncan, 5 July 2010; Cascade-Siskiyou National Monument, Pacific Crest Trail ca. 0.8 km SW of its crossing of BLM Rd 39-3E-32.3 (Soda Mountain Rd), 42°04.91′N, 122°28.90′W, elev. 1673 m, barren area on NW side of rocky knoll ca. 100 m up slope from trail, in fine gravelly, basaltic soil, associated species include *Juniperus occidentalis, Purshia tridentata* (Pursh) DC., *Artemisia tridentata* Nutt., *Penstemon deustus, Castilleja pruinosa, Balsamorhiza deltoidea, Eremogone congesta* (Nutt.) Ikonn., and *Phlox diffusa* Benth., discovered and photographed 26 June 2010 by Diane Newell Meyer, confirmed by J. T. Duncan and collected at the original site 12 July 2011, *J. T. Duncan s.n.* (OSC) with D. N. Meyer, population of ca. 15 plants in late flower and early fruit.

Previous knowledge. *Claytonia saxosa* is found in the California North Coast Range to as far north as Scott Valley, Siskiyou Co., California (near mouth of Heartstrand Gulch, *J. M. Miller 488,* OSC).

Significance. First report for Oregon, representing a range extension of ca. 60 km north of known sites in California and showing a basaltic substrate preference rather than the characteristic serpentine specialization in that state. We thank Roger Nielsen, Geology Department, Oregon State University, for his identification of gravel samples from Quarry Hill.

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