

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 (Podrutzny 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 km² (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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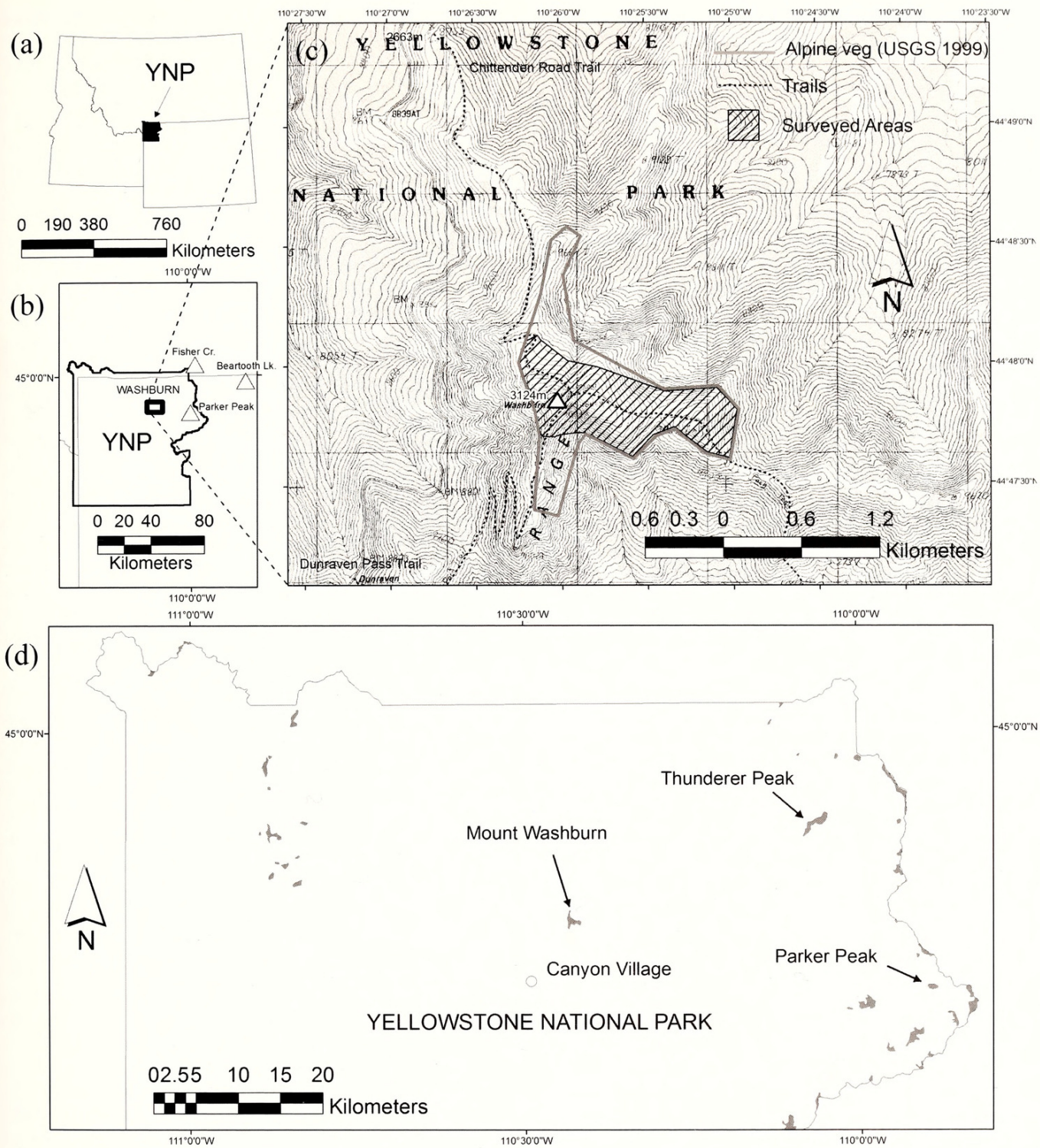


FIG. 1. Maps of study area. (a) Overview of Yellowstone National Park (YNP) with respect to Montana, Wyoming, and Idaho. (b) View of YNP showing the Washburn study area and three locations for which year-round alpine weather data is available. (c) Close up view of Washburn summit. The extent of Washburn 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 km²), 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., $<800 \text{ mm yr}^{-1}$). The mean frost-free season length (number of days with min temps $>0^{\circ}\text{C}$) 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 ($>50 \text{ km}$ for Washburn, and $<5 \text{ km}$ for the other two ranges; Aho 2006). Each plot consisted of ten $20 \times 50 \text{ cm}$ 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 non-prostrate 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*-*Astragalus 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 co-occur 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.) Rehb., 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 sub-alpine 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*

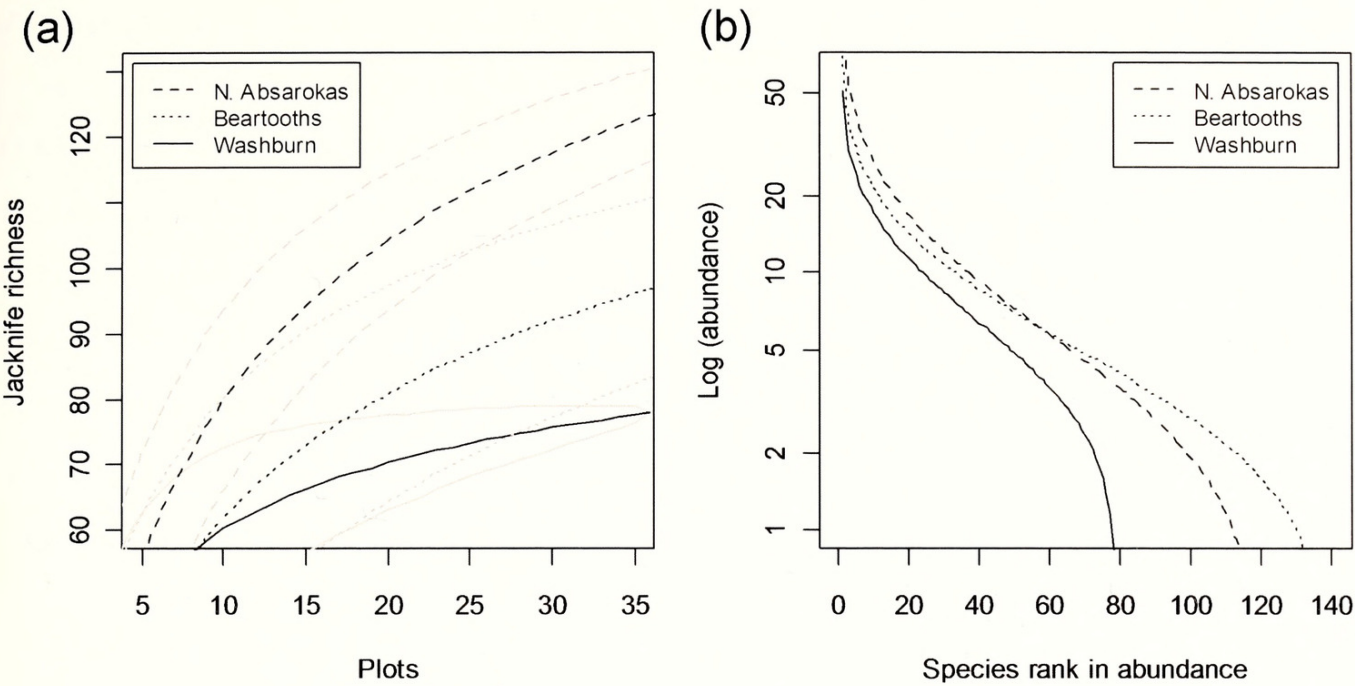


FIG. 2. Biogeographic analyses for the Washburn Range, nine mountains in the N. Absaroka-Volcanics, and six mountains on the Beartooth Plateau. (a) Species area curves from a first order jackknife procedure. Gray lines are 95% confidence intervals. (b) Rank abundance dominance (RAD) curves. Abundance 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 *Besseyia 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. unpublished). 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. unpublished), 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. [Aho 268 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 alpinum (Torr. & A. Gray.) Greene var. *haydenii* (Porter) Nesom. [Aho 249 YELLO]; unco, abund, dry to moist, *sm*, *dtf*, native (was *Aster alpinus*)

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
Symphotrichum 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. [Aho 540 IDS]; unco, abund, wet, *ta*, *sm*, native

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

Parnassiaceae

Parnassia fimbriata K. D. König [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

- Besseyia 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 wormskejoldii 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

ACKNOWLEDGMENTS

This research was made possible in part with a grant from the National Park Service (YNP-NPS #YELL-05116) and by assistantships from Montana State University. Thanks to M. Hektner (YNP-NPS), H. Anderson, J. Whipple (YELLO), T. Weaver, T. Seipel (MSU), and C. Seibert and M. Lavin (MONT).

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