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# MADROÑO

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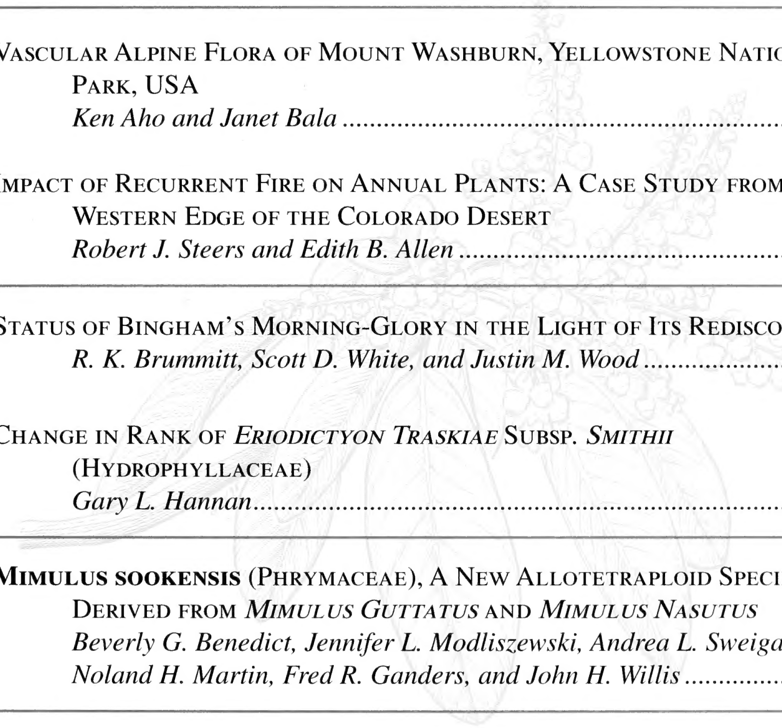
### POINTS OF VIEW

### CONTENTS

### NOTES

### NEW SPECIES

### BOOK REVIEWS



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# POINT-OF-VIEW

## COMMENT ON THE GABBRO SOILS OF PINE HILL

Burge and Manos (2011) investigated the genetic relationships of *Ceanothus roderickii* W. Knight and *Ceanothus cuneatus* Nutt. var *cuneatus* and sampled surface soils where the plants were found. They claimed to have shown that the two species are associated with chemically different gabbro soils.

The mineralogical and chemical differences among gabbro rocks are great and plant distributions from those dominated by olivine to those dominated by Ca-feldspars might be expected to be different. With respect to *C. roderickii* and *C. cuneatus* var. *cuneatus*, there are three key questions: (1) What is the range of gabbro soils on which *C. roderickii* will grow? (2) What is the range of gabbro soils on which *C. cuneatus* var. *cuneatus* will grow? (3) Considering gabbro rocks and soils where the ranges of *C. roderickii* and *C. cuneatus* var. *cuneatus* do not overlap, what are the mineralogical differences in the rocks and the chemical differences in the soils that might limit plant distributions. A final test would be to plant the two species in soils from different kinds of gabbro rocks under climatically similar or controlled.

Burge and Manos (2011) did not identify the specific gabbro rock mineralogies; they sampled only surface soils, and they ascertained only the readily extractable portions of the chemical elements. Locations where they sampled surface soils may have been in areas where the distributions of *C. roderickii* and *C. cuneatus* var. *cuneatus* do not overlap, but the methods were not adequate to distinguish different kinds of rocks and soils. Their data indicate that the greatest differences between the surface soils at sites with different ceanothus species were different amounts of Mehlich III (dilute acids and EDTA) extractable P.

Alexander (2011) sampled the parent rocks and both surface (0–15 cm) and subsoils (30–45 cm) at one site with *C. roderickii* and two sites without it on the Pine Hill gabbro. Phosphorus was ascertained from aqua regia digestion of the soils to evaluate the total elemental reserves in the soils. The soil with *C. roderickii* had subsoil P similar to that in the other soils, but the surface soil in the *C. roderickii* plant community had much more P than in the surface soils at the sites lacking *C. roderickii.* The surface soil at the *C. roderickii* site also had much more organic matter than the soils at the other two sites. Evidently, the amounts of P in the surface soils was largely dependent on the amounts of plant detritus that had been incorporated into them, which is a function of entire ecosystems, not only a single species. Perhaps the soil parent materials at the *C. roderickii* sites where Burge and Manos sampled the surface soils had as much P as the parent materials of other gabbro soils, but the plant communities at *C. roderickii* sites were cycling less P than the plant communities at the wedgeleaf ceanothus sites?

Unfortunately, the methods of Alexander (2011) are too intensive to apply broadly and the low- intensive methods of Burge and Manos are inadequate to show gabbro petrologic and soil differences related to the distributions of endemic plants. Perhaps future investigations that are less intensive than that of Alexander, but comprehensive enough to identify the kinds of gabbro parent rocks and both surface and subsoil reserves of key elements, will identify what gabbro rock and soil features lead to different plant distributions.

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MADROÑO, Vol. 59, No. 1, pp. 2–13, 2012

# VASCULAR ALPINE FLORA OF MOUNT WASHBURN, YELLOWSTONE NATIONAL PARK, USA

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## ABSTRACT

Mount Washburn, the principal peak in the volcanic Washburn Range, is an important site for both tourism and research in Yellowstone National Park. This paper provides: 1) descriptions of plant community types on Mt. Washburn, 2) biogeographic comparisons of species diversity for several ranges in the North-Central Rockies, and 3) an annotated species list of the alpine vascular flora, including summaries of constancy, local abundance, and preferred habitats. The alpine flora consists of one hundred and twenty-six vascular plant species from seventy-five genera and twenty-eight families. Biogeographic analyses suggest that the flora is depauperate for the region, with relatively low rates of colonization. These results agree with the predictions of the theory of island biogeography for small isolated ecosystems, and emphasize the vulnerability of Washburn to sub-alpine encroachment as the result of climate change.

Key Words: Alpine flora, andesitic substrates, biogeography, Mount Washburn, Yellowstone National Park.

Mount Washburn (3124 m), a volcanic formation in north-central Yellowstone National Park (YNP), has long been an important destination for tourism and scientific research. Washburn is one of the most frequently climbed alpine summits in the Rocky Mountains (Aho and Weaver 2010). Previous scientific research on Mt. Washburn includes studies of geology (Feeley et al. 2002), conifer distributions (Kokaly et al. 2003), whitebark pine ecology (Weaver and Dale 1974; Mattson and Reinhart 1990; Tomback et al. 2001), and grizzly bear ecology (Podruzny 1999).

While alpine vegetation has been described for volcanic substrates in the coastal Cordillera (Douglas and Bliss 1977; Hunter and Johnson 1983) and southern Rocky Mountain regions (Baker 1983; Rottman and Hartman 1985; Taye 1995; Seagrist and Taylor 1998), comparable descriptions for northern Rocky Mountain volcanic peaks are scarce. Aho and Weaver (2010) identified distinct alpine communities on Mt. Washburn, and described community evolutionary trends. This work, however, provided neither a formal inventory of Washburn alpine species, nor a comparison of the Washburn flora to those of other alpine locations.

Annotated species lists are valuable tools for monitoring/management (O'Kane 1988), hypothesis generation (Bell and Johnson 1980), and floristic comparisons (Baker 1983). The absence of an inventory for Mt. Washburn is notable given the existence of such lists for the Beartooth Mountains to the north (Johnson and Billings 1962; Lackschewitz 1994), the Tetons to the south (Spence and Shaw 1981), and the Madison, Gallatin, and Tobacco Root Mountains to the west (Pemble 1965; Cooper et al. 1997).

The Mt. Washburn alpine zone may have been overlooked because of its insular characteristics (i.e., small size and isolation; cf. Billings 1978). The extent of Mt. Washburn alpine vegetation is less than 1.2 km$^2$ (Despain 1990), while the nearest neighboring areas of alpine vegetation are in the region of Thunderer Peak, approximately 30 km to the northeast (Fig. 1). The insularity of the Washburn alpine is notable since it may result in increased vulnerability to subalpine encroachment as a result of climate change (cf. Hadley 1987; Bruun and Moen 2003; Halloy and Mark 2003).

This paper describes the flora of the alpine zone of Mt Washburn (not subalpine zones, nor the more general Washburn Range). First, it describes the alpine communities and environments of Mt. Washburn, including comparisons to other alpine ranges, particularly those on andesitic substrates. Second, biogeographic analyses of species diversity are presented to provide a regional context for the Washburn alpine flora. Third, an annotated alpine vascular species list is provided, based on both current and historical collections.

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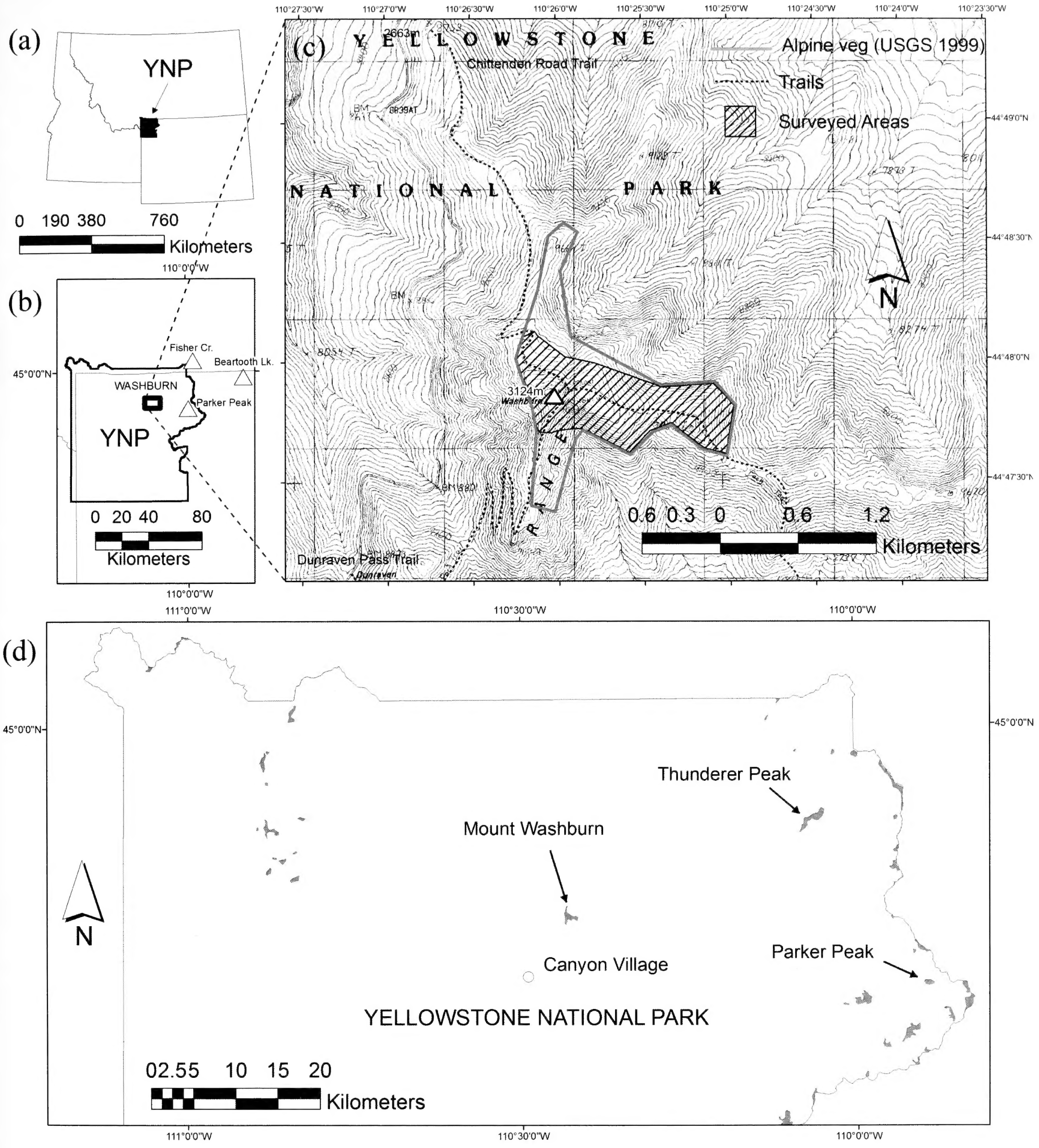

FIG. 1. Maps of study area. (a) Overview of Yellowstone National Park (YNP) with respect to Montana, Wyoming, and Idaho. (b) View of YNP showing the Washburn study area and three locations for which year-round alpine weather data is available. (c) Close up view of Washburn summit. The extent of Washburn alpine vegetation is from a ARC-GIS shapefile based on the vegetation classification of YNP by Despain (1990). (d) Alpine vegetation areas in Yellowstone National Park.

## METHODS

### Study Area

Mount Washburn (3124 m) is the highest peak in the Washburn Range, a volcanic formation in north-central Yellowstone National Park (44°48′N, 110°26′W; Fig. 1). The area above treeline (>2950 m) is small (1.2 km$^2$), and dominated by cushion plants, perennial forbs, and deep rooted graminoids (Aho and Weaver 2010).

The plant-supporting surficial rock of the Washburn Range is from the Langford Formation of the Thorofare Creek Group, a unit of the Absaroka Volcanic Supergroup (Smedes and Protska 1972). The Langford Formation consists of both light colored lava flows and alluvial facies composed of hornblende and pyroxene andesite fragments deposited between 47–49 million years ago (Smedes and Prostka 1972). On Mount Washburn the Langford Formation unconformably overlies strata of the Washburn Group, the oldest member of the Absaroka Volcanic Supergroup. Glaciers, most recently from the Pinedale Glaciation have scoured the Washburn Range resulting in the present-day rounded appearance of its ridges and northern slopes (Pierce 1979).

Detailed year-round and seasonal weather for Mt. Washburn is summarized in Aho and Weaver (2010). These data indicate that precipitation on Washburn is lower than at adjacent alpine ranges (i.e., $<$800 mm yr$^{-1}$). The mean frost-free season length (number of days with min temps $>$0°C) on Mt. Washburn is 93 days. This is comparable to other nearby alpine and high subalpine sites (Aho 2006).

### Voucher Collection

Vascular alpine species on Mount Washburn were inventoried during growing seasons (approx. June 25–Aug 30) over 5 years (2000–2004). During this period thirty-four one day collections were made from four contiguous summits that constitute the majority of the Mt. Washburn alpine (Fig. 1). As species were collected, voucher data were recorded, as well as qualitative information concerning species constancy, local abundance, moisture regime, and species association with eight broad habitat types. These habitat types were: 1) dense turf, 2) rocky turf, 3) ridgetops, 4) talus/scree, 5) late melting snowbanks, 6) ledges on south-facing cliffs, 7) disturbed, and 8) treeline. Types 1–6 have been previously recognized as distinct nodal communities on Mt. Washburn (Aho and Weaver 2010). Turf, ridgetops, talus, and snowbanks sites are well documented circumboreal alpine ecosystem components which often contain distinct communities (Billings 2000; Körner 2003). The "disturbed" habitat included areas such as roads, trails, and structures which are frequent throughout the Mt. Washburn alpine. The "treeline" habitat constituted subalpine/alpine ecotonal sites. Following field collection and identification, voucher specimens were deposited at the Yellowstone National Park herbarium (YELLO) in Gardiner, WY, and at the Idaho State herbarium (IDS) in Pocatello, ID.

To provide a comprehensive species list, our inventory includes not only species collected in 2000–2004, but those collected in the alpine zone by others and vouchered at YELLO over the last 90 years (the earliest vouchers from Mt. Washburn date from 1922). The quality of voucher labels dictated the degree to which environments for these species could be described. Species whose vouchered location was uncertain are not included here. Nomenclature and IDs for all species follows Dorn (2001).

### Biogeographic Analyses

To estimate the effects of alpine size and isolation in the region, plots were established on Mt. Washburn (36 plots), and in the alpine of two other ranges: the Northern Absarokas (82 plots; 9 peaks), and the Beartooth Plateau (60 plots; 6 peaks). The three ranges are adjacent (Fig. 1), but differ widely in their planar area above treeline (1.2 km$^2$, 2384 km$^2$, and 768 km$^2$ for Washburn, the Northern Absarokas, and the Beartooths respectively; Hadley 1987), and distance to other alpine ranges ($>$50 km for Washburn, and $<$5 km for the other two ranges; Aho 2006). Each plot consisted of ten 20 × 50 cm subplots situated at each meter on a 10 m line. In each subplot ocular estimates of cover were made for each vascular species. Plots were established randomly within each of five environments (N face, S face, ridgetop, talus, and late-melt). Whenever possible the environments on each mountain range were sampled in the same proportions, i.e., each environment made up approximately 20% of total number of samples from each range.

To compare richness of floras, species area curves were constructed from these data using first order jackknife procedures (Palmer 1990). To compare the importance of rare species, rank abundance dominance (RAD) plots were fit with Preston log-normal models (Preston 1948), this approach often effectively describes local community rank/dominance patterns (Hubbell 2001). Jackknife and RAD analyses were conducted using the software package R (R development core team 2010) with functions from the library vegan, a package for plant community ecology (Oksanen et al. 2010).

## RESULTS AND DISCUSSION

One hundred and twenty-six vascular plant species from seventy-five genera and twenty-eight families were identified from the alpine zones of Mt. Washburn. The species list includes one family and one genus from Lycophyta, two families, four genera, and four species of Gymnosperms, and twenty-five families, seventy genera, and one hundred twenty-two species of Angiosperms. Important families included Asteraceae (24 species), Brassicaceae (14 species), Poaceae (14 species), Cyperaceae (6 species), Polygonaceae (6 species), and Scrophulariaceae (6 species).

### Washburn Communities

Aho and Weaver (2010) used cluster and pruning analysis to objectively identify six nodal community types on Mt. Washburn. These included two turf communities (dense turf and rocky turf), along with ridgetop, snowbank, talus, and ledge types. This paper adds two other general Mt. Washburn associations: treelines and disturbed environments. Descriptions of these communities, which follow, include comparisons to similar communities reported for our region (Northern-Central Rockies), the larger Rocky Mountains region, and coastal Cordilleras. A primary objective of this survey was to compare the flora of Mt. Washburn to those of other North American andesitic-alpine locations.

*Dense turf.* North-facing slopes on Washburn were characterized by dense dry meadows dominated by *Carex elynoides* Holm, secondary graminoids including *Carex obtusata* Lilj., *Luzula spicata* (L.) DC., and *Poa glauca* Vahl var. *rupicola* (Nash ex Rydb.) Boivin, and perennial forbs including *Minuartia obtusiloba* (Rydb.) House, *Cerastium arvense* L., *Polemonium viscosum* Nutt., *Potentilla diversifolia* Lehm.var. *diversifolia*, and *Sedum lanceolatum* Torr.

Dry *Carex elynoides* turf is ubiquitous to the Rocky Mountain alpine from Montana (Bamberg and Major 1968; Cooper et al. 1997; Damm 2001; Aho 2006) through Idaho (Caicco 1983; Urbanczyk and Henderson 1994; Richardson and Henderson 1999), Utah (Lewis 1970), Wyoming (Billings and Bliss 1959), Colorado (Komárková and Weber 1978; Komárková 1979; Willard 1979; Hartman and Rottman 1988), and New Mexico (Baker 1983). On andesitic substrates *C. elynoides* turf occurs locally in the northern (Aho 2006) and southern Absarokas (Thilenius and Smith 1985), and at most other documented andesitic/alpine ranges in the Rockies including Buffalo Peaks and San Juans of southern Colorado (Rottman and Hartman 1985; Seagrist and Taylor 1998), and the Sangre de Cristo Mountains in New Mexico (Baker 1983).

Notably, *Trifolium dasyphyllum* Torr. & A. Gray is co-dominant with *Carex elynoides* on andesitic substrates in the southern Absarokas (Thilenius and Smith 1985) and on Latir Mesa in the Sangre de Cristo Mountains (Baker 1983). These species also co-occur on both granitic and limestone substrates in the nearby Beartooths (Aho 2006). The genus *Trifolium* L., however, does not occur in the alpine of Mt. Washburn, or on the northernmost peaks of the nearby andesitic Northern Absarokas (Aho 2006).

*Rocky turf.* Rocky turf communities occupied heterogeneous patches on steep, south facing slopes. These were often dominated by *Packera cana* (Hook.) W. A. Weber & Á. Löve, and *Astragalus kentrophyta* A. Gray var. *tegetarius* (S. Watson) Dorn, with associates *Minuartia obtusiloba, Cerastium arvense, Erigeron compositus* Pursh var. *discoideus* A. Gray, *Lomatium cous* (S. Watson) J. M. Coult & Rose, *Phlox pulvinata* (Wherry) Cronquist, and *Sedum lanceolatum.*

This association is similar to windswept dry nonprostrate communities in the Tendoy and Tobacco Root Mountains in southwest Montana dominated by *Lomatium cous, Phlox pulvinata, Sedum lanceolatum* and *Smelowskia calycina* (Steph. ex Willd.) Meyer var. *americana* (Regel & Herder) W. H. Drury & Rollins (Cooper et al. 1997).

On andesitic substrates an *Erigeron compositus-Astragus kentrophyta* cushion plant community occurs locally in northern Absarokas (Aho 2006). A similar *Packera cana-A. kentrophyta-E. compositus* association occurs in andesitic rocky environments in the Sweetwater Mountains in the Sierra Nevada (Hunter and Johnson 1983).

*Ridgetop environments.* Ridgetops were often dominated by *Erigeron rydbergii* Cronquist, *Oxytropis lagopus* Nutt., and cushion plants species, including *Minuartia obtusiloba, Astragalus kentrophyta, Phlox pulvinata, Draba densifolia* Nutt., *Draba incerta* Payson, *Eriogonum ovalifolium* Nutt., *Erigeron compositus*, and *Selaginella densa* Rydb.

*Erigeron rydbergii* is endemic to the Greater Yellowstone Ecosystem, and is limited in distribution to southern Montana and northwestern Wyoming and parts of Idaho (Pemble 1965; Hitchcock and Cronquist 1973; Lackschewitz 1994). *Selaginella densa* and *Erigeron compositus* frequently co-occur in cushion plant communities in the Pioneer, Tobacco Root, Madison, Beaverhead and Tendoy Ranges in southwestern Montana (Cooper et al. 1997), although these associations often include and *Dryas octopetala* L.var. *hookeriana* (Juz.) Breitung and *Geum rossii* (R. Br.) Ser. Both *G. rossii* and *D. octopetala* are absent from Mt. Washburn. *Astragalus kentrophyta*, *Draba densifolia*, *Erigeron compositus*, and *Phlox pulvinata* occur frequently on rocky andesitic substrates in the Sweetwater Mountains in the Sierra Nevada (Hunter and Johnson 1983).

*Talus and scree. Elymus scribneri* (Vasey) M. E. Jones frequently dominated heterogeneous patches in talus with *Erigeron compositus* and *Cerastium arvense.* Other infrequent associates included *Chaenactis alpina* (A. Gray) M. E. Jones, *Carex haydeniana* Olney, and *Polemonium viscosum.*

Species composition on scree is similar to that at other north-central Rocky Mountains locations. In particular, rocky areas in southwestern Montana are often dominated by *Elymus scribneri, Festuca brachyphylla* Schult. & Schult. var. *coloradensis* (Fred.) Dorn, *Trisetum spicatum* (L.) K. Richt., *Achillea millefolium* L. var. *lanulosa* (Nutt.) Piper, and *Lomatium cous* (Cooper et al. 1997). Rocky grassland communities of the Copper Basin in Idaho are dominated by *Elymus scribneri, Poa glauca* var. *rupicola*, and *Erigeron compositus* (Caicco 1983). While *E. scribneri* is widespread from Utah (Hayward 1952; Lewis 1970), to Colorado (Hartman and Rottman 1988) to Montana (Pemble 1965) and New Mexico (Hitchcock and Cronquist 1973), it has only been noted as a major alpine community component in the northern and north-central Rocky Mountains (e.g., Caicco 1983; Cooper et al. 1997).

With regard to andesitic substrates *Elymus scribneri* and *Erigeron compositus* frequently cooccur in the northern (Aho 2006) and southeastern Absarokas (Thilenius and Smith 1985). *Elymus scribneri* occurs mostly in dry meadows in the andesitic Buffalo Peaks of southern Colorado (Seagrist and Taylor 1998).

*Snowbank environments.* Snowbank areas on Mount Washburn were dominated by *Carex paysonis* Clokey and *Artemisia scopulorum* A. Gray. Secondary species included the graminoids *Carex phaeocephala* Piper, *Festuca brachyphylla* var. *coloradensis* and *Luzula spicata*, and the forbs *Achillea millefolium* var. *lanulosa, Minuartia obtusiloba, Cerastium arvense, Erigeron simplex* Greene, *Polygonum bistortoides* Pursh, *Sibbaldia procumbens* L., and *Stellaria monantha* Hultén.

Locally this association appears to be similar to several *Carex paysonis* snowbank communities on sedimentary ranges of southwestern Montana (Cooper et al. 1997). *Carex paysonis* communities also occur in the granitic Beartooths (Aho 2006), and on neo-glacial deposits in the Tetons (Spence and Shaw 1981).

*Carex paysonis* associations appear frequently on andesitic substrates in the Rocky Mountain and coastal cordilleras. *Carex paysonis- Artemisia scopulorum* late-melt communities occur locally on peaks in the andesitic northern Absarokas (Aho 2006). Similar associations also occur on moist and wet andesitic meadows in the distant Buffalo Peaks (Seagrist and Taylor 1998), and in the San Juan and Sangre de Cristo Mountains in the Southern Rockies (Baker 1983; Rottman and Hartman 1985). Wet meadows in the San Juan Mts. include *A. scopulorum*, *Erigeron simplex*, *Sedum integrifolium* (Raf.) A. Nelson, and *Sibbaldia procumbens* (Rottman and Hartman 1985), while similar sites in Sangre de Cristo Mountains include *A. scopulorum, Lloydia serotina* (L.) Rchb., and *Salix arctica* Pall. var. *petraea* (Andersson) Bebb (Baker 1983). *Carex paysonis* late melt communities also occur on volcanic Mount St. Helens in Washington (del Moral and Jones 2002) and on Mount Hood in Oregon (Titus and Tsuguzaki 1999).

*Ledges under cliff formations.* The upright forb *Arnica rydbergii* Greene frequently dominated runnels along cliff bases, and unstable, steep, rocky volcanic slopes. *Arnica rydbergii* often occurs as a patchy monoculture, although infrequent associates include *Elymus scribneri*, and *Cirsium eatonii* (A. Gray) Robins.

The northern Rockies support other similar *Arnica* associations. A community dominated by *Arnica diversifolia* Greene, *Epilobium anagallidifolium* Lam., *Poa alpina* L., and *Poa cusickii* Vasey var. *pallida* (Soreng) Dorn pioneers wet, rocky, recently deglaciated substrates in Glacier National Park (Damm 2001). *Arnica longifolia* Eaton, *Poa reflexa* Vasey & Scribn. ex Vasey, and *Ranunculus eschscholtzii* Schlecht. dominate subalpine ledges and draws in Grand Teton National Park (Gregory 1983). Monoculture stands of *Arnica* sp. occur in rocky cirques, and under limestone outcrops of the Bridger Range of southern Montana (S. Forcella unpublished data).

With regard to andesitic substrates, *Arnica rydbergii-Epilobium clavatum* Trel. communities often dominate low alpine cliff runnels in the northern Absarokas (Aho 2006), while *A. rydbergii* occurs at alpine/subalpine ecotonal environments in the volcanic northern Cascades (Douglas and Bliss 1977).

*Disturbed environments.* Despite the general resistance of alpine areas to weed invasion (Billings and Mooney 1968), six exotic species were collected within the Washburn alpine. These included a rhizomatous grass (*Bromus inermis* Leyss.), a taprooted perennial forb (*Taraxacum officinale* Weber), and annual/biennial forbs (*Polygonum aviculare* L., *Chenopodium rubrum* L., *Descurainia sophia* [L.] Webb ex Prantl, and *Lepidium* sp. L.). It should be emphasized that these species persisted not only at subalpine-alpine ecotonal elevations, but also in areas far above treeline.

The number of non-natives is notable given exotic species reports in other alpine studies. For instance, only one species (*Artemisia biennis* Willd.) out of 173 was reported to be exotic in the alpine regions in the Mosquito Range in central Colorado (Seagrist and Taylor 1998), while several alpine species lists report no exotics whatsoever (e.g., Spence and Shaw 1981; Baker 1983; Hunter and Johnson 1983; Hartman and Rottman 1988). The large number of exotics on Washburn is surely due to invasion vectors provided by frequent human visitors and associated disturbance at trails and roadsites (cf. Weaver et al. 2001). With the exception of *T. officinale*, which also inhabited wet turf sites, exotic species were generally limited to areas within and alongside roads, and other areas of heavy anthropogenic disturbance.

*Treeline environments.* Because treelines on Washburn are the result of historical patterns of forest fires as well as altitudinal and topographic gradients (Barrett 1994; Peet 2000), it was often difficult to distinguish alpine and high-subalpine ecotones. Species distributions were also inadequate in distinguishing the zones. For instance, *Eriogonum flavum* Nutt., *Delphinium bicolor*

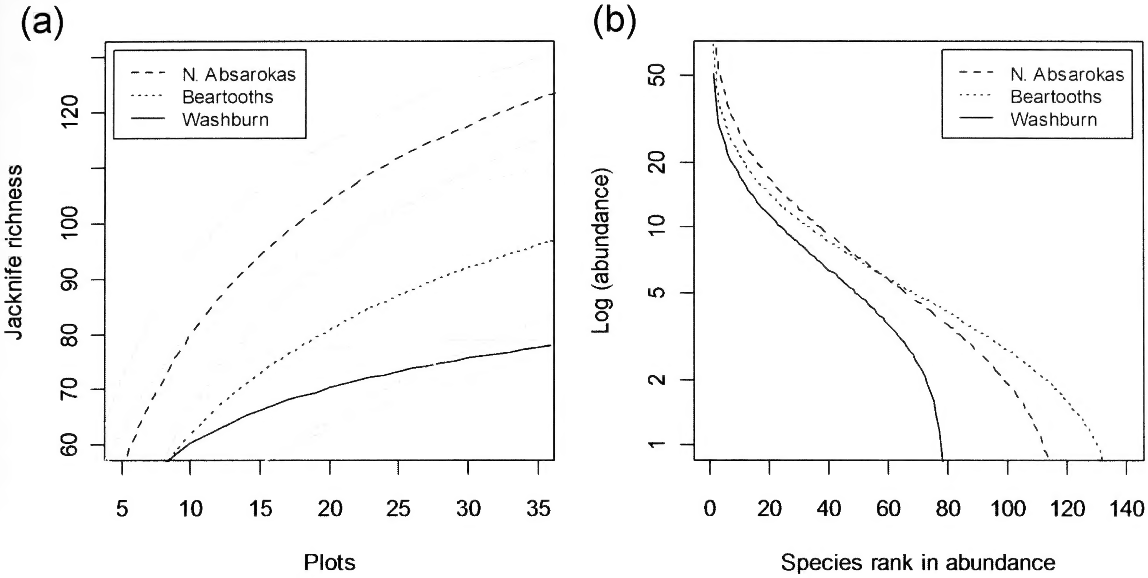

FIG. 2. Biogeographic analyses for the Washburn Range, nine mountains in the N. Absaroka-Volcanics, and six mountains on the Beartooth Plateau. (a) Species area curves from a first order jackknife procedure. Gray lines are 95% confidence intervals. (b) Rank abundance dominance (RAD) curves. Abundance responses were fit to a log-Normal distribution (Preston 1948).

Nutt., and *Geum triflorum* Pursh dominated high subalpine slopes, while being absent from definitive alpine areas (and so are not included in this list). Conversely, other species, such as *Besseya wyomingensis* (A. Nelson) Rydb., *Poa pattersonii* Vasey, *Erigeron compositus*, *Androsace septentrionalis* L.var. *subulifera* A.Gray, *Antennaria microphylla* Rydb., *Agoseris glauca* (Pursh) Raf. var. *dasycephala* (Torr.& A. Gray) Jeps., and *Achillea millefolium* var. *lanulosa* had broad altitudinal distributions and frequently occurred at both the highest altitudes and at areas far below treeline (and are included here). Species which were representative of the treeline ecotone included *Arnica latifolia* Bong., *Linum lewisii* Pursh, *Phleum alpinum* L., *Penstemon attenuatus* Douglas ex Lindl., and *Vaccinium scoparium* Leiberg ex Coville. Ecotonal tree species (i.e., *Pinus albicaulis* Engelm., *Picea engelmannii* Parry ex Engelm. and *Abies lasiocarpa* (Hook) Nutt. are included in the species list to indicate the species which demark the treeline.

## Mt. Washburn in a Biogeographic Context

Results from biogeographic analyses indicate that, for the region, Mt. Washburn has both lower levels of richness (Fig. 2a), and lower levels of immigration (Fig. 2b). In particular, Washburn was predicted to have 78 species per 36 plots, while the Beartooths and northern Absarokas were predicted to have 97 and 123 species per 36 plots. Lower immigration rates can be deduced by the sharp decline and the end of the Washburn rank abundance curve in Fig. 2b, indicating few rare species (Hubbell 2001). Both of these results fit with predictions of the theory of island biogeography for small, isolated environments (MacArthur and Wilson 1963, 1967). That Mt. Washburn may be affected by its island characteristics gives rise to management concerns, particularly given recent climate models for Yellowstone National Park. These models generally predict an increase in treeline elevation, further decreasing alpine island area, and increasing fragmentation (Romme and Turner 1990).

As a result of its depauperate flora, a large number of species are missing from the Mt. Washburn alpine that are common to surrounding alpine regions. These include: *Agrostis variabilis* Rydb., *Bupleurum americanum* J. M. Coult. & Rose, *Carex scirpoidea* Michx., *Eritrichium nanum* (Vill.) Schrad. ex Gaudin var. *elongatum* (Rydb.) Cronquist, *Deschampsia cespitosa* (L.) P. Beauv., *Dryas octopetala*, *Geum rossii*, *Pedicularis groenlandica* Retz., *Silene acaulis* (L.) Jacq.var. *subacaulescens* (F. N. Williams.) Fernald & H. St. John, and the genus *Trifolium* (e.g., *T. dasyphyllum, T. haydenii* Porter, and *T. parryi* A. Gray). Hypothetically these absences may be due to several factors including Mt. Washburn's small size and isolation (discussed above), and its andesitic-volcanic substrate. Two of the missing species are documented calciophiles: *Dryas octopetala* (Bamberg and Major 1968; Komárková 1979; Willard 1979), and *E. nanum* var. *elongatum* (Bamberg and Major 1968). *D. octopetala*, *B. americanum*, and *Eritrichium nanum* var. *elongatum* are also absent from andesitic alpine areas in the southern Rockies (Baker 1983; Rottman and Hartman 1985) and the coastal Cordillera (Hunter and Johnson 1983). All three species however occur on southern peaks of the andesitic northern Absarokas (Hartman et al. unpublilshed). Alpine species in the genus *Trifolium* (e.g., *T. dasyphyllum, T. haydenii*, and *T. parryi*) are also absent from the alpine of the northernmost peaks of the nearby andesitic northern Absarokas (Aho 2006). *Trifolium*, however, is present on andesitic substrates of southern peaks in the northern Absarokas (Rosenthal 1999; Hartman et al. upublished), and in the southern Absarokas (Thilenius and Smith 1985; Rosenthal 1999). Little evidence exists to link other missing species to substrate effects.

## Annotated Species List for the Mount Washburn Alpine

The annotated list which follows includes species names along with qualitative information about constancy, local abundance, moisture regime, habitat preference, and native/exotic status. The constancy of each species (i.e., rare = rare, unco = uncommon, comm = common, wide = widespread), is reported first in the annotated list. Constancy records the tendency of a species to occur in all possible examples of its preferred habitat. Local abundance (i.e., scarce = scarce, abund = abundant, dom = dominant) reflects species dominance within its preferred habitat. Soil water preference (i.e., dry, moist, wet) was quantitatively determined, using soil sensors, for 59 species growing within >5% of plots examined by Aho and Weaver (2010); also see Aho (2006, Chapter 2). Water preference was subjectively evaluated for species found outside of plots. General habitat preference is denoted as: *dtf* = dense turf, *rtf* = rocky turf, *rt* = ridgetop, *ta* = talus, *sm* = late melt, *d* = disturbed, *tr* = treeline, *l* = ledges, *all* = all habitats. Constancy, abundance, and water preferences are not inferred for species unless they were modeled by Aho (2006).

It should be acknowledged that while the list of species in this paper is based on a large number of current and historical collections, additional rare species may still be found (J. Whipple, Yellowstone National Park, personal communication). Still other unlisted species may exist intermittently in the Washburn alpine as a product of random ecological drift (Hubbell 2001).

### Lycophyta

#### Selaginellaceae

*Selaginella densa* Rydb. [*Aho 303* YELLO]; wide, abund, dry, *dtf, rtf, rt,* native

### Anthophyta-Monocotyledoneae

#### Cyperaceae

*Carex albonigra* Mack. [*Gentholts, D.* YELLO *4702*]; wet, *ta* , native

*Carex elynoides* Holm [*Aho 152, 381* YELLO]; wide, dom, dry, *dtf, rt,* native

*Carex haydeniana* Olney [*Gentholts, D.* YELLO *4653*]; unco, abund, wet, *sm,* native

*Carex obtusata* Lilj. [*Aho 146, 335* YELLO]; comm, dom, dry, *dtf,* native

*Carex paysonis* Clokey; [*Aho 145, 380* YELLO]; comm, dom, wet, *sm*, native

*Carex phaeocephala* Piper [*Aho 144* YELLO]; unco, abund, moi to wet, *sm, d*, native

#### Juncaceae

*Juncus drummondii* E. Mey. [*Aho 544* YELLO]; unco, abund, wet, *sm*, native

*Luzula spicata* (L.) DC. [*Aho 564* YELLO]; wide, abund, wet to dry, *al*, native *l*

#### Liliaceae

*Allium cernuum* Roth [*Aho 108* YELLO]; unco, abund, dry to moist, *d, tr*, native

#### Poaceae

*Bromus inermis* Leyss. var. *inermis* [*Aho 94* YELLO]; unco, dom, dry to moist, *d*, exotic

*Elymus scribneri* (Vasey) M. E. Jones [*Aho 557* IDS]; comm, abund, dry to wet, *ta, rt*, native

*Elymus trachycaulus* (Link) Gould ex Shinners var. *andinus* (Scribn. & J. G. Sm.) Dorn [*Aho 88* YELLO]; unco, abund, dry to wet, *d*, exotic

*Festuca brachyphylla* Schult. & Schult. var. *coloradensis* (Fred.) Dorn [*Aho 576* IDS]; wide, abund, dry to wet, *all*, native

*Phleum alpinum* L. [*Aho 567* IDS]; unco, abund, wet to moist, *tr, d*, native

*Poa alpina* L. [*Aho 541* IDS]; comm, abund, dry to wet, *dtf, sm*, native

*Poa cusickii* Vasey var. *pallida* (Soreng) Dorn [*Aho 360, 85* YELLO]; wide, abund, dry to wet, *all*, native

*Poa cusickii* Vasey var. *epilis* (Scribn.) C. L. Hitchc. [*Aho 80* YELLO]; wide, abund, dry to wet, *all*, native

*Poa glauca* Vahl var. *rupicola* (Nash ex Rydb.) B. Boivin [*Aho 75, 382* YELLO]; comm, abund, dry to wet, *dtf* , *rtf*, native

*Poa interior* Rydb. [*Aho 379* YELLO]; unco, scarce, wet to moist, *ta, sm*, native

*Poa pattersonii* Vasey [*Aho 77* YELLO]; wide, abund, dry to wet, *dtf, rtf* , native

*Poa reflexa* Vasey & Scribn. ex Vasey [*Aho 549* IDS]; unco, scarce, wet, *sm*, native

*Poa secunda* J. Presl var. *incurva* (Scribn. & T. A. Williams. ex Scribn.) Beetle [*Aho 72 73* YELLO]; unco, abund, dry to moist, *ta*, native

*Trisetum spicatum* (L.) K. Richt. [*Caprio, T.* YELLO *4588*]; wide, abund, dry to wet, *all*, native

## ANTHOPHYTA-DICOTYLEDONEAE

### Apiaceae

*Lomatium cous* (S. Watson) J. M.Coult. & Rose [*Aho 559* IDS]; wide, abund, dry to wet, *all*, native

### Asteraceae

*Achillea millefolium* L. var. *lanulosa* (Nutt.) Piper [*Aho 271* YELLO]; wide, abund, wet to dry, *all*, native

*Agoseris glauca* (Pursh) Raf. var. *dasycephala* (Torr. & A. Gray) Jeps. [*Aho268* YELLO]; wide, abund, dry to wet, *all*, native

*Antennaria media* Greene; [*Aho 482* YELLO]; unco, abund, wet, *sm*, native

*Antennaria microphylla* Rydb. [*Aho 577* IDS]; wide, abund, dry to wet, *all*, native

*Antennaria umbrinella* Rydb. [*Aho 565* IDS]; wide, abund, dry to wet, *all*, native

*Arnica latifolia* Bong. [*Aho 572* IDS]; unco, abund, wet, *sm, tr*, native

*Arnica longifolia* D. C. Eaton [*Condon, D.* YELLO *2688*]; Frequent, *tr*, native

*Arnica rydbergii* Greene [*Aho 558* IDS]; comm, dom, wet, *ta, l, d, tr*, native

*Artemisia scopulorum* A. Gray [*Aho 252* YELLO]; unco, abund, wet, *sm*, native

*Chaenactis alpina* (A. Gray) M. E. Jones var. *alpina* [*Aho 244* YELLO]; unco, abund, dry to moist, *ta, d*, native

*Cirsium eatonii* (A. Gray) B. L. Rob. [*Aho 243* YELLO]; unco, abund, dry to moist, *ta, l, d*, native

*Ericameria suffruticosa* (Nutt.) G. L. Nesom [*Aho 228* YELLO]; unco, abund, dry to moist, *ta, rt, d*, native

*Erigeron compositus* Pursh var. *discoideus* A. Gray; comm. [*Aho 556* IDS]; abund, dry, *rt, ta*, native

*Erigeron rydbergii* Cronquist [*Aho 234, 378* YELLO]; Frequent, dry, *dtf, rt*, native

*Erigeron simplex* Greene [*Aho 233* YELLO]; Frequent, dry to wet, *sm, dtf* , native

*Erigeron ursinus* D. C. Eaton [*Currie, M C.* YELLO *4265*]; native

*Oreostemma alpigenum* (Torr. & A. Gray.) Greene var. *haydenii* (Porter) Nesom. [*Aho 249* YELLO]; unco, abund, dry to moist, *sm, dtf*, native (was *Aster alpigenus*)

*Packera cana* (Hook.) W. A. Weber & Á Löve [*Aho 224* YELLO]; comm, abund, dry to moist, *ta, rt*, native

*Packera subnuda* (DC.) Trock & T. M. Barkley [*Caprio, T.* YELLO *4402*]; native

*Senecio fremontii* Torr. & A. Gray [*Aho 220* YELLO]; comm, abund, dry to moist, *ta, rt*, native

*Senecio integerrimus* Nutt. var. *integerrimus* [*Aho 218* YELLO]; unco, abund, moist to wet, *sm, tr*, native

*Solidago multiradiata* Aiton var. *scopulorum* A. Gray [*Aho 212* YELLO]; comm, abund, dry to moist, *ta, d*, native

*Symphyotrichum foliaceum* (Lindl. ex DC.) G. L. Nesom var. *apricum* (A. Gray) G. L. Nesom [*Aho 248* YELLO]; comm, abund, wet, *sm*, native (was *Aster foliaceus* var.*apricus*)

*Taraxacum ceratophorum* (Ledeb.) DC. [*Conrad, H. S.* YELLO *3193*]; comm, abund, dry to moist, *all*, native

*Taraxacum eriophorum* Rydb. [*Aho 210* YELLO]; rare, scarce, moist, *ta*, native

*Taraxacum officinale* Weber [*Aho 208* YELLO]; comm, abund, moist to wet, *d*, exotic

*Townsendia parryi* Eaton [*Aho 207* YELLO]; *tr*, native

### Boraginaceae

*Mertensia alpina* (Torr.) G. Don [*Aho 205* YELLO]; comm., abund, dry to moist, *dtf, rtf, sm*, native

*Myosotis alpestris* F. W. Schmidt [*Aho 204* YELLO]; comm., abund, dry to moist, *dtf, rtf, sm*, native

### Brassicaceae

*Boechera angustifolia* (Nutt.) Dorn [*Smith, F. H.* YELLO *1203*]; unco, abund, dry to moist, *ta, d*, native

*Boechera exilis* (A. Nelson) Dorn [*Aho 199, 190* YELLO]; unco, abund, dry to moist, *ta, d*, native

*Boechera lemmonii* S. Watson [*Caprio, T.* YELLO *4363*]; unco, abund, dry to moist, *ta, d*, native

*Boechera lyallii* (S. Watson) Dorn [*Aho 547* IDS]; unco, abund, dry to moist, *dtf*, native

*Boechera microphylla* Nutt. [*Aho 568* IDS]; unco, abund, dry to moist, *ta, d*, native

*Descurainia sophia* (L.) Webb ex Prantl [*Aho 562* IDS]; unco, abund, dry to moist, *d*, exotic

*Draba cana* Rydb. [*Aho 189* YELLO]; rare, abund, dry to moist, *ta, tr*, native

*Draba crassifolia* Graham [*Aho 324* YELLO]; comm, scarce, moist to wet, *sm*, native

*Draba densifolia* Nutt. [*Smith, F. H.* YELLO *1266*]; unco, abund, dry, *rt*, native

*Draba incerta* Payson [*Aho 326* YELLO]; comm, abund, dry to moist, *ta, rt*, native

*Draba paysonii* J. F. Macbr. var. *treleasii* (O. E. Schulz) C. L. Hitchc. [*Aho 186* YELLO]; rare, scarce, dry to moist, *ta, rt*, native

*Lepidium* sp. L. [*Aho 178* YELLO]; unco, scarce, dry to moist, *d, t*, exotic

*Noccaea parviflora* (A. Nelson) Holub [*Aho 176* YELLO]; unco, abund, dry to moist, *tr, dtf*, native

*Smelowskia calycina* (Stephan ex Willd.) C. A. Meyer var. *americana* (Regel & Herder) W. H. Drury & Rollins [*Woolf, A.* YELLO *1317*]; comm, abund, dry to moist, *all*, native

### Caryophyllaceae

*Cerastium arvense* L. [*Aho 546* IDS]; comm, dom, moist to wet, *sm, dtf, rtf, ta*, native

*Eremogone congesta* (Nutt.) Ikonn. var. *lithophila* (Rydb.) Dorn [*Aho 174* YELLO]; comm, abund, moist to wet, *sm, dtf, rtf, ta*, native

*Minuartia obtusiloba* (Rydb.) House [*Aho 363* YELLO]; comm., abund, moist to wet, *sm, dtf, ta*, native

*Minuartia rubella* (Wahlenb.) Hiern [*Aho 170* YELLO]; widespread, abund, dry to wet, *sm, dtf, ta*, native

*Silene kingii* (S. Watson) Bocquet [*Aho 165* YELLO]; unco, dom, moist to wet, *sm, dtf*, native

*Stellaria monantha* Hultén [*Aho 161* YELLO]; unco, abund, moist to wet, *sm, dtf*, native

*Stellaria umbellata* Turcz. ex Kar. & Kir. [*Conrad, H. S.* YELLO *1026*]; unco, scarce, wet, *sm*, native

### Chenopodiaceae

*Chenopodium rubrum* L. [*Aho 551* YELLO]; unco, abund, *d*, exotic

### Crassulaceae

*Sedum lanceolatum* Torr. [*Aho 159* YELLO]; wide, dom, dry to wet, *all*, native

### Ericaceae

*Vaccinium scoparium* Leiberg ex Coville [*Aho 560* YELLO]; unco, abund, wet, *sm, tr*, native

### Fabaceae

*Astragalus alpinus* L. [*Conrad, H. S.* YELLO *1596*]; comm, abund, dry to wet, *sm, dtf*, native

*Astragalus kentrophyta* A. Gray var. *tegetarius* (S. Watson) Dorn [*Aho 578* IDS]; comm, abund, dry to moist, *rt, ta*, native

*Astragalus miser* Douglas [*Conrad, H. S.* YELLO *1587*]; unco, dom, dry to moist, *tr, dtf*, native

*Lupinus argenteus* Pursh [*Aho 129* YELLO]; wide, dom, dry to moist, *dtf, rt, sm*, native

*Oxytropis borealis* DC. var. *viscida* (Nutt.) S. L. Welsh [*Aho 127* YELLO]; unco, abund, dry, *rt*, native

*Oxytropis lagopus* Nutt. [*Aho 126* YELLO]; comm, abund, dry, *dtf, rt*, native

*Oxytropis parryi* A. Gray [*Aho 125* YELLO]; rare, scarce, dry to moist, *dtf*, native

### Grossulariaceae

*Ribes montigenum* McClatchie [*Aho 118* YELLO]; unco, abund, moist, *tr, sm*, native

### Hydrophyllaceae

*Phacelia hastata* Douglas ex Lehm. [*Aho 579* IDS]; unco, abund, dry to moist, *ta*, native

*Phacelia sericea* (Graham ex Hook.) A. Gray [*Aho 116* YELLO]; unco, abund, dry to moist, *ta*, native

### Linaceae

*Linum lewisii* Pursh [*Aho 56 1* IDS]; unco, abund, dry to moist, *ta, dtf, tr*, native

### Onagraceae

*Epilobium clavatum* Trel. [*Aho540* IDS]; unco, abund, wet, *ta, sm*, native

*Epilobium halleanum* Hausskn. [*Aho 101* YELLO]; rare, scarce, wet, *sm*, native

### Parnassiacea

*Parnassia fimbriata* K. D. Konig [*Condon, D.* YELLO *1385*]; wet, *tr*, native

### Polemoniaceae

*Phlox multiflora* A. Nelson [*Aho 580* IDS]; wide, dom, dry to moist, *tr, dtf, rtf*, native

*Phlox pulvinata* (Wherry) Cronquist [*Aho 168*, *398*, *399* YELLO]; comm, abund, dry, *rt, dtf, rtf*, native

*Polemonium pulcherrimum* Hook. [*Aho 555* IDS]; unco, abund, dry to moist, rocky *dtf, ta*, native

*Polemonium viscosum* Nutt. [*Woolf, A.* YELLO *2129*]; comm, dom, dry to moist, *dtf, ta*, native

### Polygonaceae

*Eriogonum ovalifolium* Nutt. [*Aho 65* YELLO]; unco, abund, dry, *rt, rtf, dtf*, native

*Oxyria digyna* (L.) Hill [*Aho 552* IDS]; infr, abund, moist, *ta*, native

*Polygonum aviculare* L. [*Aho 62* YELLO]; unco, abund, *d*, exotic

*Polygonum bistortoides* Pursh [*Aho 12* YELLO]; comm., abund, dry to moist, *dtf,* native

*Polygonum douglasii* Greene var. *microspermum* (Engelm.) Dorn [*Aho 539* IDS]; unco, scarce, dry to moist, *ta, d*, native

*Rumex paucifolius* Nutt. [*Aho 56* YELLO]; *rt, ta*, native

### Portulacaceae

*Claytonia lanceolata* Pursh [*Aho 553* IDS]; comm, abund (early spring), dry to moist, *dtf*, native

*Lewisia pygmaea* (A. Gray) B. L. Rob. [*Aho 368* YELLO]; unco., abund, wet to moist, *dtf, sm*, native

*Cistanthe umbellata* (Torr.) Hershk. var. *caudicifera* (A. Gray) Kartesz & Gandhi [*Aho 545* IDS]; unco, abund, moist, *ta, d*, native

### Primulaceae

*Androsace septentrionalis* L. var. *subulifera* A. Gray [*Aho 542* IDS]; wide, scarce, dry to moist, *all*, native

*Dodecatheon conjugens* Greene [*Woolf, A.* YELLO *2017*]; *dtf*, native

*Dodecatheon pulchellum* (Raf.) Merr. [*Aho 51* YELLO]; unco, abund, moist to wet, *dtf, sm*, native

### Ranunculaceae

*Delphinium bicolor* Nutt. [*Aho 330*, *369* YELLO]; dry to moist *dtf, tr,* native

*Ranunculus eschscholtzii* Schlecht. [*Aho 43* YELLO]; comm, dom (early spring), moist to wet, *ta, sm*, native

### Rosaceae

*Potentilla diversifolia* Lehm. var. *diversifolia* [*Aho 35, 36* YELLO]; comm, dom, dry to moist, *dtf, rtf*, native

*Potentilla ovina* J.M. Macoun [*Aho 32* YELLO]; comm, abund, dry, *dtf, rtf, rt*, native

*Sibbaldia procumbens* L. [*Aho 74* YELLO]; unco, abund, *sm, dtf*, native

### Salicaceae

*Salix arctica* Pall. var. *petraea* (Andersson) Bebb [*Aho 543* IDS]; unco, abund, wet, *sm*, native

### Saxifragaceae

*Saxifraga cespitosa* L. [*Conrad, H. S.* YELLO *1565*]; unco, scarce, wet, *sm*, native

*Saxifraga rhomboidea* Greene [*Aho 400, 401* YELLO]; comm, abund, dry to moist, *dtf*, native

### Scrophulariaceae

*Besseya wyomingensis* (A. Nelson) Rydb. [*Aho 582* IDS]; comm, abund, dry to moist, *dtf*, native

*Mimulus lewisii* Pursh [*Condon, D.* YELLO *2490*]; infrequent, wet, *tr*, native

*Pedicularis cystopteridifolia* Rydb. [*Aho 10* YELLO]; infrequent, wet, *sm*, native

*Penstemon attenuatus* Douglas ex Lindl. [*Aho 6* YELLO]; infrequent, dry to moist, *dtf, tr*, native

*Penstemon procerus* Douglas ex Graham [*Aho 583* IDS]; infrequent, dry to moist, *dtf*, native

*Veronica wormskjoldii* Roem. & Schult. [*Aho 538* YELLO]; infrequent, wet, *sm*, native

## CONIFEROPHYTA

### Pinaceae

*Abies lasiocarpa* (Hook.) Nutt. [*Condon H. S.* YELLO *49*]; infrequent, dry to moist, *tr*, native

*Picea engelmannii* Parry ex Engelm. [*Aho 537* YELLO]; infrequent, dry to moist, *tr*, native

*Pinus albicaulis* Engelm. [*Condon H. S.* YELLO *56*]; infrequent, dry to moist, *tr*, native

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# IMPACT OF RECURRENT FIRE ON ANNUAL PLANTS: A CASE STUDY FROM THE WESTERN EDGE OF THE COLORADO DESERT

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## ABSTRACT

Limited information exists regarding the impact of fire on annual plant composition in creosote bush scrub vegetation. The impact of recurrent fires on annual plants is even less understood. To investigate this matter, annual vegetation was sampled in a stand of creosote bush scrub in western Coachella Valley, California that had recently experienced two wildfires. The wildfires fragmented the once contiguous shrubland into three sections: unburned, once-burned, and twice-burned stands, all of which were separated by fuel breaks that contained each fire. For all three stands, annual plant cover and species richness were determined in the field, soil seed bank samples were collected and assayed in a glasshouse, and soil chemistry and physical properties were measured. We found that invasive annual grass cover was highest in the twice-burned stand and native annual plant cover was greatest in the unburned stand. Native annual species richness significantly decreased each time a stand burned resulting in low native annual plant diversity. Seed bank assays revealed that invasive annual grass germinants were orders of magnitude greater in the twice-burned stand compared with the other two stands. Lastly, soil total N, C, and soil pH were elevated in both burned stands. Overall, we found that recurrent fire can result in strong impacts to annual vegetation; however, the twice-burned stand was sampled only three years after burning while the once-burned stand was sampled 20 years after burning. Thus, longer-term fire effect studies plus replication with additional study sites are still needed to improve our understanding of how recurrent fire impacts annual plants.

Key Words: Diversity, feedback, grass/fire cycle, invasive plant, richness, seed bank.

Invasive grasses can alter the fire regime by increasing the frequency, intensity, extent, and seasonality of fire (Brooks et al. 2004). In creosote bush scrub vegetation of southern California, the invasive grasses are annuals that differ fundamentally from the native annual forbs that they displace. For example, unlike most native annual plants, invasive annual grasses senesce earlier and have persistent standing biomass throughout the dry season (Brooks 1999). One problematic result of grass invasion for creosote bush scrub is longer-lasting fine fuel that connects widely spaced shrubs (Brooks et al. 2004). In addition, invasive grasses can form higher density assemblages than native vegetation (Steers and Allen 2010), thus increasing the fuel packing ratio and consequently, fire intensity.

The primary foci of previous studies examining fire in desert shrublands of the Mojave and Sonoran Deserts have been on the impacts to perennial species. These studies have documented reductions in cacti and long-lived shrubs, such as *Larrea tridentata* Coville, and increases in relatively short-lived perennials (O'Leary and Minnich 1981; McLaughlin and Bowers 1982; Brown and Minnich 1986; Alford et al. 2005; Brooks and Minnich 2006; Abella 2009; Abella 2010). However, most of these studies did not measure annual vegetation.

Previous studies that have focused on fire and desert annual plants documented post fire decreases in *Bromus madritensis* L. subsp. *rubens* (L.) Husn. and increases in *Schismus* spp. (either *S. arabicus* Nees, *S. barbatus* [L.] Thell., or both), which are both invasive annual grasses. These studies also documented little change in the abundance of the invasive forb, *Erodium cicutarium* (L.) Aiton, and either an increase or decrease in native annuals, depending on the species (Cave and Patten 1984; Brooks 2002; Esque et al 2010a, b; Steers and Allen 2011a). Native annual plant species richness has also been shown to decline in shrub understories after fire but no response was detected in interspace habitat (Brooks 2002). Besides these studies, little information exists on the impacts of fire on desert annual plants. Brooks et al. (2004) and Brooks and Esque (2002) warn that post fire increases in invasive annual grasses may promote recurrent fire, *sensu* the grass/fire cycle (D'Antonio and Vitousek 1992). However, documentation of the impact of recurrent fire on annual vegetation is lacking.

The goal of this study was to document the impact of fire on the annual plant community in creosote bush scrub that partially burned in 1988 and in 2003. The fire history of this study site

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resulted in an unburned, once-burned, and twice-burned stand. Our objective was to measure the response of invasive annual grasses and forbs to fire, and the impact of fire on native annual plants. We were especially interested in documenting the response of native annual plant species richness and diversity measures to recurrent fire, as this is relatively unknown. In addition to vegetation surveys, seed bank samples collected from the three stands were also assayed and soil parameters (nutrients, texture, and pH) were measured to provide additional insight.

## MATERIALS AND METHODS

### Study Area

The study site was located in Whitewater Canyon (33°56′50″N, 116°38′43″W) on the western edge of the Colorado Desert in Riverside County, California. Vegetation along the floor of Whitewater Canyon was composed of desert riparian and desert dry wash communities. Creosote bush scrub occurred throughout the valley bottom, upland of the riparian and wash areas. On steeper slopes of the canyon, *Encelia farinosa* Torr. was dominant. Coastal scrub shrubs, such as *Artemisia californica* Less. and *Salvia apiana* Jeps., were occasional on north and east facing hill slopes. Within unburned creosote bush scrub of the study site, perennial vegetation was about 21% cover (Steers and Allen 2011b). *Larrea tridentata* contributed about 10% cover, *Ambrosia dumosa* (A. Gray) W. W. Payne 6%, *Krameria grayi* Rose & Painter 3%, and the following species individually contributed less than 2% cover: *Psorothamnus arborescens* (A. Gray) Barneby, *Ephedra californica* S. Watson, *Encelia farinosa*, and cacti, including *Echinocereus engelmannii* (Engelm.) Lem., *Opuntia basilaris* Engelm. & J. M. Bigelow and *O. echinocarpa* Engelm. & J. M. Bigelow (Steers and Allen 2011b). The slope at the study site was 5 to 6 degrees, facing east, at an elevation of about 525 m. Soils were alluvial (NRCS 2010) and about 80% sand (this study). Annual average precipitation is assumed to be between 9.5 ± 5.6 SD and 29.9 ± 16.4 SD cm, based on records for Palm Springs, about 19 km to the southeast, and Cabazon, about 14 km to the southwest, respectively (WRCC 2008). Precipitation at the Palm Springs weather station was 3.1, 4.8 and 16 cm for calendar years 2006, 2007 and 2008, respectively. Summer precipitation was negligible during these three years, which is typical for the area (WRCC 2008). Fire disturbance in this part of the Colorado Desert is not uncommon, and severalburned stands of creosote bush scrub have been previously investigated nearby (O'Leary and Minnich 1981; Brown and Minnich 1986; Steers and Allen 2011b).

### Fire History Determination

The fire history of the study site was determined based on stereoscope validation of fire perimeters from a series of aerial photographs of the study landscape, spanning from 1949 to 2005. Aerial photos were obtained from Riverside County Flood Control and Water Conservation District, Coachella Valley Water District, and UC Riverside Science Library. The years when aerial photos were taken include the following: 1949, 1957, 1974, 1980, 1984, 1985, 1986, 1987, 1989, 1990, 1995, 1996, 1998, 2000, and 2005. For fires that occurred after the 2005 aerial photographs, additional fires were recorded from personal observation. Aerial photography revealed that the year of the first fire occurred sometime between 1987 and 1989. Because fires in desert vegetation are more common following winter seasons with above average rainfall (Brooks and Matchett 2006), the wettest year, which was 1988, is reported as the assumed burn year. Based on personal observations, the second fire occurred in the summer of 2005, following a winter of above average precipitation (WRCC 2008).

Based on aerial photography, the pattern of fire at the study site transformed an area with similar creosote bush shrub cover into three stands, one of which was a 1.7 ha remnant unburned stand, a 2.7 ha once-burned stand (burned in 1988), and a 3.3 ha twice-burned stand (burned in 1988 and 2005). At the time of both fires, fuel breaks (dozer-lines) were implemented to contain each fire from spreading into adjacent areas. Therefore, differences in vegetation among all three investigated stands prior to the first fire, and differences between the vegetation in the once- and twice-burned stands prior to the second fire, are assumed to be negligible.

### Soil and Vegetation Sampling

In August of 2006, six vegetation sampling plots were implemented in a stratified random design within each unburned, once-burned, and twice-burned vegetation stand. A sampling plot consisted of one, 7.32 m radius, modified – National Weed Management Association (mod-NAWMA) plot (Stohlgren et al. 2005). Slope and aspect were measured from the center of each plot using a compass and clinometer. Soil was collected to determine nutrient levels, physical characteristics, and to assess the seed bank. For soil nutrients, four soil samples per mod-NAWMA plot were taken to 5 cm depth with a 2.5 cm diameter corer and pooled into one composite sample per plot. The four samples were collected at the center and at three edge locations (7.32 m from plot center), at 30, 150, and 270 degrees from plot center. For soil seed bank samples, four cores per plot were also collected within a 20 cm radius of the soil nutrient sample plugs, except 5 cm diameter cores were used instead. These cores were also pooled into one composite sample per plot. One core with the same dimensions used for seed bank samples was taken at the center of the plot, within a 20 cm radius of where the other soil samples were collected, for bulk density, coarse fraction (>2 mm), and soil texture measures. All soil sampled was taken at a 5 cm depth and placed in one of three plastic Ziploc bags per plot, for soil nutrient, seed bank, and physical (bulk density, coarse fraction, and soil texture) measurements, and then transported back to UC Riverside. At UC Riverside, samples taken with the 2.5 cm diameter corer were split, and 50 g were used to measure pH in a 1:1 soil:water slurry using a Fisher Scientific® Model 50 pH meter. The remaining portion of the soil nutrient samples were then sent to the University of California, Division of Agriculture and Natural Resources Analytical Laboratory at UC Davis for carbon (C), total nitrogen (N), KCl-extractable $NH_4^+$ and $NO_3^-$, and texture (% sand, silt and clay) analyses (http://groups.ucanr.org/danranlab).

Soil seed bank samples were assayed by growing them out in a glasshouse and counting the number of germinants per species (Cox and Allen 2008). First, a composite sample was sieved through a 6 mm × 6 mm mesh to remove coarse materials, making sure not to remove any seeds, and then spread out on a 20 cm × 20 cm styrofoam tray. Soil depth in each tray ranged from 1 cm to 2 cm. Then, trays were kept moist and germinants were removed when identifiable or at a stage where they could be transplanted safely to pots to await identification. Watering continued in all trays until no new seeds germinated and then trays were left to dry. Once the soil in each tray was completely dry, it was mixed before the next watering cycle. Three cycles of watering and drying took place from September 2007 to May 2008. Trays were allowed to dry from 3 to 6 weeks between watering periods. By the third cycle, negligible numbers of seeds germinated so further cycles were not implemented. Throughout the watering, trays were reorganized several times to minimize localized effects within the glasshouse.

During the winter wet-season of 2006–07, insufficient rainfall prevented the germination of annual plants at the study site, and no vegetation measurements were taken. In the winter of 2007–08, precipitation was about average and vegetation was sampled in March 2008 during peak-flowering. In each established mod-NAWMA plot, percent cover by species was measured in three 1 $m^2$ (1 m × 1 m) quadrats, located 4.57 m from plot center at 30, 150, and 270 degrees. Species richness was measured within each of the three 1 $m^2$ quadrats per plot and also within each plot (out to a 7.32 m radius from plot center). All species names follow nomenclature in Hickman (1996).

### Data Analyses

Annual plant composition between the three stands (unburned, once-burned, and twice-burned) was compared using presence/absence data for all annual species recorded in the six mod-NAWMA plots per stand. Plots were ordinated with Nonmetric Multidimensional Scaling using a Sorenson distance measure (McCune and Mefford 2006). A random starting configuration with 50 runs of real data was used in the autopilot mode with medium speed. Then, a Multiresponse Permutation Procedure, using a Sorenson distance measure, was performed on the same data to determine if there were any significant pairwise difference between annual species composition in the three stands at $\alpha = 0.05$ (McCune and Mefford 2006).

Other comparisons between the three stands were also conducted based on categorizations of species (e.g., native versus invasive), species richness, and species similarity indices. Annual vegetation cover was categorized into invasive grass, invasive forb, total invasive annuals (grass + forb), and native annuals (grass + forb) at the 1 $m^2$ scale (in quadrats). Native annual grasses and forbs were combined and not treated separately because the number of native annual grass species was very low (Appendix 1). Species richness of native annuals was calculated at both the quadrat and mod-NAMWA plot scales while species richness of herbaceous perennials and shrubs were only calculated at the mod-NAMWA plot scale. To determine the impact of fire on seed banks, germinants were grouped into four categories: invasive grasses, invasive forbs, native annuals, and shrubs plus cacti. No herbaceous perennials were found in the seed bank assays.

Shannon Diversity ($H'$) was calculated at the quadrat scale based on native annual richness and cover by species (Shannon and Weaver 1963). Also, within-plot native annual plant species similarity ($S$) was also calculated from the three 1 $m^2$ quadrats per mod-NAMWA plot. This was done using a multiple-quadrat community coefficient based on a modification of the Sorenson index (Diserud and Ødegaard 2007): $S = (3/2)([ab + ac + bc - abc]/[a + b + c])$, where $a$ is the number of species in quadrat (plot frame) A, $b$ is the number of species in quadrat B, etc… and $ab$, $ac$, $bc$ and $abc$ are the number of species shared between quadrats A and B, A and C, B and C and A, B and C, respectively.

To improve the normality of data, germinant density and native annual plant richness were square-root transformed. One-way ANOVA and Fisher's LSD test were used to compare the soil and vegetative variables among unburned, once-burned, and twice-burned conditions at $\alpha = 0.05$. Vegetation parameters that were constituted of more than one sub-sample per mod-NAWMA

TABLE 1. AVERAGE SOIL AND PERENNIAL PLANT PARAMETERS FOUND IN UNBURNED, ONCE-BURNED (1988), AND TWICE-BURNED (1988 AND 2005) STANDS. For each parameter, F test statistics based on one-way ANOVA are shown. Differences in superscript letters indicate significant differences between stands based on post-hoc LSD tests. Parameters that did not differ significantly between paired stands do not contain letter superscripts. n = 6 and α = 0.05 for all statistical analyses.

| Parameters | Unburned (avr. ± SE) | Once-burned (avr. ± SE) | Twice-burned (avr. ± SE) | F |
|---|---|---|---|---|
| SOIL | | | | |
| Total N (%) | 0.08 ± 0.01$^{A}$ | 0.10 ± 0.01$^{AB}$ | 0.13 ± 0.01$^{B}$ | 5.6115 |
| Total C (%) | 0.75 ± 0.09$^{A}$ | 0.96 ± 0.07$^{AB}$ | 1.23 ± 0.11$^{B}$ | 6.8488 |
| $NH_4^+$ (ppm) | 13.1 ± 1.3 | 13.7 ± 1.4 | 14.2 ± 2.1 | 0.1046 |
| $NO_3^-$ (ppm) | 11.3 ± 1.9 | 11.9 ± 1.2 | 14.6 ± 2.1 | 0.9811 |
| Sand (%) | 77.8 ± 1 | 80 ± 1.1 | 80.5 ± 0.8 | 2.1964 |
| Silt (%) | 17 ± 0.7 | 16.7 ± 1 | 15 ± 0.7 | 1.8023 |
| Clay (%) | 5.2 ± 0.5$^{A}$ | 3.3 ± 0.4$^{B}$ | 4.5 ± 0.2$^{AB}$ | 5.6707 |
| pH | 7.4 ± 0.1$^{A}$ | 7.6 ± 0$^{B}$ | 7.7 ± 0$^{B}$ | 9.1424 |
| Bulk density (g/cm$^3$) | 1.29 ± 0.09 | 1.15 ± 0.06 | 1.15 ± 0.08 | 1.0887 |
| Coarse fraction (g/cm$^3$) | 0.31 ± 0.03 | 0.42 ± 0.13 | 0.49 ± 0.03 | 1.3802 |
| Bare ground cover (%) | 7.1 ± 2.2$^{A}$ | 12.3 ± 5.3$^{AB}$ | 18.9 ± 3.4$^{B}$ | 2.4091 |
| Rock cover (%) | 3.4 ± 1.5$^{A}$ | 5.7 ± 2$^{A}$ | 12.1 ± 2.5$^{B}$ | 4.8556 |
| Litter cover (%) | 3.7 ± 1.1 | 5.8 ± 2.9 | 1.6 ± 0.6 | 1.3029 |
| HERBACEOUS PERENNIALS | | | | |
| Richness (species/168.3 m$^2$) | 0.8 ± 0.4 | 0 ± 0 | 0.5 ± 0.3 | 1.9000 |
| SHRUBS | | | | |
| Richness (species/168.3 m$^2$) | 6 ± 0.5$^{A}$ | 2 ± 0.5$^{B}$ | 1.2 ± 0.2$^{B}$ | 46.8182 |
| Live cover (%) | 10.6 ± 3 | 18.6 ± 9.3 | 18.6 ± 5.1 | 0.5323 |
| *Encelia farinosa* cover (%) | 0 ± 0$^{A}$ | 17.9 ± 9.4$^{B}$ | 16.4 ± 4.8$^{B}$ | 2.6668 |

plot (e.g., percent cover and species richness per m$^2$) were averaged together before analyses. Thus, for all soil and vegetation analyses, n = 6. Similar statistical procedures have been utilized when comparing paired burned and unburned vegetation in low replication contexts (Haidinger and Keeley 1993; Brooks and Matchett 2003; Abella et al. 2009).

## RESULTS

### Impact of Fire on Soils

Some soil parameters were influenced by fire while others were not (Table 1). Extractable nitrogen ($NH_4^+$ and $NO_3^-$) did not differ between paired burned and unburned areas. However, total N and C, and soil pH were greater in the twice-burned area than the unburned area. Also, percent cover of bare ground and rock were greatest in the twice-burned area (Table 1).

### Impact of Fire on Seed Banks

A total of 6357 germinants belonging to 14 species were recorded from the seed bank study. About 97% of the seed bank germinants were *Schismus barbatus* and *S. arabicus,* which are collectively referred to as *Schismus* spp. Invasive forbs, *Erodium cicutarium* and *Brassica tournefortii* Gouan, made up about 0.6%, with 29 and 12 individuals counted, respectively. Only four *Bromus madritensis* ssp. *rubens* individuals were counted, all of which only occurred in soils from the unburned area. Eight native annual species made up about 1.8% of the total germinants counted. The most abundant native species were *Camissonia californica* (Torr. & A. Gray) P. H. Raven, *Crassula connata* (Ruiz & Pav.) A. Berger, and *Plantago ovata* Forssk. Only *Encelia farinosa* and one unknown cactus that died prematurely made up the six germinants in the shrub plus cacti category.

Analyses of the seed bank at a scale of 78.5 cm$^2$ showed that the twice-burned stand had greater invasive annual grass density than the once-burned and unburned stands (Fig. 1). No differences in invasive forb and native annual germinants were found between stands (Fig. 1). At this small scale, mean native annual plant richness also was not different between the unburned (1.33 ± 0.33 SE species), once-burned (1 ± 0.52 SE), and twice-burned (1.33 ± 0.33 SE) stands.

### Impact of Fire on Aboveground Vegetation

Five exotic annuals and 38 native annual species (Appendix 1) were documented. Of the exotics encountered, the invasive forbs, *Brassica tournefortii* and *Erodium cicutarium,* were widespread in all three areas, as were the invasive grasses, *Schismus* spp. When comparing annual plant species composition among the three paired stands, the Nonmetric Multidimensional Scaling (NMS) analysis resulted in a two-dimensional solution.

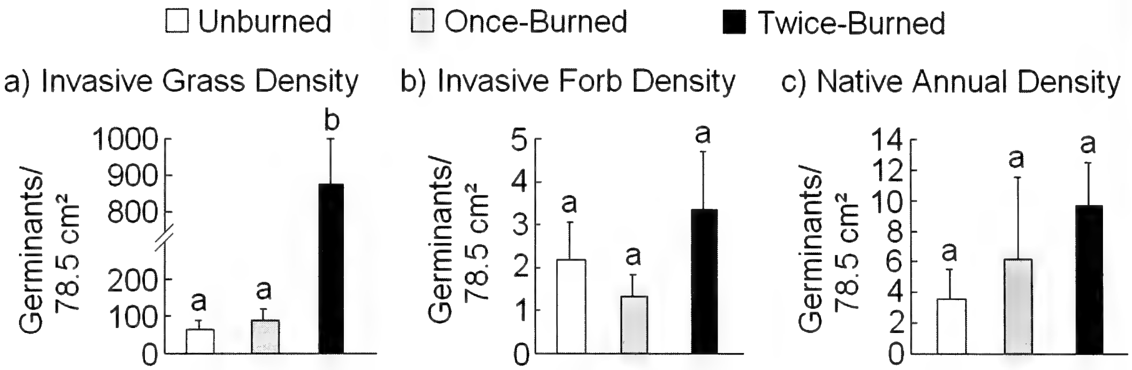

FIG. 1. Average density and SE bars for invasive grass (a), invasive forb (b), and native annual (c) germinants from seed bank assays of the unburned, once-burned, and twice-burned stands. Differences in letters above bars indicate significant differences between stands based on ANOVA and LSD tests ($\alpha = 0.05$).

The final stress for the best solution was low, at 12.23 out of 100. The proportion of variance represented by each axis, based on the $r^2$ between distance in the ordination space and distance in the original space was 0.681 and 0.209 for axis 1 and 2, respectively. Thus, the separation that was revealed among the three stands was primarily along axis 1 (Fig. 2). Species that had the strongest correlation with axis 1 were *Bromus madritensis* ssp. *rubens* ($r = -0.851$), *Plantago ovata* ($r = -0.851$), *Chaenactis fremontii* A. Gray ($r = -0.841$), *Vulpia octoflora* (Walter) Rydb. ($r = -0.819$), *Pectocarya linearis* DC. ($r = -0.696$), *Stylocline gnaphaloides* Nutt. ($r = -0.658$), *Pholistoma membranaceum* (Benth.) Constance ($r = -0.653$), and *Phacelia distans* Benth. ($r = -0.652$). When the three stands were compared using the Multi-Response Permutation Procedure, the unburned stand had a significantly different annual plant community than the once-burned ($A = 0.296$; $P < 0.001$) and twice-burned ($A = 0.299$; $P < 0.001$) stands. Similarly, the once-burned and twice-burned stands were also significantly different from each other ($A = 0.134$; $P < 0.001$).

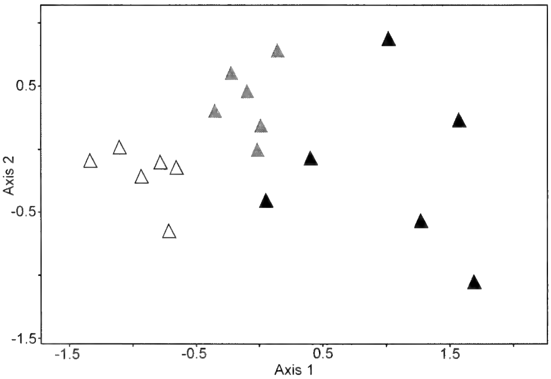

FIG. 2. A Nonmetric Multidimensional Scaling ordination of unburned, once-burned, and twice-burned sample units (white, grey, and black triangles, respectively) based on presence/absence of annual species recorded in 168.3 m$^2$ mod-NAWMA plots.

No difference in total invasive annual plant cover between the unburned, once-burned and twice-burned stands was detected (Fig. 3). However, invasive grass cover was greater and invasive forb cover was lower in the twice-burned compared to the once-burned stand (Fig. 4). In addition, relative cover of invasive grasses was greatest in the twice-burned stand versus the other two stands (Fig. 3). Native annual plant cover and species richness at the 1 m$^2$ scale were lower in both of the burned stands compared to the unburned stand (Figs. 3 and 4). Also at the 1 m$^2$ scale, the stand that had burned twice did not have lower native cover or richness compared to the stand that had only burned once. However, native annual plant diversity (Shannon Diversity – *H'*) was lower in the twice-burned stand compared to the other two stands (Fig. 3). Also, only in the twice-burned stand was within-plot native annual plant similarity (based on shared species among the three 1 m$^2$ quadrats per plot) greater than the unburned stand (Fig. 3). In other words, the variety of annual species found in twice-burned vegetation was lower compared to the unburned stand. At a larger scale (168.3 m$^2$ mod-NAWMA plot), native annual species richness was lower within each burned stand (Fig. 3). Also at this larger scale, shrub richness was lower for the first burn, but showed no further decrease after the second burn. Herbaceous perennial richness was very low in general and did not differ among the three stands (Table 1).

## DISCUSSION

### Impact of Fire on Soils

Soil pH, and total N and C were greatest in the twice-burned stand, which last experienced fire three years prior to sampling. Elevated pH is

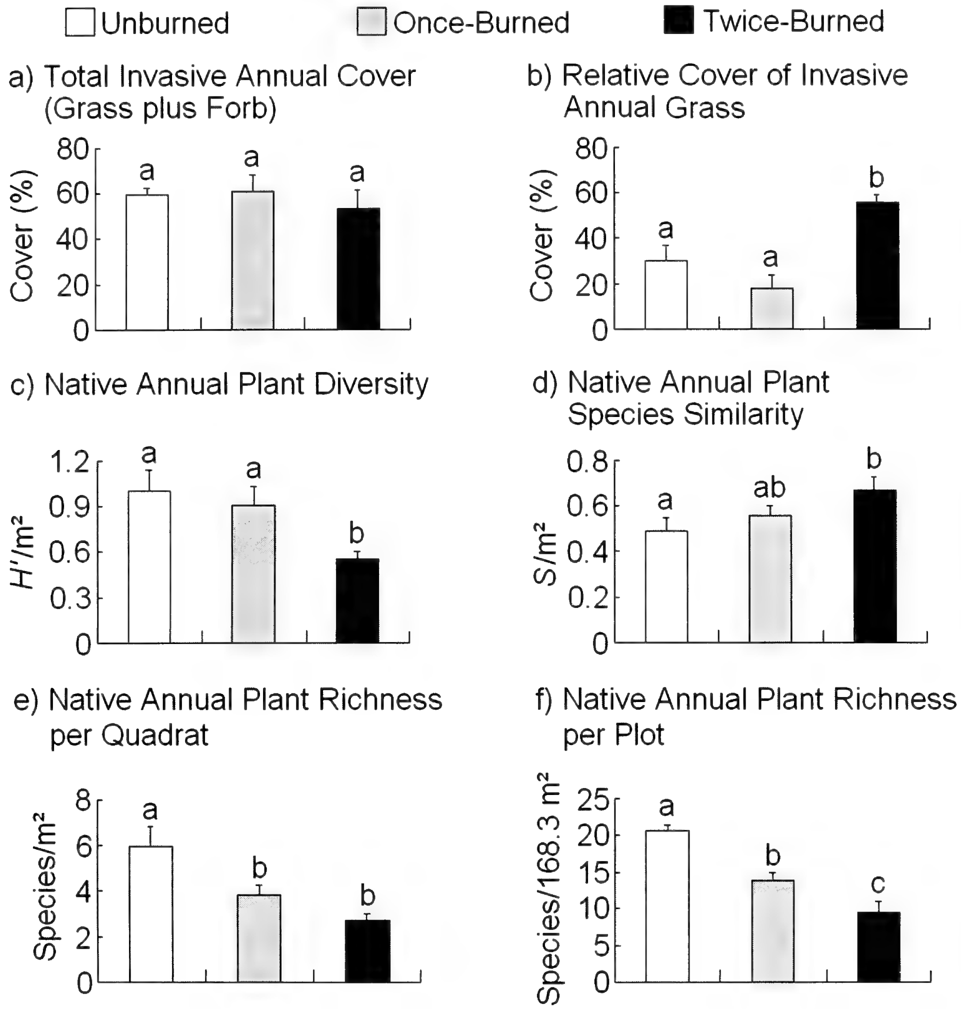

FIG. 3. Invasive annual plant cover (a), relative invasive annual grass cover (b), and various native annual plant diversity measures: Shannon index (c), Sørenson index (d), richness per 1 $m^2$ quadrat (e), and richness per 168.3 $m^2$ mod-NAWMA plot (f). Values in each graph are averages per stand with SE bars. Differences in letters between paired stands within each graph indicate significant differences at $\alpha = 0.05$.

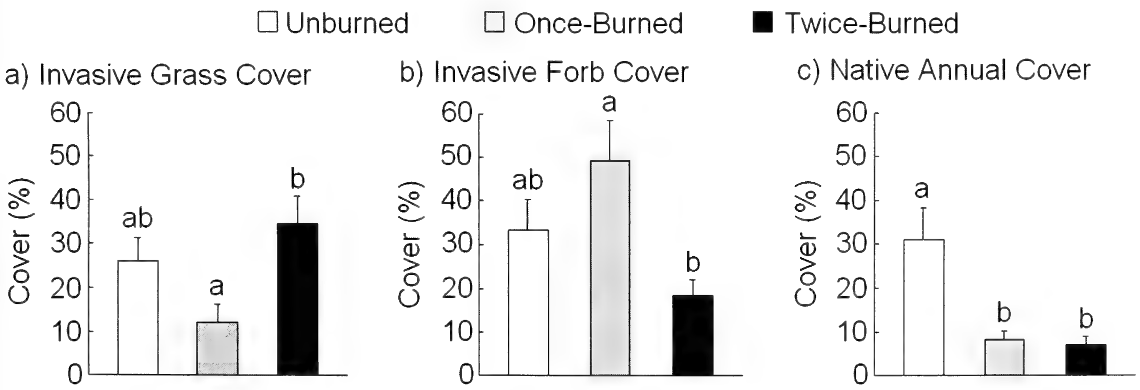

FIG. 4. Average cover and SE bars for invasive grasses (a), invasive forbs (b), and native annuals (c) in the unburned, once-burned, and twice-burned stands. Differences in letters above bars indicate significant differences between stands per graph based on ANOVA and LSD tests ($\alpha = 0.05$).

common following fire due to increased ash (Raison 1979; Abella et al. 2009). The response of total N and C to fire, however, is variable (Raison 1979; Brooks 2002; Allen et al. 2011). Pre-fire *Encelia* cover was assumed to be high in the twice-burned stand based on conditions in the once-burned stand, which likely accounts for the elevated C and N found in post fire soils (Xie and Steinberger 2001). Soil $NH_4^+$ and $NO_3^-$ were highest in the twice-burned stand but not significantly so. These mobile, inorganic forms of nitrogen are typically elevated in post-fire environments (Wan et al. 2001), even in creosote bush scrub (Esque et al. 2010b). It is possible that both $NH_4^+$ and $NO_3^-$ were significantly elevated immediately after the 2005 fire in the twice-burned stand but by the time the sites were sampled in August of 2006, these nitrogen sources had decreased due to leaching and/or immobilization.

Post-fire bare ground and rock cover was elevated in the twice-burned stand. Adams et al. (1970) reported higher bare ground after fire in creosote bush scrub of the Colorado Desert due to hydrophobic soils that were characterized by water repellant layers found at various depths under burned shrubs. Large bare areas under burned shrubs, as they described, were not observed during this study. In general, the altered soil properties that resulted from fire were not dramatic and are expected to return to pre-fire conditions as vegetation recovers (Allen et al. 2011). However, persistent invasive species, a continuation of a short fire return interval or heightened soil erosion could cause long-term alterations to soil properties (Morris and Moses 1987; Belnap 1995; Allen et al. 2011).

### Impact of Fire on Seed Bank Germinants

In general, propagule abundance is linked to above ground plant performance (Olano et al. 2005; Cox and Allen 2008). Therefore, seed bank composition can elucidate potential aboveground vegetation, especially in the context of future disturbances (Cox and Allen 2008; Satterthwaite et al. 2007; Fisher et al. 2009). Results from the seed bank assays revealed that invasive grass propagules of *Schismus* spp. are ubiquitous and abundant in the seed bank at this site. Future fires or other disturbances will likely promote these plants (Cox and Allen 2008; Fisher et al. 2009). Native species also did not differ among stands, which suggests that invasive species removal could be an effective strategy for native seed bank management, especially because native annual plants exhibit density dependent inhibition of germination (Inouye 1980).

When scaled up, the number of invasive annual grass propagules in the twice-burned stand was 111,952.9 ± 15,760 SE per $m^2$. To our knowledge, this is vastly greater than any value previously reported for exotic annual grasses from the American southwest (Young and Evans 1975; Nelson and Chew 1977; Reichman 1984; Hassan and West 1986; Guo et al. 1998; Angoa-Roman et al. 2005; Cox and Allen 2008; Abella et al. 2009; Esque et al. 2010a). The relative lack of other germinants besides *Schismus* spp. may indicate that the methods used to assay the seed bank were not ideal for detecting the full suite of species that could occur in the seed bank. Native desert annuals, in particular, are known to exhibit high interannual variation (Freas and Kemp 1983; Philippi 1993; Pake and Venable 1996). While multiple watering cycles were utilized to address this potential variation, and while *Schismus* germinants were removed immediately to minimize interference, it is possible that not all viable native seeds in the seed bank samples germinated during the assays. For example, Esque et al. (2010a) treated seed bank samples with gibberellic acid to stimulate germination and observed native annual germinants to be magnitudes greater than what we found.

### Impact of Fire on Annual Plants

Invasive annual grasses and forbs can severely reduce the abundance and species richness of native annual plants in unburned vegetation (Huenneke et al. 1990; Crimmins and McPherson 2008; Davies and Svejcar 2008; Minnich 2008). This study suggests that fire disturbance is also a serious threat to native annuals because it promotes invasive plants like *Schismus* spp. Abundance of *Bromus madritensis* ssp. *rubens* typically decreases in the immediate post-fire years (Abella et al. 2009; Esque et al. 2010a) although it is expected to return to or even exceed pre-fire abundance levels within three years after fire, if precipitation is adequate (Brooks 2003). The mechanism whereby *Schismus* spp. increases immediately after fires relates to the small size of its seeds, which fall into cracks and escape damage from fire, plus its ability to take advantage of elevated inorganic nitrogen levels in the post-fire environment (Esque et al. 2010b). Because nitrogen-use traits may not differ between invasive and native annuals, the relative early germination and more rapid phenology of *Schismus* spp. contributes to its success (Marushia et al. 2010; Steers et al. 2011).

At this study site, fire reduced the quadrat- and plot-level species richness of native annual plants, and recurrent fire magnified this outcome at the plot-level. Recurrent fire also significantly decreased species diversity, which led to a highly simplified assemblage of annual plants in the twice-burned stand. Despite the negative impact of fire on native annuals, if invasive annuals are removed post-fire, then native annual species richness can increase greatly, likely exceeding prefire levels (Steers and Allen 2010, 2011c).

## Relevance to the Grass/Fire Cycle

At our study site, invasive annual grass cover within the first three years after a fire was greater in the burned compared to the unburned stand, due almost entirely to *Schismus* spp, which is similar to other studies (Cave and Patten 1984; Minnich and Dezzani 1998; Brooks 2002; Esque et al. 2010b; Steers and Allen 2011a). This difference in invasive annual grasses may translate to greater potential for a consequent fire (Brooks et al. 2004). *Schismus* spp. are generally considered less effective at carrying fire than larger annual grasses like *Bromus madritensis* ssp. *rubens* (Brooks 1999). However, in this region *Schismus* spp. can attain relatively large sizes due to high anthropogenic nitrogen deposition, especially in wet years (Rao and Allen 2010; Rao et al. 2010) and are known to carry stand-replacing fires. For example, in the summer of 2005, at least four other creosote bush scrub fires within a 10 km radius of the study site were primarily fueled by *Schismus* spp. (R. Steers personal observations). Therefore, given adequate precipitation, results from this study suggest that fire can promote invasive annual grasses (i.e., *Schismus* spp.), which in turn, could fuel additional fires in a positive feedback, as described by the grass/fire cycle (D'Antonio and Vitousek 1992; Brooks et al. 2004).

## Management Implications

Removal of invasive grasses and forbs should favor natives through decreased competition (Brooks 2000; Schutzenhofer and Valone 2005; Barrows et al. 2009; Steers and Allen 2010) and through limiting future fire disturbance (Brooks et al. 2004). Because native annual richness is linked to the spatial and structural heterogeneity of creosote bush scrub (Schmida and Whittaker 1981), some native species may not find suitable micro-habitats until the shrub components are returned, regardless of invasive plant removal. For example, *Pholistoma membranaceum* was the most abundant annual forb in the unburned stand (Appendix 1) where it occurred almost exclusively in shrub understories of long-lived species, like *Larrea tridentata* (R. Steers personal observation). *Pholistoma membranaceum* was virtually eliminated in the once-burned and twice-burned stands even though *Encelia farinosa* shrubs were prevalent. Unfortunately, reestablishment of long-lived shrubs, like *Larrea tridentata*, has been speculated to take decades or longer (Vasek 1983; Lovich and Bainbridge 1999; Abella 2009, 2010; Steers and Allen 2011b). Because of invasive species and the long time scale required for desert vegetative succession, intervention through restoration practices may be required to ensure the return of certain native annual species, although this may only be feasible at small scales or where special status plant species are at risk.

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APPENDIX 1. Average cover of each annual species recorded per quadrat (1 m$^2$) and their respective frequency score per stand (unburned, once-burned, or twice-burned stands). Frequency is the number of occurrences per six 168.3 m$^2$ mod-NAWMA plots per stand.

| | | Unburned | Once-burned | Twice-burned |
|---|---|---|---|---|
| Family | Species | Cover (%)/ frequency per six plots | Cover (%)/ frequency per six plots | Cover (%)/ frequency per six plots |
| INVASIVE FORBS | | | | |
| Brassicaceae | *Brassica tournefortii* Gouan | 22.1/6 | 41.9/6 | 5.2/6 |
| Geraniaceae | *Erodium cicutarium* (L.) Aiton | 11.2/6 | 7.3/6 | 13.4/6 |
| INVASIVE GRASSES | | | | |
| Poaceae | *Bromus madritensis* L. subsp. *rubens* (L.) Husn. | 4.1/6 | <0.1/6 | 0/3 |
| | *B. tectorum* L. | 0/4 | <0.1/1 | <0.1/1 |
| | *Schismus barbatus* (L.) Thell. and *S. arabicus* Nees | 22.1/6 | 11.9/6 | 34.7/6 |
| NATIVE ANNUALS | | | | |
| Asteraceae | *Chaenactis fremontii* A. Gray | 5.7/6 | 0.8/6 | 0/2 |
| | *Filago californica* Nutt. | 0.6/6 | 0/5 | 0.2/4 |
| | *F. depressa* A. Gray | <0.1/2 | 0/0 | 0/0 |
| | *Lasthenia californica* Lindl. | <0.1/5 | 0/3 | <0.1/5 |
| | *Malacothrix glabrata* A. Gray | 0/0 | 0/3 | 0.2/3 |
| | *Rafinesquia neomexicana* A. Gray | 0.1/6 | 0/0 | 0/0 |
| | *Stephanomeria exigua* Nutt. | 0/0 | 0/0 | <0.1/2 |
| | *Stylocline gnaphaloides* Nutt. | 1.4/6 | 0/1 | 0/0 |
| | *Uropappus lindleyi* (DC.) Nutt. | 0/0 | <0.1/1 | 0/1 |
| Boraginaceae | *Amsinckia menziesii* A. Nelson & J. F. Macbr. | 1/6 | 0/1 | 0/1 |
| | *Cryptantha barbigera* Greene | 0/5 | 0.8/6 | 1/5 |
| | *Pectocarya heterocarpa* I. M. Johnst. | 0.3/5 | 0/0 | 0/0 |
| | *P. linearis* DC. | 0.7/5 | <0.1/5 | <0.1/1 |
| | *P. recurvata* I. M. Johnst. | 0.8/5 | 0.1/5 | 0/2 |
| Brassicaceae | *Descurainia pinnata* (Walter) Britton | 0/0 | <0.1/3 | 0/1 |
| | *Lepidium lasiocarpum* Torr. & A. Gray | 0/0 | 0/3 | <0.1/1 |
| | *Tropidocarpum gracile* Hook. | 0/1 | 0/0 | 0/0 |
| Caryophyllaceae | *Loeflingia squarrosa* Nutt. | <0.1/5 | 0/0 | 0/0 |
| Crassulaceae | *Crassula connata* (Ruiz & Pav.) A. Berger | 1.3/6 | 0.1/4 | <0.1/4 |
| Fabaceae | *Lotus strigosus* (Nutt.) Greene | <0.1/5 | 0/0 | <0.1/1 |
| | *Lupinus sparsiflorus* Benth. | 0/2 | 0/0 | 0/0 |
| Hydrophyllaceae | *Emmenanthe penduliflora* Benth. | 0.1/6 | 3.3/6 | 2.5/6 |
| | *Phacelia campanularia* A. Gray | 0/0 | 0/2 | <0.1/2 |
| | *P. distans* Benth. | 1.4/5 | <0.1/6 | 0/0 |
| | *Pholistoma membranaceum* (Benth.) Constance | 13.2/6 | 0/1 | 0/0 |
| Lamiaceae | *Salvia columbariae* Benth. | 0/0 | 0/0 | 0/1 |
| Loasaceae | *Mentzelia involucrata* S. Watson | 0/0 | 0/1 | 0/0 |
| | *Mentzelia* sp. | <0.1/2 | 0/0 | 0/0 |
| Onagraceae | *Camissonia californica* (Torr. & A. Gray) P. H. Raven | 0.1/6 | 1.1/6 | 2/6 |
| | *C. pallida* (Abrams) P. H. Raven | 0.1/4 | 0/2 | <0.1/4 |
| Plantaginaceae | *Plantago ovata* Forssk. | 0.1/6 | 0.7/6 | 1.11/3 |
| Poaceae | *Vulpia microstachys* (Nutt.) Benth. | 0/1 | 0/0 | 0/0 |
| | *V. octoflora* (Walter) Rydb. | 3.9/6 | 0.9/6 | 0/1 |
| Polemoniaceae | *Gilia angelensis* V. E. Grant | 0.2/1 | 0/0 | 0/0 |
| | *Linanthus bigelovii* Greene | 0/2 | 0/0 | 0/0 |
| Polygonaceae | *Chorizanthe brevicornu* Torr. | 0/2 | 0/0 | 0/0 |
| | *Pterostegia drymarioides*Fisch. & C. A. Mey. | 0/1 | 0/0 | 0/0 |
| Portulaceae | *Calyptridium monandrum* Nutt. | 0/0 | 0/1 | 0/1 |

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# STATUS OF BINGHAM'S MORNING-GLORY IN THE LIGHT OF ITS REDISCOVERY

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## ABSTRACT

*Calystegia sepium* (L.) R. Br subsp. *binghamiae* (Greene) Brummitt (Convolvulaceae), until recently presumed extinct, is elevated to species status. The basionym *Convolvulus binghamiae* Greene was published without identifying a type; therefore, a lectotype is selected from among the specimens cited in Greene's description.

Key Words: *Calystegia sepium* subsp. *binghamiae*, Convolvulaceae, lectotype, new combination, rare species.

*Calystegia sepium* (L.) R. Br subsp. *binghamiae* (Greene) Brummitt has been presumed extinct (California Native Plant Society 2011) until its rediscovery in May 2011 in the City of Chino, San Bernardino County, California. The rediscovery and subsequent conservation efforts will be described elsewhere by others. The availability of new specimens and live material prompted a taxonomic review, which indicates that recognition at the species level is warranted.

## TAXONOMIC TREATMENT

**Calystegia binghamiae** (Greene) Brummitt, comb. nov.—Basionym: *Convolvulus binghamiae* Greene, Bull. Calif. Acad. Sci. 2: 417. 1887. Greene referred to collections by Bingham and himself "in marshy places about Burton's Mound in Santa Barbara," but did not cite the specimens. Synonyms: *Convolvulus sepium* var. *binghamiae* (Greene) Jepson, Fl. Calif. 3:118. 1939. *Calystegia sepium* subsp. *binghamiae* (Greene) Brummitt, Ann. Missouri Bot. Gard. 216. 1965.—Type: USA, California, Santa Barbara Co. City of Santa Barbara, August 1886, *Mrs. R.F. Bingham s.n.* UC 335392 (lectotype chosen here; isolectoype: *Mrs. R.F. Bingham s.n.,* Columbian Collection F). Jepson cited Bingham's collection, but did not specify the UC or the F specimen as the lectotype.

## Review

*Convolvulus binghamiae* Greene (Convolvulaceae) was described from specimens collected by Mrs. R. F. Bingham and E. L. Greene in Santa Barbara, coastal southern California, in 1886. In 1965 Brummitt transferred it to the genus *Calystegia* R. Br. and ranked it as a subspecies within *C. sepium* (L.) R. Br., a decision he has regretted since. Its only verified localities are coastal regions of Santa Barbara and Los Angeles counties and Chino Creek, San Bernardino County, all in southern California (Consortium of California Herbaria 2011). Abrams (1951) also mentioned it extending to Orange County. We have seen specimens from Bolsa Chica (*L.M. Booth 1214,* POM) and east of Huntington Beach (*L.M. Booth 1359,* POM) that were labeled as *Convolvulus binghamiae* or *C. sepium* subsp. *binghamiae* as of 1951. Both of these were annotated by Brummitt as *Calystegia sepium* subsp. *limnophila* (Greene) Brummitt. We are not aware of any other records from Orange County.

One of us, Brummitt, has worked on this genus for many years, both in the herbarium and in the field. In 1998 he determined material at RSA as *Calystegia binghamiae*, adopting specific rank, but, in view of the lack of clear evidence in the very sparse material available to him, he did not publish this name. In *The Jepson Manual* (Brummitt 1993) and its second edition (Baldwin et al. 2012), which went to press before the rediscovery was appreciated, he retained subspecific rank under *C. sepium*. However, he has now examined the recent specimen collected in Chino (*J.M. Wood 4092,* K), as well as Greene's original description, and photographs of the original material, and as a result is now convinced that inclusion in *C. sepium* is inappropriate.

In *C. sepium*, with numerous subspecies in pantemperate regions of the world, the large paired bracteoles are inserted close to the calyx and largely overlap and conceal it. This seems to be

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an apomorphy suggesting a derived position in the likely evolution of the genus. *Calystegia binghamiae,* by contrast, usually (see below) has smaller, much narrower bracteoles, with at least one of them inserted remote from the calyx. Such bracteoles are characteristic of a number of species of the *Calystegia* complex that is endemic to California. This character is not found elsewhere among *Calystegia* taxa, and is thought to represent a more plesiomorphic condition. *Calystegia sepium* may well be a polyphyletic taxon (Brummitt 1963) even without including *C. binghamiae*, and would probably be even more so with *C. binghamiae* included (the taxonomic details of the Californian species in the 1963 thesis were based on inadequate herbarium material and have been superseded by the author in more recent work). The rhizomatous habit, which *C. binghamiae* shares with *C. sepium*, apparently evolved independently within the California *Calystegia* lineage.

Although available specimens referable to *C. binghamiae* are rather limited in number, we have noted surprising variation in both bracteole and leaf shape characters. The bracteoles on the original collections by Bingham and Greene from Santa Barbara are broadly elliptic, 8–12 × 4–8 mm, and inserted almost adjacent to the sepals (probably influencing earlier decisions to include the taxon in *C. sepium*). They differ markedly, however, from those of *C. sepium* in being only about half as long as the sepals. All specimens we have seen from further east have linear to narrowly elliptic bracteoles with at least one inserted clearly below the sepals. Field observations at different times by one of us (J. M. Wood) on the newly located population at Chino have noted that early in the season the bracteoles tend to be more similar to those of the specimens collected by Bingham and Greene in Santa Barbara, whereas later in the season they are much narrower with at least one of them usually remote from the sepals. A good illustration of the latter may be seen in Abrams (e.g., Fig. 3855, 1951).

The leaves on the material from Santa Barbara have relatively well developed posteriorly-directed basal lobes with a tendency to a parallel-sided sinus. Ivan Johnston's specimens, collected at Chino Creek in 1917 (*1274*, below) have very similar leaves. However, the new collection from Chino, *J.M. Wood 4092*, has poorly developed basal lobes (especially on young leaves) with a broadly rounded sinus or almost cuneate leaf base. This is unlike anything found in *C. sepium*. Further specimens or observations on both leaves and bracteoles would be of interest.

While excluding *Calystegia binghamiae* from *C. sepium*, one must consider whether it is possible to regard it as conspecific with any other Californian species, but this does not seem to be the case. Indeed it is not clear which of the Californian taxa would be most similar based on character states of the rhizomes, pubescence, leaves and bracteoles. An annotation made by Brummitt in 1973 on one the Johnston specimens at RSA suggested it was a hybrid possibly between *C. sepium* subsp. *limnophila* and *C. occidentalis* (Gray) Brummitt subsp. *fulcrata* (Gray) Brummitt or *C. longipes* (Watson) Brummitt, but this is now discounted.

One misidentified specimen, *R. Zembal s.n. 21 May 1977* RSA, labeled as *Calystegia sepium* subsp. *binghamiae* and reported as such in California Department of Fish and Game (2011), is *C. macrostegia* (Greene) Brummitt. One of us (S. D. White) has annotated the specimen and entered the correction on the Consortium of California Herbaria web site.

*Calystegia binghamiae* has been known by the common names "Santa Barbara morning-glory" (Abrams 1951) and "Bingham's false-bindweed" (USDI Natural Resources Conservation Service 2011). Its geographic range is (or was) wider than the first common name implies, and the native California *Calystegia* species are commonly known as morning-glories rather than false-bindweeds (Brummitt 1993). Therefore, we suggest the common name "Bingham's morning-glory." Mrs. R.F. Bingham was a naturalist of the Santa Barbara area, and published notes on the local vascular flora, marine algae, natural history, and medicinal plants (e.g., Bingham 1887, 1890). A genus of marine algae, *Binghamiella*, is named in honor of a Mrs. C. P. Bingham of the Santa Barbara area in the 1870s (Setchell and Dawson 1941); this may have been the same Mrs. Bingham, perhaps identifying herself at times by her husband's initials.

## Specimens Examined

USA. CALIFORNIA. **Santa Barbara Co.**: Santa Barbara, August 1886, *Mrs. R.F. Bingham s.n.* (UC 335392 lectotype chosen here; F, presumed duplicate of previous cited collection; photos K, RSA); Santa Barbara, 1886 *E.L. Greene s.n.* NDG 39692, and July 1886, *E.L. Greene s.n.* NDG 39691 and 39693; photos K, RSA); lagoon near ocean, Ellwood, May 30 [no year] *Alice Eastwood s.n.* (UC 879470). **Los Angeles Co.**: Riveria [probably what is now Pico Rivera], 1 May 1902, *Anstruther Davidson 1892* (RSA; mixed collection with one stem of *C. binghamiae* including leaves, one flower, and one bud, mounted with several *C. sepium* stems); near University Station [presumably a Pacific Electric station near the USC campus], 1899, *Anstruther Davidson 2144* (RSA). **San Bernardino Co.**: Chino Creek, 30 May 1917, *Ivan Johnston 1274* (two sheets at RSA/POM; one at UC); city of Chino, SE corner of Edison Ave. and Oaks Ave., near entrance to Chaffey college campus, ca. 2.5 mi N of Chino Creek (Prado Basin), irrigated landscaped area adjacent to ruderal grasslands, 17 May 2011, *Justin M. Wood 4090* (to be distributed) and *4092* with *S.D. White, N. Gale & A. Parikh* (K, RSA; one duplicate to be distributed). We understand that at least one other collection has been made at the Chino site this year, but we have not seen it.

## ACKNOWLEDGMENTS

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# CHANGE IN RANK OF *ERIODICTYON TRASKIAE* SUBSP. *SMITHII* (HYDROPHYLLACEAE)

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In preparing a taxonomic treatment of *Eriodictyon* (Hydrophyllaceae) for the Flora of North America North of Mexico, it has become necessary to standardize ranks of infraspecific taxa. Infraspecific taxa in two species in the Flora have been named as varieties: *E. trichocalyx* A. Heller var. *trichocalyx* with *E. trichocalyx* var. *lanatum* (Brand) Jeps., and, *E. crassifolium* Benth. var. *crassifolium* with *E. crassifolium* var. *nigrescens* Brand. The operationally, if not evolutionarily, preferable approach to achieving nomenclatural consistency in the treatment is to treat *E. traskiae* Eastw. subsp. *smithii* Munz as a variety. In the interest of nomenclatural consistency, therefore, the following nomenclatural change is proposed:

## TAXONOMIC TREATMENT

**Eriodictyon traskiae** Eastwood var. **smithii** (Munz) Hannan stat. nov. Basionym: *Eriodictyon traskiae* Eastw. subsp. *smithii* Munz, A California Flora: Supplement, 90. 1968. —Type: USA, California, Santa Barbara Co., San Marcos Pass, July 4, 1950, *Clifton F. Smith 1621* (holotype: POM 310992; isotypes: CAS 384681!, NY 337110).

The resulting autonym is:

**Eriodictyon traskiae** Eastw. var. **traskiae** —TYPE: USA, California, Los Angeles Co., Santa Catalina Island, Avalon, "one volcanic upland, 1500 ft. elevation", May, 1897, *Blanche Trask s.n.* (holotype: CAS 369!).

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# MIMULUS SOOKENSIS (PHRYMACEAE), A NEW ALLOTETRAPLOID SPECIES DERIVED FROM *MIMULUS GUTTATUS* AND *MIMULUS NASUTUS*

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## ABSTRACT

A new species of monkeyflower, **Mimulus sookensis**, is described. This species is found throughout the southern portion of Vancouver Island, the Gulf Islands of British Columbia, the San Juan Islands of Washington state, the Willamette and Umpqua River Valleys in Oregon, and has been collected at one location in Mendocino County, California. **Mimulus sookensis** is a tetraploid species ($n = 28$) derived from the predominately outcrossing *Mimulus guttatus* DC. ($n = 14$) and the predominately self-pollinating *Mimulus nasutus* Greene ($n = 14$). **Mimulus sookensis** is similar phenotypically to the small-flowered *M. nasutus*, but differs in chromosome number, height, and by a slightly more narrowed corolla tube than that of *M. nasutus*. It is commonly found on wet hillsides, seeps, cutbanks, and in roadside ditches, often co-occuring with *M. guttatus* but infrequently with *M. nasutus*.

Key Words: Allotetraploid speciation, *Mimulus*, *Mimulus guttatus*, *Mimulus nasutus*, monkeyflower, new species, Oregon, Vancouver Island.

A small-flowered monkeyflower similar to *Mimulus nasutus* Greene was first observed on Vancouver Island, Canada, by Fred Ganders, and later collected for scientific study in May 1991 by Beverly Benedict. Although phenotypically similar to *M. nasutus* (Fig. 1), allozyme analysis revealed that some of the small-flowered monkeyflowers on Vancouver Island were always heterozygous at allozyme markers. This was in contrast to allozyme data from another small-flowered monkeyflower found on the island, *M. nasutus* (snouted monkeyflower), and the common yellow monkeyflower, *M. guttatus* DC. These results were intriguing because while the large-flowered, chasmogamous *M. guttatus* is known to be highly outcrossing, both *M. nasutus* and the heterozygous, small-flowered monkeyflowers were known to be highly selfing, given their floral structure, small flower size, and often cleistogamous nature (Ritland and Ritland 1989; Dole 1992; Willis 1993). Morphological analysis of *M. guttatus*, and the two small-flowered monkeyflowers (*M. nasutus* and the species described here, **M. sookensis**) revealed that while *M. nasutus* and **M. sookensis** overlapped a great deal in floral morphology, subtle morphological differences did exist (Fig. 1, e.g., pistil length, corolla tube width). Because of fixed heterozygosity in some of the small-flowered *Mimulus* on Vancouver Island, and slight differences in floral morphology, F. Ganders suspected that the heterozygous monkeyflowers in question were actually a distinct taxon of allopolyploid origin (Benedict 1993). Chromosome squashes conducted at the time revealed that these new monkeyflowers, **M.**

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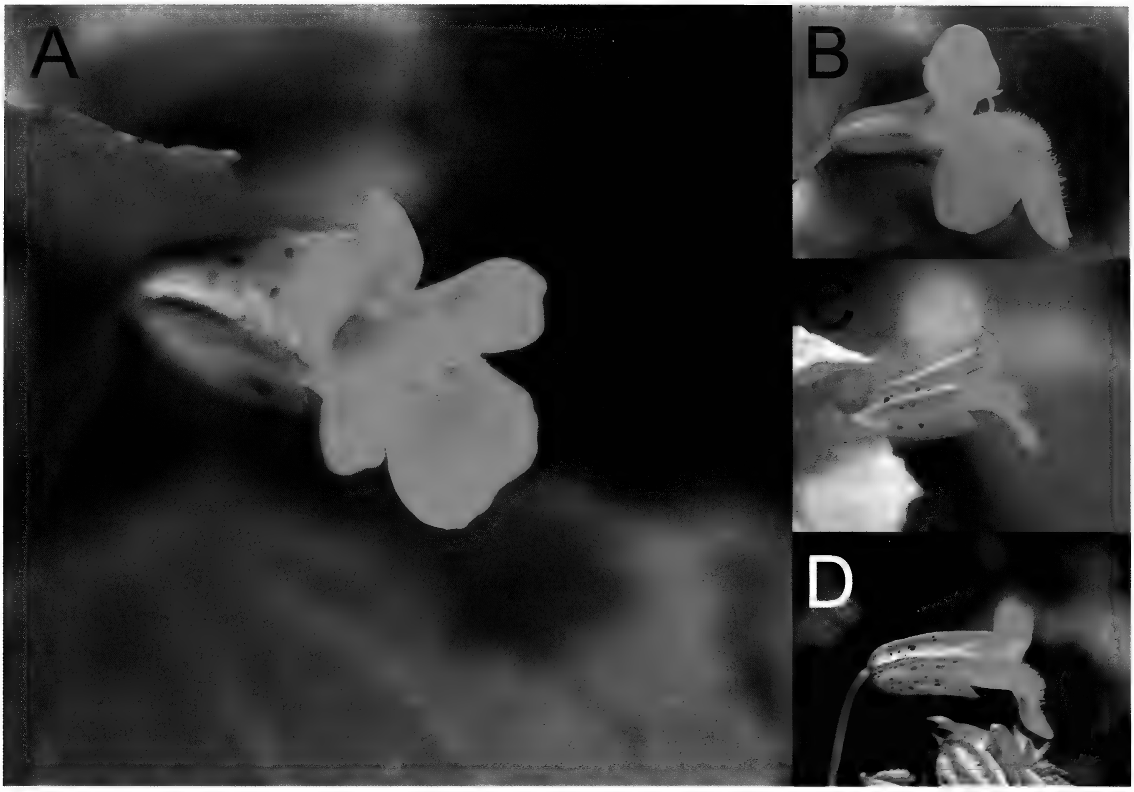

FIG. 1. Photographs of *M. sookensis* and its progenitor species. Side profile photographs are taken on approximately the same scale. A. *M. sookensis*, B. *M. guttatus*, C. *M. sookensis*, D. *M. nasutus*.

**sookensis**, had more than $n = 14$ chromosomes, but an exact count was not obtained.

Following the work of B. G. Benedict, flow cytometry data from three **M. sookensis** collections revealed that the small-flowered monkeyflowers from Vancouver Island and surrounding areas, as well as the valleys of western Oregon and northern California, had approximatey twice the DNA content of *M. guttatus* and *M. nasutus*, suggesting again that this taxon was of tetraploid origin (Sweigart et al. 2008). Sequence data from two nuclear genes confirmed that this new species was a hybrid tetraploid derived from *M. guttatus* and *M. nasutus*. Furthermore, crossing data revealed that the allotetraploids were reproductively isolated from their diploid progenitors due to failure of seed development, a result consistent with the triploid block that is commonly observed in interploidy crosses (Sweigart et al. 2008). Although **M. sookensis** is a cryptic species due to its phenotypic similarity to *M. nasutus*, the fact that it is reproductively isolated from its diploid progenitors illustrates the concept of instant or rapid speciation of polyploids, which has long been recognized (e.g., Winge 1917; Dobzhansky 1937; Coyne and Orr 2004). Polyploidy not only has the propensity to quickly create new species (according to the biological species concept, e.g., Mayr 1996) but has contributed significantly to angiosperm evolution (Stebbins 1971; Grant 1981; Masterson 1994; Otto and Whitton 2000).

Here, we present evidence that **M. sookensis** is historically taxonomically unrecognized, and provide new chromosome data that provide conclusive evidence that **M. sookensis** is a cytologically distinct species, which has previously been shown (Sweigart et al. 2008) to be of polyploid origin, and reproductively isolated from its diploid progenitors, as well as a description of this hitherto unnamed species of monkeyflower.

## REVIEW OF PREVIOUSLY PUBLISHED *MIMULUS* TAXA

*Mimulus guttatus* is an herbaceous wildflower distributed throughout much of western North America (Vickery 1978), while *Mimulus nasutus* has a restricted range relative to *M. guttatus* (Kiang and Hamrick 1978; Vickery 1978). *Mimulus guttatus*, *M. nasutus*, and **M. sookensis** all belong to the *M. guttatus* species complex, and are part of the Simiolus clade (Beardsley et al. 2004) of the genus *Mimulus*. *Mimulus guttatus* and its close relatives have been extensively

TABLE 1. COMPLETE LIST OF PREVIOUSLY PUBLISHED *MIMULUS* TAXA WHICH MIGHT HAVE BEEN A DESCRIPTION OF *M. SOOKENSIS*, WITH A DESCRIPTION OF HOW THEY ARE DIFFERENT FROM *M. SOOKENSIS*. Taxa are listed in alphabetical order, although subspecies and varieties are listed in parentheses if variety or subspecies was given specific rank. For synonyms examined, three sources were used: the synonyms listed in Grant (1924) and Pennell (1951) for *M. nasutus*, and the synonyms listed for both *M. guttatus* and *M. nasutus* in IPNI. Many of the large flowered varieties of *M. guttatus* were not included in this list for the purpose of brevity. All references are included in the literature cited. Evidence sources refers to all herbarium specimens, drawings and descriptions, in both the nomenclatural citation and established floras or monographs, that were used in determining differences. For each candidate taxa, the characters that most easily illustrate the difference between the listed taxa and *M. sookensis* are described for the listed taxa.

| Previously published taxa | Synonym (source) | Evidence sources | Distinguishing characters from *M. sookensis* |
|---|---|---|---|
| *M. arvensis* Greene (*M. guttatus* DC. var. *arvensis* Grant) | *M. guttatus* (IPNI) | Greene (1887); Grant (1924); Pennell (1951); Mukherjee and Vickery (1962) | Diploid ($n$ = 14), easily hybridizes with *M. guttatus*; Greene describes the leaves as lyrate, and the species as perhaps synonymous with *M. lyratus* Benth. Grant describes the variety as having an upper calyx tooth not markedly longer than others, elongated internodes, teeth not usually folded over each other at maturity |
| *M. bakeri* Gandoger | *M. nasutus* (Grant 1924, Pennell 1951) | CAS 22488 (isotype), NY 20798 (possible isotype); Gandoger (1919) | CAS specimen appears to be hybrid between *M. guttatus* and *M. nasutus*, while description doesn't match specimen, description suggests that difference between *M. nasutus* and *M. bakeri* is the impunctate calyx of *M. bakeri* |
| *M. cordatus* Greene | *M. nasutus* (Grant 1924) | Greene (1910); Pennell (1951); Mukherjee and Vickery (1962) | Corolla lacking in spotting, diploid ($n$ = 14) that hybridizes easily with *M. guttatus* |
| *M. cuspidatus* Greene | *M. nasutus* (Grant 1924; Pennell 1951) | DS 771002 (isotype); description in Greene (1910) | *M. nasutus* found in wet shades exhibiting phenotypic plasticity in a classic shade avoidance response (see text for discussion) |
| *M. decorus* (Grant) Suksd. (*M. guttatus* DC. var. *decorus* Grant) | *M. guttatus* (IPNI) | CAS 22445; Pennell (1951) | Corolla large |
| *M. erosus* Greene | *M. nasutus* (Grant 1924) | Greene (1910) | Corolla exserted from tube, synonym of *M. nasutus* |
| *M. glareosus* Greene | *M. nasutus* (Grant 1924; Pennell 1951) | Greene (1889, 1894) | Leaves toothed or lobed, slimy, synonym of *M. nasutus* |
| *M. guttatus* DC. subsp. *scouleri* (Hook.) Pennell | *M. guttatus* (IPNI) | Pennell (1947) | Stoloniferous variant of *M. guttatus* with more linear leaves (perhaps synonymous with *M. tilingii* Regel or *M. caespitosus* Greene) |
| *M. hallii* Greene (*M. guttatus* DC. var. *hallii* Grant) | *M. guttatus* (IPNI) | Greene (1885); Grant (1924) | Leaves parallel-veined and almost entire, calyx highly inflated |
| *M. guttatus* DC. var. *lyratus* (Benth.) Pennell ex M. Peck | *M. guttatus* (IPNI) | Pennell (1941); Pennell (1951) | Leaves pinnately lobed at the base, corolla long (2–3 cm) |
| *M. guttatus* var. *depauperatus* Grant (*M. luteus* var. *depauperatus* A. Gray) | *M. guttatus* (IPNI) | Gray (1867); Grant (1924); Hitchcock and Cronquist (1987) | Grant (1924) thought to be synonymous with *M. puncticalyx* and *M. microphyllus*, based on Hitchcock and Cronquist (1987) and Gray, appears to be simply a description of small *M. guttatus* or *M. nasutus* plants with few or small flowers – a condition most likely caused by environment |
| *M. guttatus* var. *glaucescens* (Greene) Jeps. (*M. glaucescens*) | *M. guttatus* (IPNI) | Greene (1885); Jepson (1925); Pennell (1951) | Leaves glaucous, synonymous with *M. glaucescens* (Greene) |

TABLE 1. CONTINUED.

| Previously published taxa | Synonym (source) | Evidence sources | Distinguishing characters from *M. sookensis* |
|---|---|---|---|
| *M. guttatus* var. *gracilis* (A. Gray ex Torr.) Campbell | *M. guttatus* (IPNI) | CAS 23523 (isotype for *M. pardalis*); Campbell (1950); ORE96554 | Campbell lumps all synonyms of *M. nasutus* and *M. nasutus* itself under this variety. CAS specimen is *M. pardalis*, corolla described as being twice as long as the calyx, diploid ($n$ = 14) |
| *M. guttatus* var. *nasutus* Jeps. | *M. nasutus* (Pennell 1951) | | Synonym of *M. nasutus* |
| *M. guttatus* var. *puberulus* A. L. Grant | *M. guttatus* (IPNI) | Grant (1924) | Listed as perennial, large-flowered |
| *M. inflatulus* Suksd. | *M. breviflorus* (Pennell 1951) | CAS 152750 (isolectotype); Pennell (1951) | Calyx equal-toothed, leaves more linear and narrow, synonym of *M. breviflorus* Piper |
| *M. laxus* Pennell ex. M. Peck | *M. guttatus* (Mukherjee and Vickery 1962) | CAS 329746 (isotype); NY 90734 (isotype); Mukherjee and Vickery (1962) | Variant of *M. guttatus*, diploid ($n$ = 14) |
| *M. marmoratus* Greene | *M. nasutus* (Pennell 1951) | Greene (1895b) | Description of *M. marmoratus* matches that of a hybrid between *M. guttatus* and *M. nasutus*, with large red blotch on middle lower lobe, with a corolla that is longer than *M. nasutus* (>3 cm) |
| *M. micranthus* A. Heller (*M. guttatus* var. *micranthus* (A. Heller) G. R. Campb., *M. nasutus* Greene var. *micranthus* A. L. Grant) | *M. guttatus*, *M. nasutus* (IPNI) | DS 74105; NY 90746 (isotype Heller 7410); Heller (1912); Grant (1924); Pennell (1951); Munz (1959) | Narrow-range endemic of CA; calyx even toothed and lower teeth not curled upward and inward upon maturity, stem weak, lower leaves described as being lyrate and long-petioled, calyx puberulent, diploid used in multiple genetic studies (see text) |
| *M. microphyllus* Benth. (*M. guttatus* var. *microphyllus* Pennell in M. Peck) | | Greene (1885), Pennell (1941, 1951) | Leaves small, stems rounded, pistil much exserted from calyx, located mostly in the mountains |
| *M. minusculus* Greene | *M. nasutus* (Grant 1924) | Greene (1910) | Perennial, shorter than *M. sookensis*, leaves ovate, flowers large |
| *M. minutiflorus* R. K. Vickery | | CAS 961575 (isotype); Vickery (1997) | Corolla superficially similar in appearance to *M. sookensis*, but lacking ridges, and stems wiry; closely related to *M. wiensii*, $n$ = 32 |
| *M. nasutus* Greene var. *eximius* Green A. L. Grant ex J. T. Howell | *M. nasutus* (IPNI) | Howell (1949) | Howell (1949) bases his description of this variety on *M. nasutus*, but does not realize that what he considers *M. nasutus* is actually a hybrid between *M. guttatus* and *M. nasutus*, also appears to be synonymous with *M. nasutus* var. *insignis* |
| *M. nasutus* Greene var. *insignis* A. L. Grant | *M. nasutus* (IPNI) | Grant (1924); and Pennell (1941) | Flower size outside the range of *M. sookensis* and large blotch of anthocyanin spotting on lower corolla lobe, both suggest that description matches that of a hybrid between *M. guttatus* and *M. nasutus* |
| *M. guttatus* DC. var. *insignis* Greene | *M. guttatus* (IPNI) | JEPS 2938 (the very type!) | Large flowered, hybrid between *M. guttatus* and *M. nasutus* |
| *M. parishii* Gand. | *M. nasutus* (Grant 1924; Pennell 1951) | Gandoger (1919) | Leaves deeply cut or laciniate; only a single specimen was examined in the naming |
| *M. puberulus* Greene | | Greene (1910) | Corolla large (>3 cm), stem round and viscidly puberulent |
| *M. puberulus* Gand. | *M. nasutus* (Grant 1924; Pennell 1951) | Gandoger (1919) | Only distinguishing feature from typical *M. nasutus* is that it is minutely pubescent; only a single specimen was examined, a synonym of *M. nasutus* |

TABLE 1. CONTINUED.

| Previously published taxa | Synonym (source) | Evidence sources | Distinguishing characters from *M. sookensis* |
|---|---|---|---|
| *M. puncticalyx* Gand. | *M. nasutus* (Pennell 1951) | ORE96654 (isotype); ORE96655; Gandoger (1919) | Leaves tiny upper tooth hardly more prominent than others; only a single specimen was examined in the naming |
| *M. subreniformis* Greene | *M. nasutus* (Grant 1924; Pennell 1951) | UC 27111 (holotype); Greene (1895a) | Appears to be a diminuitive variant of *M. nasutus*, but without anthocyanin spotting on corolla |
| *M. washingtonensis* Gand. | | CAS 152669 (isotype); Gandoger (1919) | Calyx equal-toothed, flowers large |

collected and examined throughout western North America, by both early botanists and contemporary botanists and geneticists. Historically, *M. guttatus* and its close relatives have been subject to extraordinarily divergent taxonomic treatments by different authors. Pennell (1951) recognized 28 taxa closely allied with *M. guttatus* from the Pacific Northwest, and in a recent treatment of California, Thompson (1993) recognized only five. In contemporary times, the genus *Mimulus* has seen a proliferation of scientific interest: a Google Scholar search for articles published between 1980–2011 including the word *Mimulus* in the title found 436 articles, with 194 written on *M. guttatus* alone. Although many of these recent publications do not necessarily include field work, it is safe to assert that more has been learned of the genetics, ecology, distribution, and taxonomic status of *M. guttatus* and its close relatives, since the publications of Grant (1924), Pennell (1951) and even Thompson (1993), see Wu et al. (2008). By combining knowledge from contemporary studies with historical taxonomic wisdom, we found that **M. sookensis** is truly a previously overlooked species in this intensely studied group, in part due to its cryptic nature.

To determine if **M. sookensis** was previously taxonomically recognized, we first identified synonyms of *M. guttatus* (only the small-flowered or obscure taxa) and *M. nasutus*, from those listed in Pennell (1951), Grant (1924), and Campbell (1950), and from lists of synonyms derived from IPNI (International Plant Names Index). We also searched in Pennell (1951) and Grant (1924) for descriptions of small, yellow-flower *Mimulus* that were not listed as synonyms of *M. guttatus* or *M. nasutus*, but were considered to be closely related to the Simiolus clade (candidate taxa, Table 1). For these 31 candidate taxa, in which the author might have potentially described **M. sookensis**, we referred to herbarium specimens, the original species descriptions, crossing data and chromosome counts (when available), and drawings and descriptions in other references to determine if a previously published name could be applied to **M. sookensis** (Table 1). We did not find a previously published taxon that satisfied every aspect of the morphology and cytology of **M. sookensis** (Table 1), and thus, despite the abundance of synonyms within the *M. guttatus* species complex, no previously published names can be applied to **M. sookensis**.

Throughout the course of our examination of **M. sookensis** candidates, we found that the reasons why candidate taxa were not representative of **M. sookensis** fell into one or more categories. First, pronounced differences in habit, leaf, and even floral morphology existed (e.g., perenniality, lyrate leaves, even-toothed calyx). Second, in some cases the species described was likely either a hybrid between *M. guttatus* and *M. nasutus*, or *M. nasutus*. In the field, *M. guttatus* and *M. nasutus* are known to hybridize when they co-occur (Kiang 1973; Martin and Willis 2007). Hybrids between *M. guttatus* and *M. nasutus* have flowers that are much more similar in size to *M. guttatus*, due to dominance of the *M. guttatus* floral genes (Fishman et al. 2002). In the field, a prominent red blotch has often been observed on the lower middle corolla lobe of both *M. nasutus* (e.g., Pennell 1951; Kiang 1973) and some monkeyflowers with larger flowers than those of typical *M. nasutus*, but bearing resemblance to *M. nasutus* in shoot architecture and leaf morphology. This prominent red blotch has not been observed on **M. sookensis** flowers. The fact that the species described often had both larger flowers and a large red blotch suggests that they are either *M. nasutus* or hybrids between *M. guttatus* and *M. nasutus*. Third, there were some cases in which floral morphology differences were subtle, but differences in chromosome number existed, based on crossing studies and chromosome counts of Vickery (Campbell 1950; Mukherjee and Vickery 1962). In the special case of *Mimulus micranthus* A. Heller, it is defined in part by its endemism (Munz 1959). *Mimulus*

TABLE 2. LIST OF COLLECTIONS USED IN MEIOTIC CHROMOSOME COUNTS AND IN THE PREVIOUSLY PUBLISHED FLOW CYTOMETRY ANALYSES PRESENTED IN SWEIGART ET AL. (2008). Abbreviations: MCC, meiotic chromosome count; FC, flow cyometry.

| Collection | Taxon | Locale | Longitude | Latitude | Analyses |
|---|---|---|---|---|---|
| DRN (DEX) | *M. sookensis* | Dexter's Reservoir, OR, USA | −122.756 | 43.917 | FC |
| LSN | *M. sookensis* | Lowell, OR, USA | −122.784 | 43.930 | MCC, FC |
| NHI | *M. sookensis* | Nanoose Hill, VI, BC, CAN | −124.160 | 49.273 | MCC |
| ROG | *M. sookensis* | ca. 12 mi SE of Marial, (as the crow flies) OR, USA | −123.644 | 42.657 | MCC, FC |
| TRT | *M. nasutus* | near Troutdale, OR, USA | −122.368 | 45.520 | MCC |

*micranthus* is a diploid that has been used in multiple genetic analyses, and has been successfully crossed with other known diploids (Fenster and Ritland 1992, 1994; Ritland et al. 1993; Fenster et al. 1995). Last, we believe that the species described in some cases were possibly representative of phenotypic plasticity, the most noteable being *M. cuspidatus* Greene, found growing in shaded spots, with elongated internodes, and lack of anthocyanin spotting. In *Impatiens capensis* Meerb., this phenotype is known to be an adaptive plastic response (Schmitt et al. 1995; Dixon et al. 2001) that is characteristic of the classic shade avoidance syndrome (Smith 1982; Smith and Whitelam 1997). While it is not possible to directly test for plasticity in previously collected specimens, it seems highly plausible that many of the candidate taxa that we examined are representative of either phenotypic variation or plasticity in *M. nasutus* or *M. guttatus*. Grant (1924) noted that *M. nasutus* appeared to be quite a plastic species, and thus the taxa's earlier designations (e.g., Grant 1924; Pennell 1951) as synonyms are appropriate. Additionally, Kiang (1973) demonstrated that *Mimulus nasutus* is an exceptionally plastic species, as the flower size is dependent upon both external environmental conditions, and the position of the flower along the stem. It is also well known that *M. guttatus* harbors a great deal of phenotypic variation (reviewed in Wu et al. 2008).

## CYTOLOGICAL ANALYSIS

Meiotic counts of chromosomes were conducted to corroborate the previous indications of polyploidy as evidenced by flow cytometry (Table 2), crossing barriers, (Sweigart et al. 2008), and fixed heterozygosity at allozymes and sequenced nuclear loci (Benedict 1993; Sweigart et al. 2008). Three individuals, each from different collections considered to be **M. sookensis** (Table 2, LSN, NHI, ROG) were used for the chromosome counts. A single diploid *M. nasutus* individual (TRT) was also counted, for the purpose of comparing chromosome sizes. Immature flower buds were collected in a 3:1 95% ethanol:glacial acetic acid solution. The tissue was transferred to 70% ethanol after 24 hr and stored at −20°C until ready for use. Flower buds were then partially dissected in a 70% ethanol solution. The partially-dissected floral material was then transferred to a half-strength aceto-carmine solution, where all non-anther material was removed. Anthers were then transferred to a drop of aceto-carmine on a slide, and were eviscerated to release the pollen mother cells from the anthers. After thorough evisceration, the tissue was removed from the solution, and the slide was placed on a warming plate to facilitate staining. A drop of Hoyer's solution (Anderson 1954) was then added and the chromosomes were squashed by placing a coverslip over the solution and pressing down. Stained cells were examined with brightfield microscopy at 630–1000× magnification using a Zeiss Axioplan 2 microscope, and photographed at 1000× with a mounted Axiovision HR camera.

Meiotic chromosome counts revealed 28 distinct chromosome pairs in **M. sookensis** and 14 distinct chromosome pairs in diploid *M. nasutus* (Fig. 2). Although the sister chromatids are not easily distinguishable, it is clear from the chromosome squashes that there are twice as many of the chromosomes in **M. sookensis** as there are in diploid *M. nasutus*. This chromosome count constitutes the first published count for **M. sookensis**. Using these chromosome numbers as a calibration, we were able to confirm that the specimens used in the flow cytometry analysis of Sweigart et al (2008, Table 2) were indeed allotetraploid.

## TAXONOMIC TREATMENT

**Mimulus sookensis** B. G. Benedict, J. L. Modliszewski, A. L. Sweigart, N. H. Martin, F. R. Ganders, and J. H. Willis, sp. nov. —TYPE: CANADA, British Columbia, on a southwest facing, open, wet hillside in Sooke Potholes Provincial Park beside the Sooke River, elev. 75 m, 48°24′N 123°43′ W, 1 May 1991, *Benedict 28 V207976* (holotype: UBC).

Herba annua obligata, a *Mimulus guttatus* DC. Pistillo 5–13 mm longo, corolla 6–20 mm longa et pistillo calycem aequante vel paulo longiore

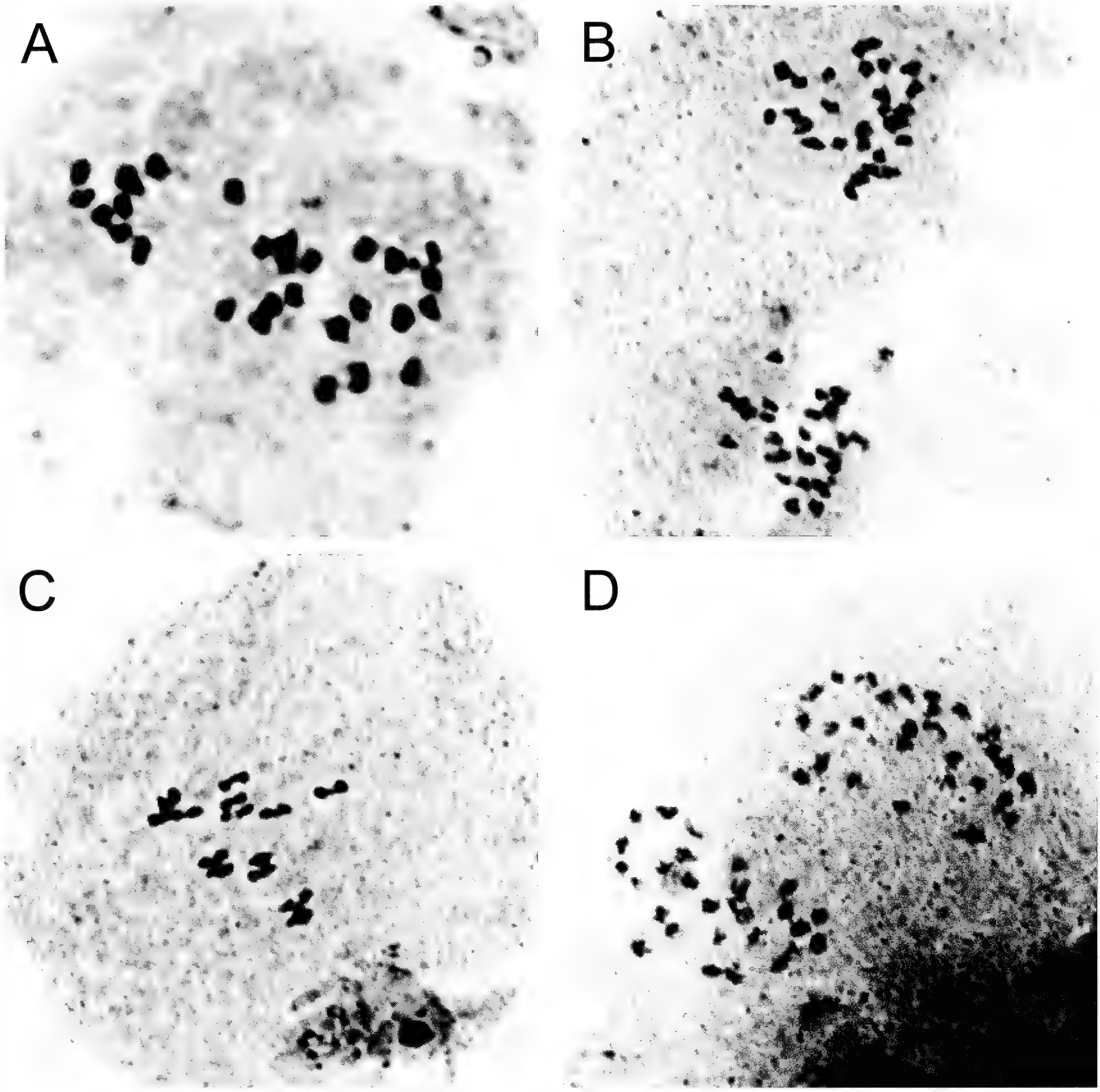

FIG. 2. Meiotic chromosome counts in *Mimulus.* A. *M. sookensis* (LSN), with 28 bivalents as seen in prophase I of meiosis. B. *M. sookensis* (NHI), shown with two daughter cells at late telophase I. Upper cell has 28 distinguishable univalents, while the lower cell has ca. 28 univalents. C. *M. nasutus* (TRT), with 14 bivalents at prophase I of meiosis. D. *M. sookensis* (ROG) as seen at late telophase I of meiosis,with two daughter cells each possessing 28 univalents.

differ; a foliis non bullatu, et caulus non alatis differ; planta tetraploidea.

Annual or winter annual herb, bearing opposite pedicillate basal leaves graduating into sessile cauline leaves, 5–25 cm high, glabrous to minutely pubescent. **Roots** fibrous. **Leaves** with leaf blade palmately veined, regularly denticulate, widely ovate, apex obtuse to acute, 0.5–3 × 0.5–2.5 cm becoming gradually reduced up the stem; leaf blade above adaxially green, frequently with anthocyanic spotting, glabrous to minutely pubescent, veins often purplish red near leafbase; leaf surface below abaxially silver-green to purple, glabrous, veins green. **Petiole** 0–2 cm long, green-white to red-white; glabrous. **Stems** tending to quadrangular but not winged, <2 mm wide. **Inflorescence** few flowered to racemose, terminal, with 1 primary raceme, occasional secondary racemes arising from leaf axils, flowers opposite in leaf axils. **Pedicel** 3–22 mm long, red, glabrous. **Calyx** 5–13 mm long, central adaxial calyx lobe longer than other four, green, often with anthocyanic spotting, white hairs on margin, somewhat inflated upon maturity. **Corolla** bilabiate or sometimes cleistogamous, 5–22 × 2–13 mm, yellow, corolla lobes subequal, palate densely hairy, red spotted, extending into tubes as two ridges, tube narrowly funnel shaped, 4–13 mm long. **Stamens** didynamous, upper stamens shorter, long stamens 4–12 mm. **Pistil** 5–13 mm; style white, minutely pubescent; stigma yellow, usually slightly exserted from calyx; ovary 2–5 mm, green; stipe 0–1 mm; stigma lobes may be thigmotropic. **Capsule** dehiscing by longitudinal slits with persistent style, crowned by a persistent calyx; lower calyx lobes curved upwards toward upper calyx lobe upon maturity. **Seeds** up to 300 per capsule, oval, brown, 0.5 × 0.2 mm. **Chromosome number** tetraploid, $n = 28$.

Found on wet, sunny, hillsides, cutbanks, and ditches on Vancouver Island and the Gulf Islands, British Columbia, on the San Juan Islands of Washington state, in the Willamette and Umqua River Valleys in Oregon, and also in one known site in Dos Rios, Mendocino Co., California, from sea level to 600 m. Flowers from late March to May.

The species is named after Sooke Potholes Provincial Park on Vancouver Island where it was found to grow abundantly and where the type specimen was collected. The common name shy monkeyflower is suggested, because this monkeyflower disguises itself as *M. nasutus*, and the flowers are small, in contrast to the 'gay' and gregarious flowers of *M. guttatus* (Vickery 1952).

## Additional *M. sookensis* Specimens Examined

CANADA. B.C.: Lasqueti Island, Trematon Mountain, 19 May 1985, *Ceska 19167* (V 144698); N. Pender Island, Oak Bluffs, 4 Apr 1983, *Ceska and Olgilve 14245* (V 133335); Saltspring Island, 5 1/2 km SW of Ganges, Lot 34, 18 April 1976, *Douglas 9716* (V 136977); Saltspring Island, clearing at the end of Isabella Road,18 May 1980, *Benedict 3* (UBC 207936); Mayne Island, Heck Hill, open bluff, 13 March 1980, *Janszen 1532* (V 107521) and 6 Apr 1979, *Janszen 978* (V 98035); Galiano Island, 12 May 1975, Wood 13 (V 97333); Galiano Island, west-facing slope overlooking ocean, Bluffs Park, 19 May 1993, *Benedict 35* (UBC 207931); Gabriola Island, 21 May 1951, *Raymer 5603135* (UBC 70999); Vancouver Island, Gonzales Hill near Victoria, April 1916, *Newcombe s.n.* (V 42590); Vancouver Island, Alberta Head, *Newcombe s.n.* (V 42592); Denman Island, wet cliffs facing Hornby Island, 7 Jul 1952, *Brink s.n.* (UBC 68843); Vancouver Island, Durrance Lake drainage on rock outcrop, 9 May 1963, *Young 63* (UBC 108599); Vancouver Island, Ucluelet, rocky ledges, 23 May 1975, *Rose 75-284* (UBC 177970); Vancouver Island, Anderson Hill in Victoria, 17 May 1950, *Krajina and Spilsbury s.n.* (UBC 55012); Vancouver Island, Mount Wells, 8 mi W of Victoria on moist rocky cliffs, 12 May 1975, *Calder and Taylor 20776* (UBC 80960); Vancouver Island, Esquimalt, 17 Apr 1917, *Darling s.n.* (UBC 45840); Vancouver Island, Victoria, 4 March 1912, *Henry s.n.* (UBC 80455); W slope of Mount Maxwell, Saltspring Island, 15 May 1963, *Young 159* (UBC 221634); Vancouver Island, 5 km N of Cowichan Lake, 19 May 1990, *Benedict 4* (UBC 207937); Vancouver Island, Nanoose Hill, N of Nanaimo, 1 May 1990, *Benedict 1* (UBC 207934); Vancouver Island, Finlayson Arm Road, near Goldstream Provincial Park, 17 May 1990, *Benedict 2* (UBC 207910); Vancouver Island, south slope of Observatory Hill, Saanich Peninsula,1 May 1991, *Benedict 27* (UBC 207935). USA. OREGON. **Josephine Co.**: above Rogue River 0.7 km W of entrance to Indian Mary Park, 3 May 1993, *Strayley 7506* (UBC 208478); N of Grant's Pass near South Hill summit, 13 Apr 1991, *Benedict 23* (UBC 208138). **Lane Co.**: S facing road cut on N side of Dorena Lake, 6 Apr 1991, *Benedict 11* (UBC 207932); **Douglas Co.**: Umpqua River Valley, 6 Apr 1991, *Benedict 26* (UBC 207995); Umpqua Valley, Roseburg Quadrangle, July 1914 *Cusick 4178a,* (UBC 149306); Umpqua River, 21 mi below Umpqua, 20 May 1954, *Steward 6641,* (UBC 197132). WASHINGTON. **San Juan Co.**: rock outcropping on Orcas Isl., 13 Apr 1975, *Gates 4,* (UBC 263239).

Gabriola Island, 21 May 1951, *Raymer s.n.* (UBC 5603135).

## Features Distinguishing *M. sookensis* and *M. nasutus*

*Mimulus sookensis* is exceedingly similar in floral morphology to *M. nasutus* (Fig. 1). All characters overlap to a degree with *M. nasutus*, but under favorable growth conditions, the following structures tend to be more reduced in *M. sookensis* (*M. nasutus* measurements are presented here in parentheses): stem width $<1$ mm ($<4$ mm), calyx length 5–13 mm (6–16.5 mm), leaves 0.5–3 × 0.5–2.5 mm (0.5–10 × 0.5–7.5 mm), height 3–25 cm (5–50 cm), pedicel length 3–22 mm (4–26 mm), stipe length 0–1 mm (0.5–2 mm). *Mimulus sookensis* tends to have a longer pistil relative to its calyx and the difference in calyx and pistil lengths range from 2.5–3.5 mm (0–6 mm). The ratio of the width of the flower to the base *in M. nasutus* is usually $>2$ ($<2$). *Mimulus nasutus* often tends to have a more sharply angled and winged stem and the leaves are often bullate, while *M. sookensis* tends to have anthocyanic red spotting on the calyx more frequently than *M. nasutus*.

## Relationships and Distribution

The genus *Mimulus* contains well over 100 species of monkeyflowers, and within the Simiolus clade, there are approximately 16–24 species, including *M. guttatus*, *M. nasutus*, and *M. sookensis* (Grant 1924; Pennell 1951). Comparable to the

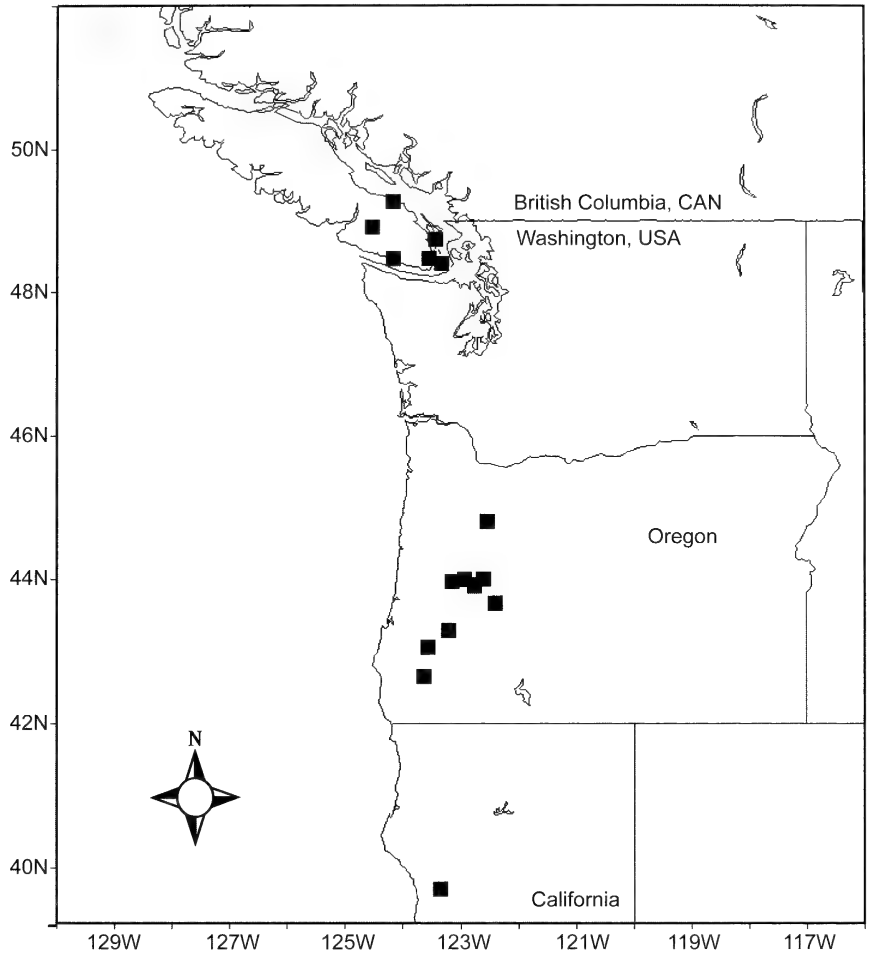

FIG. 3. Geographic distribution of *M. sookensis* in western North America, with filled squares indicating locations in which *M. sookensis* has been recorded.

rest of the genus, *M. guttatus* and its close allies are an exceedingly phenotypically and ecologically diverse group, making the *M. guttatus* complex and its close relatives an attractive system for ecological and evolutionary studies (Wu et al. 2008). Consequently, defining species relationships in this group of closely related monkeyflowers is challenging. As defined by Vickery (1978), the *M. guttatus* species complex is comprised of the common yellow monkeyflower, *M. guttatus*, and its close relatives, *M. nasutus*, *M. laciniatus* A. Gray, *M. platycalyx* Pennell, and *M. glaucescens* Greene. Pennell (1951) included a number of other taxa in the complex, including *M. nudatus* Curran, a linear-leaved serpentine endemic, and *M. pardalis* Pennell, a distinct form of monkeyflower with a prominently purple-spotted calyx, thought to be closely related to *M. nasutus* (Pennell 1947). A copper mine endemic, *M. cupriphilus* McNair, was later included in the complex (McNair 1989). Wu et al. (2008) recognize *M. guttatus*, *M. nasutus*, *M. laciniatus*, *M. platycalyx*, *M. glaucescens*, *M. cupriphilus*, and *M. nudatus* as members of the *M. guttatus* complex at the rank of species. We suggest the addition of *M. sookensis* to this species complex.

Based on present observations, it appears that *M. sookensis* is characterized by a disjunct distribution. In the northern portion of its range, *M. sookensis* is found throughout the southern end of Vancouver Island, British Columbia, in the Gulf Islands of British Columbia, including but not limited to Saltspring, Mayne, Galiano, Denman, Lasqueti, and Pender Island, and also on the San Juan Islands of Washington (Fig. 3). In the southern portion of its range, *M. sookensis* is found in the Willamette and Umpqua River Valleys of Oregon, and also in northern California. In Oregon and California, collections are known from as far north as Mehama, in Marion Co., Oregon, and as far south as Dos Rios, in Mendocino Co., California (Fig. 3). It is conceivable that many more undiscovered *M.*

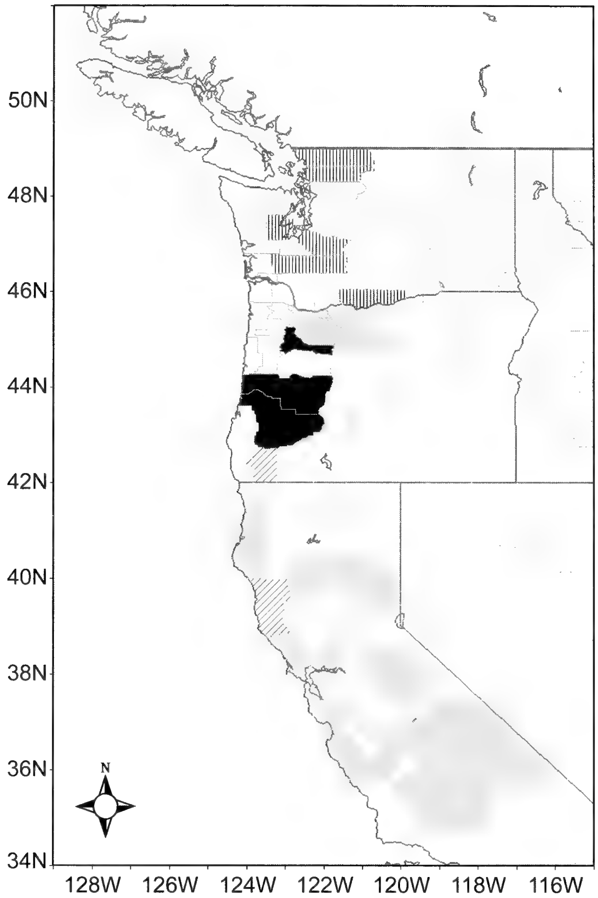

FIG. 4. Approximate location of *M. nasutus, M. guttatus*, and *M. sookensis* throughout western Washington, western Oregon, and California. U.S. counties where *M. sookensis* but not *M. nasutus* has been observed are filled in black, counties where *M. nasutus* but not *M. sookensis* has been observed are filled in grey, while counties where both species have been observed have diagonal hatching. Counties where *M. guttatus* has been observed in Washington are indicated with vertical hatching.

*sookensis* localities exist throughout the northern and southern portion of its range.

To illustrate the extent of field observations, which suggest an absence or rarity of *M. sookensis* throughout much of California, we have recorded the locations of *M. nasutus* collected in California (Fig. 4) that were used in either crossing, genetic, or flow cytometry analyses (see Table 3 and references therein). If *M. sookensis* existed further south of Dos Rios, it is likely that it would have been mistakenly collected as *M. nasutus*, and subsequent analyses would have revealed its tetraploid nature. In mainland Washington state, no *M. sookensis* have been observed to date. Kiang and Hamrick (1978) were unable to find any *M. nasutus* in the Cascades of northern California, Oregon, and Washington. Additional evidence, based on recent collections in Washington state, suggests *M. nasutus* is rare in Washington, unlike *M. guttatus* (D. Lowry, Univ. of Texas-Austin, and C. Wu, Univ. of Richmond, personal communication). At many *M. guttatus* sites in Washington, neither *M. nasutus* nor *M. sookensis* has been observed (Fig. 4). This pattern suggests that both *M. nasutus* and *M. sookensis* may be rare in Washington state, or at the very least, that *M. guttatus* and *M. nasutus* do not commonly co-occur in this region, to our knowledge. If the rarity of co-occurrence of the two progenitor taxa in Washington state is a real phenomenon and not an artifact of sampling, the limited opportunities for hybridization between *M. guttatus* and *M. nasutus* in this region may in part explain the fact that *M. sookensis* is even more rare than *M. nasutus* in this region, and perhaps does not occur at all.

We cannot exclude the possibility that isolated or ephemeral allotetraploids derived from *M. guttatus* and *M. nasutus* are found elsewhere where *M. guttatus* and *M. nasutus* co-occur and may potentially hybridize. However, determining the exact range limits of *M. sookensis* is beyond the scope of this paper, and we present here simply what is known at this time regarding the

TABLE 3. LIST OF LOCALES USED TO ILLUSTRATE LOCATIONS OF *M. NASUTUS, M. SOOKENSIS*, AND *M. GUTTATUS*, THAT HAVE BEEN CONFIRMED TO BE OF DIPLOID OR TETRAPLOID NATURE, THROUGH EITHER GENETIC ANALYSES, CROSSING EXPERIMENTS, CHROMOSOME COUNTS, OR FLOW CYTOMETRY. The locale ID may refer to: 1) the culture number given in a published chromosome count, 2) an examined herbarium specimen accession number or collector number, or 3) the ID given to the locale when published. Abbreviations used: na = not applicable.

| Species | Locale ID | County, State | Reference |
|---|---|---|---|
| *M. nasutus* | 16 | Calaveras Co., CA | Benedict 1993 |
| | KIN | Fresno Co., CA | Sweigart and Willis 2003; Sweigart et al. 2007 |
| | SNF | Fresno Co., CA | Sweigart and Willis 2003 |
| | na | Fresno Co., CA | Kiang and Hamrick 1978 |
| | KNR | Humboldt Co., CA | Modliszewski and Willis (unpublished data) |
| | Cult. No. 6060 | Inyo Co., CA | Mia et al. 1964 |
| | na | Kern Co., CA | Kiang and Hamrick 1978 |
| | BRI | Mariposa Co., CA | Sweigart and Willis 2003; Sweigart et al. 2007 |
| | na | Mariposa Co., CA | Kiang and Hamrick 1978 |
| | NDR2 | Mendocino Co., CA | Sweigart and Willis 2003; Martin and Willis 2010 |
| | SHI | Mendocino Co., CA | Modliszewski and Willis (unpublished data) |
| | Cult. No. 5044 | Monterey Co., CA | Vickery 1955 |
| | na | Plumas Co., CA | Kiang and Hamrick 1978 |
| | MHA | Santa Clara Co., CA | Modliszewski and Willis (unpublished data) |
| | Cult. No. 5751 | Santa Clara Co., CA | Vickery 1964 |
| | NBC | Santa Cruz Co., CA | Sweigart and Willis 2003 |
| | na | Sierra Co., CA | Kiang and Hamrick 1978 |
| | NMD | Solano Co., CA | Sweigart and Willis 2003 |
| | CMF | Sonoma Co., CA | Modliszewski and Willis (unpublished data) |
| | KRR | Sonoma Co., CA | Modliszewski and Willis (unpublished data) |
| | Cult. No. 5865 | Sonoma Co., CA | McArthur et al. 1972 |
| | M12 | Tehama Co., CA | Sweigart and Willis 2003; Sweigart et al. 2007 |
| | TOK | Tulare Co., CA | Sweigart and Willis 2003 |
| | na | Tulare Co., CA | Kiang and Hamrick 1978 |
| | Cult. No. 5327 | Tuolumne Co., CA | Mukherjee and Vickery 1962; n = 13 |
| | NDP | Tuolumne Co., CA | Sweigart and Willis 2003; Martin and Willis 2010 |
| | MEN | Tuolumne Co., CA | Sweigart and Willis 2003; Martin and Willis 2010 |
| | NCL | Tuolumne Co., CA | Sweigart and Willis 2003; Sweigart et al. 2007 |
| | NFN | Clackamas Co., OR | Modliszewski and Willis (unpublished data) |
| | HCN | Josephine Co., OR | Modliszewski and Willis (unpublished data) |
| | TRT | Multnomah Co., OR | See text |
| | SF | Wasco Co., OR | Fishman and Willis 2001; Sweigart and Willis 2003; Martin and Willis 2010 |
| | WSK | Klickitat Co., WA | Modliszewski and Willis (unpublished data) |
| | CLR | Klickitat Co., WA | Sweigart and Willis 2003; Sweigart et al. 2007 |
| *M. sookensis* | BVN | Douglas Co., OR | Fig. 3 |
| | WBP | Douglas Co., OR | Fig. 3 |
| | Benedict 207995 | Douglas Co., OR | See text |
| | ROG | Josephine Co., OR | See text; Sweigart et al. 2008 |
| | Strayley 208478 | Josephine Co., OR | See text |
| | Benedict 208138 | Josephine Co., OR | See text |
| | DRN | Lane Co., OR | Sweigart et al. 2008 |
| | HIL | Lane Co., OR | Fig. 3 |
| | LSN | Lane Co., OR | See text; Sweigart et al. 2008 |
| | PSG | Lane Co., OR | Sweigart and Willis 2003; Sweigart et al. 2008 |
| | SPB | Lane Co., OR | Sweigart et al. 2008 |
| | Benedict 207932 | Lane Co., OR | See text |
| | SAN | Marion Co., OR | Fig. 3 |
| | WTU 263239 | San Juan Co., WA | See text |
| | NDR | Mendocino Co., CA | Sweigart and Willis 2003; Sweigart et al. 2008 |
| *M. guttatus* | WSKG | Klickitat Co., WA | Modliszewski and Willis (unpublished data) |
| | RFA | Lewis Co., WA | Modliszewski and Willis (unpublished data) |
| | HAM | Mason Co., WA | C. Wu, personal communication |
| | HOC | Mason Co., WA | D. Lowry, personal communication |
| | CHR | Pierce Co., WA | C. Wu, personal communication |
| | AWP | Skagit Co., WA | Modliszewski and Willis (unpublished data) |
| | NCG | Whatcom Co., WA | Modliszewski and Willis (unpublished data) |

distribution of *M. sookensis* based on current collections.

Interestingly, while *M. sookensis* commonly co-occurs with *M. guttatus* throughout its range, with few exceptions, in habitats where M. *sookensis* is present, *M. nasutus* tends to be absent. *Mimulus nasutus* and *M. sookensis* are known to co-occur at only two locations. Although Vancouver Island is at the northern limit of the range of *M. nasutus*, it is found to co-occur with *M. sookensis* at one site on the southern end of Vancouver Island (Nanoose Hill). This site is at a lower elevation than many of the other locations on Vancouver Island where only *M. sookensis* was observed (Fig. 3, Benedict 1993). The second site is along the Rogue River in southern Oregon; other *M. nasutus* sites have also been found in this region (Table 3). Additionally, at the southern periphery of the range of *M. sookensis* near Dos Rios, California, *M. nasutus* and *M. sookensis* are found within ca. 3 km of one another, but not within the same collection locale (Sweigart and Willis 2003). At present, there is insufficient evidence to determine whether or not the apparent absence of *M. nasutus* at many of the *M. sookensis* collection locales is a historical artifact or if the relative rarity of co-occurrence is caused by some unknown biological or abiological factor.

## Discussion

Within just the Simiolus clade of the genus *Mimulus*, there are over 21 well-documented occurences of polyploidy or aneuploidy (reviewed in Beardsley et al. 2004). The *Mimulus glabratus* heteroploid species complex in the Simiolus clade is characterized by ploidal races that are distributed across a north-south latitudinal gradient (McArthur et al. 1972). Crossing barriers exist both between ploidal races, and to varying extents, within ploidal races (Alam and Vickery 1973; Vickery et al. 1976).

Here, together with data from previous publications (Fig. 2; Table 2; Sweigart et al. 2008), we have presented evidence of another instance of polyploid speciation–the previously undescribed *M. sookensis*. Although the triploid block is not absolutely complete between *M. sookensis* and its diploid progenitors, a triploid bridge is not likely to contribute significantly to gene flow or polyploid formation in a selfing taxa (Ramsey and Schemske 1998). Vickery found many other forms of polyploid and aneuploid monkeyflowers in the *M. guttatus* species complex during the course of his extensive cytogenetic work in *Mimulus*, but no record exists of *M. sookensis* (Mukherjee and Vickery 1959, 1960, 1962; Mia et al. 1964; Mia and Vickery 1968; Vickery et al. 1968; McArthur et al. 1972). Most of the autotetraploid *M. guttatus* that Vickery found were in the southwestern U.S. (Arizona, Colorado, New Mexico, and Utah) and Mexico or in Alaska, but one autotetraploid *M. guttatus* was found in Multnomah Falls, near Portland, Oregon. This individual was likely not *M. sookensis*, since Vickery's identification indicates that it bore more resemblance to *M. guttatus* than *M. nasutus*. Within the *M. guttatus* species complex, the autotetraploid *M. guttatus* subsp. *haidensis* Calder and Taylor is a distinct form of *M. guttatus* endemic to the Haida Gwaii (Queen Charlotte Islands) of British Columbia, Canada. Despite these autotetraploid forms of *M. guttatus*, *M. sookensis* will continue to remain a distinct species, due to the fact that the progeny of a cross between autotetraploids and allotetraploids will be tetraploid, and any backcrossing with a diploid will occur in the direction of the outcrossing species (*M. guttatus*), not the selfing species (*M. sookensis*). These backcross progeny, if existent, will likely be inviable or infertile, as was shown in Sweigart et al. (2008). Additionally, data from nuclear genes (Sweigart et al. 2008) does not show loss of *M. nasutus* gene copies, which would be expected if hybridization with autotetraploid *M. guttatus* had occurred.

The newly described *M. sookensis* is broadly distributed in scattered locations throughout the valleys of western Oregon and northern California, and also on the southern tip of Vancouver Island and the Gulf Islands of British Columbia and San Juan Islands of Washington. The seemingly disjunct distribution of *M. sookensis* raises the question as to whether or not the distribution is actually discontinuous, or if *M. sookensis* exists undiscovered in Washington; further field work in Washington could help to determine if the observed distribution is real. Data from plants of the Pacific Northwest suggest that the glaciations of the Pleistocene created discontinuous distributions that were later recolonized (Soltis et al. 1997). If *M. sookensis* formed post-Pleistocene glaciation events, it may be that *M. nasutus* has yet to extensively recolonize Washington state, in contrast to the more common *M. guttatus*, and that the rarity of *M. nasutus* in Washington has contributed to more extreme rarity of *M. sookensis* in Washington. If *M. sookensis* formed throughout the Pacific Northwest prior to Pleistocene glaciations, it may have existed in glacial refugia on Vancouver Island and Oregon (Soltis et al. 1997; Brunsfield et al. 2001; Shafer et al. 2010), and has not yet extensively recolonized Washington.

Of final note is the observation that *Mimulus sookensis* from different collection locations all appear to be phenotypically quite similar to *M. nasutus*. It would be interesting to know if *M. sookensis* was formed by multiple polyploidization events, as suggested by sequences from one of two nuclear genes sequenced to date (Sweigart et al. 2008), or if individuals from as far apart as British Columbia and California originated once, and then spread geographically to occupy their current distribution. If *M. sookensis* was indeed formed by multiple allopolyploidization events, as is common among polyploid plants (Soltis and Soltis 1993, 1999) it would be of great interest to know how these interspecific polyploid hybrids between *M. guttatus* and *M. nasutus* all came to have the appearance of *M. nasutus*.

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# REVIEW

*Northwest California: A Natural History.* By JOHN O. SAWYER. 2006. University of California Press, Berkeley, CA. 264 pp. ISBN 9780520232860, $75.00, hardcover.

In this authoritative but refreshingly slim volume, veteran botanist and plant ecologist John Sawyer describes the majestic landscapes and natural inhabitants of northwest California, an area that has occupied most of his professional career. Dr. Sawyer is an engaging and confident guide through the varied landscapes of northwest California, expertly weaving together physical and biological patterns with environmental and human history.

As the author says in the opening pages, the book is not an encyclopedia of organisms of northwest California. Rather, it is a tour of an ancient and complex region that is at once at the edge of a state and a center of biodiversity in the western United States. The book is laid out in broad themes, first describing the geography of the region, next exploring major ecological themes in sequence, including patterns in vegetation, environmental history, the evolution of species diversity, fire regimes and other agents of change, and the current and future conservation status of the region. The book is an integration of a lifetime of ecological study and learning. One cannot study botany without becoming at least a little curious about geology, environmental history, and the effects of humans on the land, and Dr. Sawyer discusses all of these topics with uncommon ease and authority. Lovers of wildlife, on the other hand, may find this volume less rich than it could be, but will still find useful insights and information.

Even the most casual visitor will notice that northwest California is diverse in its climates, landscapes, and vegetation types, so one must break up the landscape to discuss its natural history. The book takes the approach of dividing northwest California into two geologic regions, then into smaller landscape units called countries (e.g., the middle Sacramento country). The latter is unconventional, but appealing in its informality and descriptiveness. This framework is used throughout the book to describe the various ecological phenomena, from geology to vegetation to disturbance regimes.

For lovers of botanical nuts and bolts, this is no regional manual, but the author does provide broad floristic information and species lists for selected habitats. He begins by presenting a counterintuitive but interesting and, I believe, accurate view of the regional vegetation patterns. Despite its well-known floristic diversity, he describes the region as being dominated by several climatic and elevationally driven zones that are dominated by just seven tree species. Upon this broad and deceptively simple canvas, however, subordinate species and hydrology, geology, and disturbance-associated microhabitats build impressive floristic detail. Moving from the general to the more specific, the book tells us of the major tree and shrub species in different ecological zones of the region, then adds greater detail along with descriptions of selected habitats, such as montane and subalpine meadows, serpentine and limestone outcrop areas, coastal environments, and wetland and riparian zones. Some descriptions are tantalizing. I personally cannot wait to see the "outrageous shrub diversity" on the Hosselkus Limestone of Shasta County.

For decades, northwest California has been plagued by divisive perspectives on the effects of land use. However, Dr. Sawyer brings an unusually informed and moderate view to discussions of forest management and the ecology of fire. Rather than providing hackneyed and ideological arguments for or against logging or fuels restoration, he often uses the findings from a surprisingly rich pool of primary studies in the region conducted by himself and his many student colleagues at Humboldt State University. (Graciously, he credits the students first when describing such collaborative projects.) The findings are very interesting and surprising. For instance, most Californians probably envision northwest California as a land of ancient and timeless forests, yet the author's synthesis of paleoecology and disturbance ecology paints a story of a dynamic region that has rarely been in equilibrium, despite the venerable ages of some of its trees. Many seemingly ageless forest communities have existed for just a few thousand years. Moreover, particular forest stands may owe their complexity not just to their age, but to a history of patchy fires. Still other forests may be surprisingly young and very different from the landscapes experienced and managed by the region's native peoples just a couple of centuries ago.

Visually, I found the book to be a bit wanting due to the decision to collect all the plates in the middle of the volume. The images themselves are lovely and descriptive, however. Also, the maps of each "country" in the opening chapters are exceedingly plain, consisting of a simple silver digital elevation model with a black polygon delineating the area of interest. Drawings or other illustrations are infrequent and unadorned.

Nor does the writing in the book reach the artistic heights that readers have enjoyed in the writings of some California naturalists like John Muir, David Rains Wallace, or Elna Bakker. Nonetheless, the prose is well-crafted and enjoyable.

Despite these modest shortcomings, the book should be a valuable resource to anyone interested in the ecology of northwest California. It summarizes over four decades of original research in a highly readable narrative, with sufficient tables and sources to serve as a useful reference. This slim, but substantive, book provides a great introduction to the general geography and ecology of the region and provides many interesting tidbits for those already living and working there. It would undoubtedly be a good backpacking companion to be savored by a campfire somewhere in the wilds of northwest California. The price, however, at $75 for hardcover, might give pause to the zealous but cash poor.

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