MacFarlane's Four-O'clock in Hells Canyon of the Snake River

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Robust specimen of *Mirabilis macfarlanei*. Photo by Gene Yates.

MacFarlane's four-o'clock (*Mirabilis macfarlanei* Constance and Rollins), a rare, beautiful perennial, is narrowly endemic to a small range (46 by 29 km) in northeastern Oregon and adjacent west central Idaho. Many species in the genus *Mirabilis* are called four-o'clocks because their flowers open during late afternoon. *Mirabilis macfarlanei* is an exception to this pattern. Its rarity and geographic isolation may have selected for flowers open throughout the day and other adaptations that set it apart from other four-o'clocks.

Endangered Status

Mirabilis macfarlanei, currently listed as threatened under the Endangered Species Act (ESA), was first listed in 1979 as endangered, a more dire status, when only three populations totaling 20 to 25 plants were known. These populations were threatened by several factors: trampling, collecting, livestock grazing, disease and insect damage (USFWS 2000). Since then, the Idaho Conservation Data Center, US Fish and Wildlife Service (USFWS), Bureau of Land Management (BLM) and Forest Service have jointly conducted inventories in the range of the four-o'clock and discovered several additional populations harboring thousands of plants. Many of these new discoveries are located on lands managed by the BLM and Forest Service.

Currently, there are eleven known populations: six in the Salmon River canyon, three in the Hells Canyon of the Snake River, and two in the lower Imnaha River canyon. One Hells Canyon population is quite large, with hundreds plants growing in eight distinct patches. Of the four populations in Oregon, three are on federal lands within the Hells Canyon National Recreation Area. The fourth site is privately owned within the Recreation Area. In Idaho, almost half of the *M. macfarlanei*

populations grow on Forest Service or BLM administered lands; the remainder are on private land. This is worth noting because, in contrast to animal species, the ESA does not mandate protection of threatened or endangered plants growing on privately owned lands. Conservation measures undertaken by private landholders are wholly voluntary. The discovery of additional populations, plus conservation actions instituted on Forest Service and BLM sites, prompted the USFWS in 1996 to reclassify *M. macfarlanei* from endangered to threatened status.

Brief Description and Life History

Mirabilis macfarlanei grows in long-lived colonies, with herbaceous stems that emerge from a deep-seated, tuberous-thickened rhizome to form hemispheric clumps up to 1 m broad. Rarely, clumps reach a full meter in height. The broadly obtuse to ovate leaves are somewhat succulent, deep green above, glaucescent below, entire, 2.5 to 7.5 cm long, and about as wide, and progressively reduced and relatively narrower up the stem. A member of the family Nyctaginaceae, *M. macfarlanei* has a hypogynous flower (ovary superior) that lacks a corolla. The petaloid calyx, however, is strikingly showy: five sepals united into a brilliant rose-magenta funnel 1.5 to 2.5 cm long with a 1 to 3 cm broad limb. The stamens are slightly exserted, and the style extends 4 to 5 mm farther, positioning the stigma well beyond the reach of the anthers. Involucrate clusters of 4 to 7 flowers are borne in the axils of upper leaves.[1] Each flower produces one fruit, a 6 to 9 mm ellipsoid achene

The name *Mirabilis* comes from Latin meaning wonderful, a reference to the showy flowers that typify this genus. Large specimens in full bloom are indeed wonderful: broad, thigh-deep mounds of emerald green emblazoned with hundreds of brilliant magenta flowers. The specific epithet acknowledges Ed MacFarlane, the Snake River boat pilot who pointed out the plant to Lincoln Constance and Reed Rollins (see sidebar on page 5).

Around late March herbaceous stems emerge from the ground (Lowry pers. comm.). Flowering begins in mid-May and may continue until early June. The onset and duration of the bloom can vary by as much as one or two weeks. Annual variation in floral phenology is likely related to variations in temperature and precipitation, with warm, damp springs resulting in earlier flowering (Kaye and Meinke 1992). Within each cluster, flowers open sequentially and each remains open for only one day, so that each inflorescence usually displays only one, or occasionally two, open flowers at a time (Barnes 1996).

Habitat

Mirabilis macfarlanei inhabits the warm, dry canyon grasslands of the Snake, Salmon, and Imnaha Rivers on slopes between 300 and 900 meters elevation. Less than 305 mm of precipitation fall annually in these arid locales (Tisdale 1986). Habitat and associated species vary among populations. The beautiful fuzzy-tongue penstemon (*Penstemon eriantherus* var. *redactus*) is a faithful companion at most sites. Many *M. macfarlanei* sites are dominated by bluebunch wheatgrass (*Pseudoroegneria spicata*), although sparse, compared to the lush cover in stands of bluebunch wheatgrass found elsewhere in Hells Canyon. The more arid sites support strict buckwheat (*Eriogonum strictum* var. *proliferum*), hoary chaenactis (*Chaenactis douglasii* var. *glandulosa*) and prickly-pear cactus (*Opuntia polyacantha*). Two warm season grasses, sand dropseed (*Sporobolus cryptandrus*) and red three-awn (*Aristida purpurea var. longiseta*) accompany a few populations of *M. macfarlanei* at lower elevations. An unusual habitat is the one in which *M. macfarlanei* grows under and around a canopy of smooth sumac (*Rhus glabra*). The highest elevation population grows in a community of greenbush (*Glossopetalon spinescens var. aridum*), curl-leaf mountain mahogany (*Cercocarpus ledifolius*), sparse bluebunch wheatgrass and Oregon twinpod (*Physaria oregana*) on a steep southerly slope of sand, gravels and scree derived from Triassic age mudstone. Two infrequent associates include a brilliant yellow form of the clustered broom-rape (*Orobanche fasciculata*) and pallid milkvetch (*Asclepias cryptoceras*).

Bluebunch wheatgrass (*Pseudoroegneria spicata*) dominates plant cover at this *Mirabilis macfarlanei* site (scarcely visible as darker texture at lower right). Nearly all the *Mirabilis* growing at this ecologically vibrant site is obscured by the grass. Photo by Gene Yates.

Mirabilis macfarlanei habitat (in foreground) on steep southerly slope with bluebunch wheatgrass (*Pseudoroegneria spicata*), spiny green bush (*Glossopetalon spinescens* var. *aridum*) and curl-leaf mountain mahogany (*Cercocarpus ledifolius*). Photo by Gene Yates.

Biogeography

Mirabilis macfarlanei is widely distanced from its two closest relatives, *M. multiflora* var. *glandulosa* (growing 480 km to the south in Nevada) and *M. greenei*, (560 km southwest in California). During a past warmer climate, prior to the Pleistocene, *M. macfarlanei* may have been more widespread. With the onset of climatic cooling and a southward migration of most North American *Mirabilis*, *M. macfarlanei*, or its progenitor, likely found a refuge in the warm, dry canyons of the Snake and Salmon Rivers (Barnes 1996). The climate and environmental conditions at lower elevation in these canyons are similar to the environment where its related congeners (its fellow four-o'clocks) are found, and contrast sharply with conditions in the surrounding mountainous terrain. Canyon grasslands are characterized by a mild winter climate with hot, dry summers that rank among the longest growing seasons in the intermountain West (Johnson 1984). Other examples of disjunct southern xerothermic plants in Hells Canyon are netleaf hackberry (*Celtis reticulata*), spiny green-bush (*Glossopetalon spinescens* var. *aridum*) and smooth sumac (*Rhus glabra*). And, though neither disjunct nor endemic to this region, prickly-pear cactus (*Opuntia polyacantha*) is abundant in the lower elevations Hells Canyon, another acute reminder of this hot, arid climate

In addition, populations of *Mirabilis macfarlanei* in the three major drainages of the Snake, Salmon and Imnaha Rivers are more or less disjunct from each other. Jennifer Barnes (1996) studied genetic differences among the populations. Generally, *M. macfarlanei* exhibits low genetic diversity among populations, but Barnes found that genetic differentiation increased with distance between populations. As expected, populations in a given river canyon, e.g., the Salmon River, are more closely related to one another than to populations in either the Snake or Imnaha Rivers. The Imnaha River populations appear to have been isolated first; the Snake and Salmon River populations appear to have separated more recently. Currently little gene flow is evident between populations; thus isolation and small population size may be perpetuating low levels of genetic diversity.

Population Biology

Mirabilis macfarlanei forms colonies that grow from extensive lateral roots that produce thick tubers that are usually from 4 to 8 cm in diameter by 25 to 35 cm long. One large specimen was 13 cm in diameter and 43 cm long. Roots are about 1 to 1.5 cm in diameter (Lowry pers. comm.). They are usually shorter than 2 m, but can extend to 10 m. Barnes (1996) mapped *M. macfarlanei* clones at

Mirabilis macfarlanei growing with prickly pear cactus (*Opuntia polyacantha*), bluebunch wheatgrass (*Pseudoroegneria spicata*) and yarrow (*Achillea millefolium*). Photo by Gene Yates.

three sites from the Imnaha and Snake River populations and found an average of about five ramets (individual stems) per clone (genet). Mapping of three Salmon River populations produced quite different results: first, several genets had only one ramet (plants with no apparent vegetative spread); second, there was more variation between populations in the number of ramets per genet. Because the number of ramets varies from year to year, presumably in response to environmental factors (especially precipitation), Barnes *et al.* (1997) cautioned against the use of ramet counts to estimate population size.

Most populations, except the smallest, contain several genotypes. Vegetative spread has produced some colonies with intermixed growth patterns where lateral roots from different genets have grown amongst one another. Other colonies displayed less interclonal mixing; genet clumps were more or less separate. Barnes (1996) hypothesized that the colonial habit of *M. macfarlanei* would increase the amount of inbreeding, but her studies at one population found a high degree of outcrossing; slightly more than half the seeds were cross-pollinated. Because most populations comprise several genotypes, new plants have obviously been recruited via seed, but apparently quite slowly. This assumption is supported by a monitoring study by Kaye and Meinke (1992) who reported that seedlings were rare and did not survive long; 88% of seedlings died by their second year.

Pollination

Four-o'clocks are thus named because of their penchant to flower in the late afternoon. The flowers of *M. multiflora*, a close relative from the desert southwest, open at dusk then close after sunup or shortly thereafter. In contrast, Barnes (1986) recorded that *Mirabilis macfarlanei* flowers open throughout the day for various durations. The greatest number of flowers opened during the late afternoon period (1500 to 1900) and the fewest during the early morning (0700 to 1100). Flowers that opened during late afternoon and at night tended to remain open longer, up to a full day, whereas flowers that opened in the morning frequently closed within eight hours. The net result was that the number of open flowers per plant did not vary significantly over a 24-hr period.

This finding has interesting implications for the pollination biology of *Mirabilis macfarlanei*. *Mirabilis multiflora*, like many *Mirabilis* species, is adapted for nocturnal pollination (Cruden 1973). The flowers open in late in the day and emit a musk-like odor that, in one study, attracted hawkmoths within ten minutes (Cruden 1970). In contrast, Baker (1983), using only black light (no musk), failed to attract hawkmoths or other large moths overnight at one Salmon River *M. macfarlanei* population, nor did he observe moths of any kind visiting the *Mirabilis* flowers for pollination. The most frequent visitors and presumed pollinators of *M. macfarlanei* are long-tongued bees of the genera *Bombus* and *Anthophora* (Baker 1985, Barnes 1996); both were present throughout the day and were active earlier and later than other floral visitors. Barnes attributes this reliance on generalist pollinators (bees) rather than specialist pollinators (hawkmoths) to the rarity of *M. macfarlanei*.

Another noteworthy difference in *M. macfarlanei* pollination biology is its ability to self-fertilize. *Mirabilis multiflora* and *M. greenei* are both obligate outcrossing species (Pilz 1978, Levin 2000); their flowers must receive pollen from genetically different plants to produce viable seed. *Mirabilis macfarlanei* appears to be self-compatible, given the presence of pollinators, e.g., bees (Barnes 1996).

Closeup of the micro-lepidopteran *Lithariapteryx abroniaeella* on *Mirabilis macfarlanei* leaf. Photo by Gene Yates.

Pests

Although the habitat of some *M. macfarlanei* populations appears to be in excellent ecological condition, exotic invasive plants, especially cheatgrass (*Bromus tectorum*), have invaded several sites. Dalmatian toadflax (*Linaria dalmatica*) has invaded one population in Hells Canyon and Scotch thistle (*Onopordum acanthium*) is present at one site in the Imnaha River canyon. Yellow starthistle (*Centaurea solstitialis*), and rush skeleton-weed (*Chondrilla juncea*) lurk perilously close to several other four-o'clock sites in Hells Canyon.

Spittle bugs of the genera *Aphrophora* and *Philaenus* are natural pests of *M. macfarlanei*. Their nymphs feed on the shoots and inflorescences of the four-o'clock. Charles Baker (1983) found these insects so prevalent on some plants that emergent stems died back to the ground, while "stunting and general unthriftiness" accompanied other plants encumbered with "sizable" infestations. Spittle bug numbers fluctuate annually and

Larvae of the micro-lepidopteran *Lithariapteryx abroniaeella* feed between the upper and lower epidermis creating a transluscent "window" in the *Mirabilis* leaf.

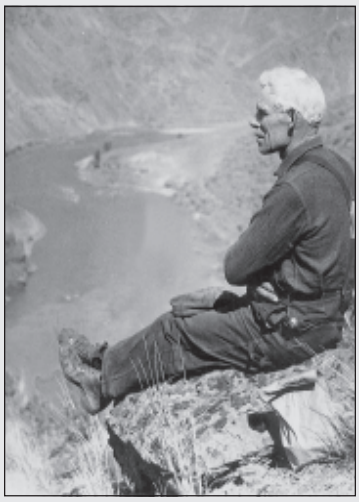
Discovery and naming of *Mirabilis macfarlanei*

Mirabilis macfarlanei was first collected and described by Lincoln Constance and Reed Rollins in 1936. Many students and scholars of botany are well aware of Constance and Rollins' contributions to the flora of North America. Lincoln Constance was a noted scholar of the Umbelliferae (Apiaceae) and patriarch of botany at UC Berkeley. Reed Rollins contributed many studies of the Brassicaceae (Cruciferae) during his long tenure as Director of the Gray Herbarium at Harvard University. Lincoln Constance's first position following completion of his PhD from Berkeley under the direction of Jepson was at Washington State College in Pullman. His first graduate student was Reed Rollins. In their two years together, these botanists investigated and collected plants from throughout this portion of the west, but to Constance (1982) their most notable trip was the "annual Spring-vacation mass foray by motor launch through dangerous white water to the bottom of mile-deep Hell's Canyon of the Snake River."

Their trusted riverboat captain on these excursions was Ed MacFarlane, who pioneered the era of commercial boat transport in Hells Canyon and is remembered as the "Father of Snake River navigation" (Carrey *et al*. 1979). In the early 1900's, MacFarlane owned a hardware store in Asotin, Washington, just north of the Oregon border along the Snake River. The stories and accounts he heard from the growing population of miners and homesteaders in need of river transport prompted the enterprising and water-oriented MacFarlane to build a boat and go into business. He launched his first vessel in 1910 and for 30 years, through a variety of partnerships and ventures, ferried supplies, goods, livestock, homesteaders, miners, mail and tourists (not to mention adventurous botanists) on the Snake River from Lewiston, Idaho, and points upstream in Hells Canyon.

"We collect type of our *Mirabilis*" Lincoln Constance noted below this photograph from his album of the May 1936 excursion up the Snake River. Used with permission, Lincoln Constance estate.

The same view where Constance and Rollins collected the type, 69 years later. Note the increase in *Celtis reticulata* cover. Most *Mirabilis* is upslope out of the picture on the right. Photo by Gene Yates.



Ed MacFarlane overlooking the Snake River during the climb to collect *Arabis crucisetosa*. MacFarlane was 64 years old. Used with permission, Lincoln Constance estate.

Mirabilis macfarlanei population growing on Bonneville flood deposits (ca. 14,500 ya). Bluebunch wheatgrass (*Pseudoroegneria spicata*) is sparse and cheatgrass (*Bromus tectorum*) is prevalent. Photo by Gene Yates.

among populations, and in some years they noticeably reduce flowering and seed production.

Another natural pest of *M. macfarlanei* is the leaf-mining micro-lepidopteran (small moth), *Lithariapterx*, whose larvae feed on the succulent palisade between leaf epidermal layers and floral buds. Charles Baker, the entomologist who collected the larvae from *M. macfarlanei* and reared them to adults, initially speculated this moth might represent a previously undescribed species that is host-specific to *Mirabilis macfarlanei* (Baker 1983, 1985). However, it was later identified as a more widespread species from the southwest, *Lithariapteryx abroniaeella*. In a review of *Lithariapteryx*, Powell (1991) assigned the insects that "Baker reared from *M. macfarlanei* in Idaho" to *L. abroniaeella*. Hsu and Powell's monograph of the Heliodinidae (2004) retained this assignment. *Lithariapteryx abroniaeella* is not known to pollinate or otherwise benefit *M. macfarlanei*.

Conservation

Livestock grazing and invasion by exotic plants were identified as the two greatest threats facing the species (USFWS 2000). Others threats included off-road vehicle impacts, pedestrian trampling, herbicide use, and road and trail construction. To date, several conservation actions are facilitating recovery of the four-o'clock. The Wallowa-Whitman National Forest excluded grazing with fences around some populations in Hells Canyon and the single Forest Service administered site in the Imnaha River canyon. On the Idaho side of Hells Canyon, the Forest Service has temporarily discontinued livestock grazing in the allotment where *M. macfarlanei* grows. The Oregon side of Hells Canyon is no longer grazed. In the Salmon River, the BLM has fenced one site previously accessible to livestock; other BLM sites are so steep that livestock do not frequent them (Lowry pers. comm.).

The Oregon Department of Agriculture released a biological control insect on Dalmatian toadflax at one four-o'clock location in Hells Canyon and the Forest Service continues to control weeds in the vicinity of other four-o'clock sites in Hells Canyon.

The Berry Botanic Garden, in coordination with the Forest Service, BLM, and USFWS, has collected and placed into long-term cold storage thousands of *M. macfarlanei* seeds from throughout its range. The Berry Botanic Garden has also conducted propagation experiments on *M. macfarlanei* and is currently partnered with the Forest Service to establish *Mirabilis macfarlanei* in suitable habitat in Hells Canyon.

These conservation efforts, plus the fact that most *Mirabilis macfarlanei* populations occur on federal lands, greatly improve the prospects for survival of this threatened species.

[1]In the classic *Mirabilis* subgenus *Quamoclidion* inflorescence, a solitary, ebracteate, central flower is surrounded by 5 flowers borne on the bases of their fused involucral bracts (Pilz 1978). Reported variations from this pattern are likely due to floral abortion and herbivory, which are well documented in *M. macfarlanei* (Baker 1983, Kaye and Meinke 1992, Barnes 1996).

Hiking in Hells Canyon

The month of May is a wonderful time to visit Hells Canyon. The weather is not hot and the sharp-tipped awns in cheatgrass (*Bromus tectorum*) florets haven't yet cured to the point where they become an unbearable pestilence in footwear and socks. The third or fourth week of may is a great time to catch the four-o'clock in flower, and many of the plants listed here also bloom in May. If conditions are right, the end of flowering for the four-o'clock will coincide with the beginning of the prickly-pear cactus bloom. I caution visitors about the prevalence of rattlesnakes. I encounter rattlesnakes with each visit, though I find them neither a threat nor a bother. Definitely watch out for western poison ivy (*Toxicodendron rydbergii*), common along the lower slopes and bottoms of the Snake River in Hells Canyon and its tributaries.

Plants Endemic to Hells Canyon

Arabis crucisetosa Constance and Rollins (collected during same trip with *M. macfarlanei*)
Arabis hastatula Greene
Astragalus arthurii M.E. Jones
Astragalus vallaris M.E. Jones
Calochortus macrocarpus Dougl. var. *maculosus* (A. Nels. & J.F. Macbr.) A. Nels. & J.F. Macbr.
Calochortus nitidus Douglas
Lomatium rollinsii Mathias and Constance
Lomatium serpentinum (M.E. Jones) Mathias
Mimulus hymenophyllus R.J. Meinke
Phlox colubrina Wherry and Constance
Ribes cereum Dougl. var. *colubrinum* C.L. Hitchc.
Rubus bartonianus M.E. Peck

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