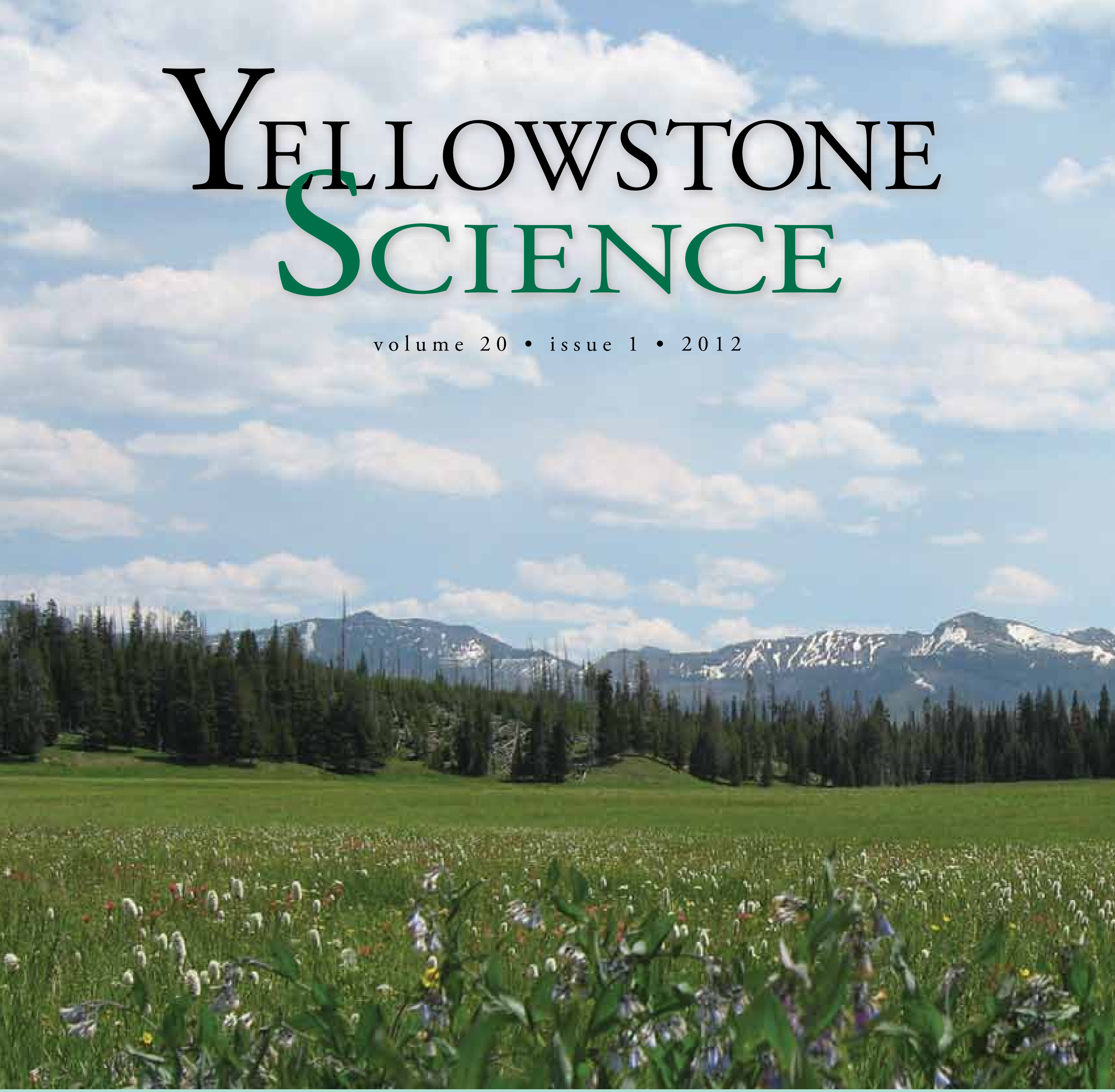
Yellowstone Science

volume 20 • issue 1 • 2012



Yellowstone Vegetation

Fungi Inventory

Endemic Plants of Yellowstone

Restoration of Native Vegetation in Gardiner Basin

Twenty Years of *Yellowstone Science*

For two decades, *Yellowstone Science* has been devoted to presenting significant and reliable science about the natural and cultural resources of Yellowstone National Park. I am so pleased to be able to address this milestone for our twentieth volume.

In the first of these editorials in 1992, then editor Paul Schullery presented the aims of *Yellowstone Science*.

> *Our primary goal is to explore the full breadth of the work being done in the park–to celebrate, through the eyes and ears and voices of the researchers themselves, the knowledge and wonder they so often find in this amazing place. At the same time, and with younger readers especially in mind, we'd like to show, through example, how science works: what its limitations and strengths are, and what it means to all of us who care about Yellowstone.*

As I tried to reflect on the significance of 20 years of scientific publications, I found myself wondering how we had measured up to that lofty goal. So many changes have taken place in that time. The prominence of the internet and the resulting availability of scientific information have certainly changed the role and the goals of *Yellowstone Science*. The ongoing development of information technology will assuredly affect how it continues to evolve. What will not change, however, is our commitment to providing our readers with accessible and engaging articles about research across the spectrum of topics important to Yellowstone.

We will continue to nurture our readers' knowledge of the resources that make Yellowstone so unique, as Jennifer Whipple does in this issue by sharing her work on Yellowstone's endemic plant species. We will strive to foster a better understanding of the relationships among those resources, as Bill Hamilton and Eric Hellquist do in their study of the interdependence of microbial and plant communities in the Gardiner Basin. We will also provide context and perspective for the role of Yellowstone's resources, as Kathy Cripps does when she brings the ecological role of fungi to light by combining an investigation into historical records about Yellowstone fungi with results from a recent bioblitz.

All that we have done, and hope to do, is only possible with a great deal of help. We thank our contributors–the scientists and researchers whose passion for the park leads them to devote their time and energy to the exploration of Yellowstone's wonders, and whose exuberance inspires them to share the fruits of that labor with us. And we thank you, our readers, for twenty years of interest, encouragement, and support.

We hope you enjoy the issue.

Janine Waller

Yellowstone Science

a periodical devoted to
natural and cultural resources

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For back issues of *Yellowstone Science*, please see *www.greateryellowstonescience.org/ys*.

Submissions are welcome from all investigators conducting formal research in the Yellowstone area. To submit proposals for articles, to subscribe, or to send a letter to the editor, please write to the following address: Editor, *Yellowstone Science*, PO Box 168, Yellowstone National Park, WY 82190. You may also email: yell_science@nps.gov.

Yellowstone Science is printed on recycled paper with a soy-based ink.

Cover photo: Southeast view of Pelican Valley, near Pelican and Astringent creeks. NPS photo by Canyon backcountry rangers.

C. E. HELLQUIST

C. Barre Hellquist examining *Potamogeton foliosus* which grows in hydrothermally influenced water, an unusual habitat for aquatic plants.

FEATURES

DEPARTMENTS

News & Notes

Citizen Scientists Conduct Mid-winter Bald and Golden Eagle Survey

Volunteers from Yellowstone National Park took part in the US Geological Survey (USGS) Mid-winter Eagle Survey for the first time since 2005.

The National Wildlife Federation initiated the mid-winter surveys in 1979 to focus specifically on bald eagles (*Haliaeetus leucocephalus*), one year after they were listed as "Threatened and Endangered" under the federal Endangered Species Act. Initially, the survey tried to determine eagle distribution during winter, identify previously unrecognized areas of important winter habitat, and estimate the wintering bald eagle population in the lower 48 states. The annual survey continued even after the bald eagle was removed from the Endangered Species List in 1997.

A mature golden eagle (*Aquila chrysaetos)* takes to the air after feeding on what appeared to be a goldeneye duck (*Bucephala*) near the Lamar River trailhead.

Park Ranger, ecologist, and bird expert Katy Duffy behind the spotting scope.

Surveys typically occur during the first two weeks of January, usually on one of two target days. Regional coordinators in each state organize local surveys, enlist participants, and verify survey route consistency.

Yellowstone National Park began monitoring bald eagles in 1984, and later added golden eagles (*Aquila chrysaetos*) to the midwinter survey. In Yellowstone, the survey is coordinated by ornithologist Lisa Baril, working with the Bureau of Land Management and the US Fish and Wildlife Service. Baril organized online and classroom training for survey volunteers the week before the event. Identification was the primary focus of the training since proper identification is essential to collecting accurate data.

In the early morning hours of Saturday, January 14, 2012, a record number of volunteers took to the survey routes within and north of the park. Survey participants were assigned to count eagles along these standardized routes, in order to provide consistent and readily comparable data for identifying long-term population trends.

The 43 volunteers conducted the four- to five-hour survey in teams, travelling a total of 337 miles in 11 designated territories, including 8 inside the park and 3 adjacent to the park boundary travelling through Jardine, Gardiner, Tom Miner Basin, Paradise Valley, and Cooke City. Survey areas were reached by car or truck when accessible; more remote areas were accessed by snowmobile.

Surveyors recorded a total of 57 eagles this year, including 45 bald eagles (40 adults and 5 subadults), 10 golden eagles (7 adults and 3 subadults), and 2 unidentified eagles. The overall totals and proportional breakdown by species were fairly typical of surveys in previous years, though this year's survey covered a more extensive area. Other raptor species reported along survey routes included rough-legged hawks, red-tailed hawks, northern goshawks, prairie falcons, northern harriers, Cooper's hawks and one snowy owl.

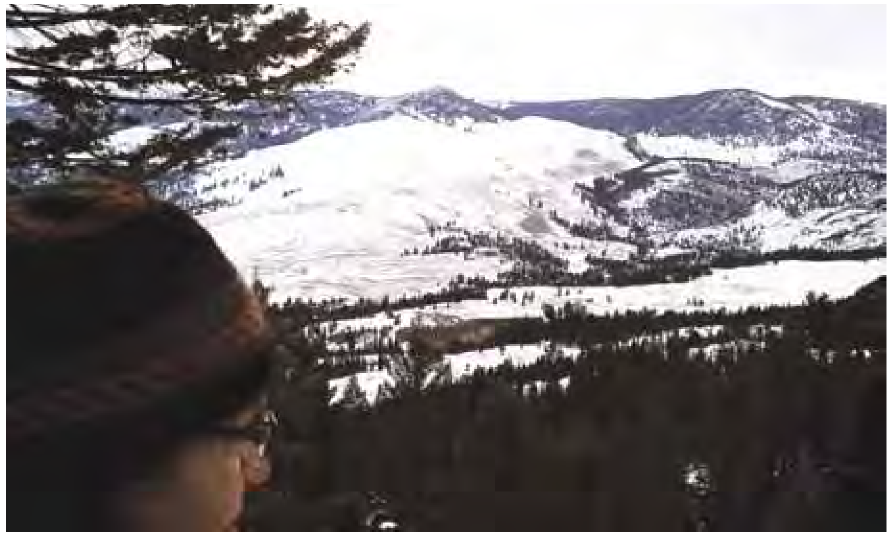
Coordinator Lisa Baril suggested that the low number of subadult bald eagles reported may be because the subadults range much farther than the adults do during winter, typically migrating to the coast during autumn. "Since they are not breeders, they don't have territories to get back to and defend in early spring as the adults do. Most of the adult bald eagles observed are likely residents making small seasonal movements to take advantage of local food resources, but some of the golden eagles could be from as far away as the Brooks Mountain Range in Alaska," she noted.

"As usual, golden eagle numbers were lower than bald eagle counts," Baril reported. "Only 10 [goldens] were counted during the survey, but wolf project technicians recently observed 14 golden eagles on a single carcass." Most eagles were observed in the Paradise Valley, likely due to the availability of open water there.

Once volunteers had completed a clear identification by species and age group, additional data were collected and recorded on precise location and map coordinates where the sighting occurred. Participants were also asked to note related information on time of day and weather conditions at time of observation, as well as related observations about the bird's behavior and surroundings when sighted.

This year's unusually mild winter may contribute to greater abundance of food, which could mean that the eagles are more widely and evenly dispersed across the survey area. The abundant food can also make them more difficult to spot than in colder winters, when groups of eagles are more likely to converge and feed at the same source together. These factors could influence the survey data.

The annual mid-winter survey represents a unique source of long-term, baseline data. Unlike nesting surveys, it provides information on both breeding and non-breeding segments of the population at a potentially limiting time of year. In addition to providing information on eagle trends, distribution, and habitat, the count has helped to involve the public in the stewardship and conservation of the raptors of Yellowstone.



NPS/BASEDEN

Photographer Jennifer Whipple is caught on the other side of the camera while surveying for eagles along the northern range of Yellowstone.

Among other sightings during the survey were a great blue heron, northern shrike, American dippers, rosy-finches, numerous Bohemian waxwings, trumpeter swans, a belted kingfisher, Barrow's and common goldeneyes, American robins, and black-capped and mountain chickadees. Future volunteer opportunities and events for International Migratory Bird Day are being planned for late May.

Tonnessen Receives 2011 Wilderness Stewardship Award

Kathy Tonnessen, the Intermountain Region Coordinator for the Rocky Mountain Cooperative Ecosystem Studies Unit, has received a 2011 Leader in Wilderness Stewardship Award by the National Park Service Intermountain Region. The award program highlights and recognizes employees who work in the region.

Kathy has an outstanding record of wilderness accountability, consistency and continuity. She helps promote the Aldo Leopold Wilderness Research Institute, the Arthur Carhart National Wilderness Training Center, the University of Idaho Wilderness Research Center, the University of Montana Wilderness Management Distance Education Program, and the University of Montana Wilderness Institute. Under Kathy's leadership, the Rocky Mountain CESU has hosted a Wilderness Stewardship in the Rockies workshop, every winter since 2002, bringing wilderness managers together from throughout the U.S. and Canadian Northern Rockies. The commitment and passion she brings to the management of wild places is greatly appreciated.

COURTESY OF K. TONNESSEN

Kathy Tonnessen, coordinator for the Rocky Mountain Cooperative Ecosystem Studies Unit.

11th Biennial Scientific Conference on the Greater Yellowstone Ecosystem Announced

The Greater Yellowstone Biennial Scientific Conference series, initiated in 1991, encourages awareness and application of wide-ranging, high-caliber scientific work on the region's natural and cultural resources. These conferences provide a forum for knowledge-sharing among hundreds of researchers, park managers, and the general public. They attract world-class speakers and are interdisciplinary by design.

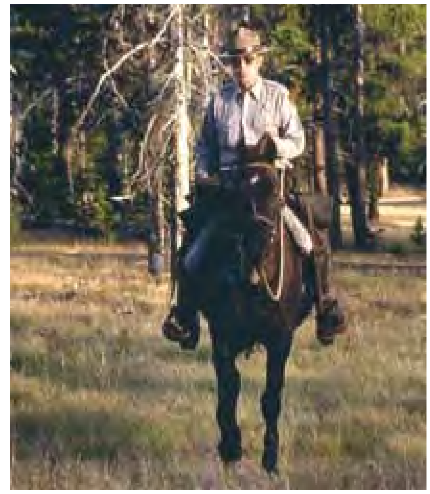
The theme of 11th Biennial Scientific Conference on the Greater Yellowstone Ecosystem will be Greater Yellowstone in Transition: Linking Science and Decision Making. It will be held on October 8–10, 2012 in Mammoth Hot Springs, Yellowstone National Park, Wyoming.

The conference will bring together scientists, managers, and other decision makers to examine resources from a variety of perspectives. The goals are to exchange information relevant to management and to identify resource challenges that require new research.

The conference's program comittee has representatives from state universities, several government agencies, and non-profit research organizations. The committee hopes that forums and presentations will help to establish management targets or desired conditions, examine the interactions between humans and the environment, and determine how best to preserve a record of scientific research and management actions.

For additional information, please visit: *gyesciconf.greateryellowstonescience.org*

Passing of Jerry Mernin a "Ranger's Ranger"


NPS

Gerald "Jerry" Mernin was known and respected for his dedication to Yellowstone and his superior horsemanship.

On December 13, 2011, the National Park Service family and community lost a good friend when retired Ranger Gerald "Jerry" Mernin passed away. Although he suffered with Parkinson's disease for the past several years, Jerry's mind, wit, and memory remained unaffected. A mentor and leader, Jerry showed us how to handle the debilitating disease with dignity and grace. "We hired on to be rugged," he would remind new rangers to Yellowstone and he remained rugged to the very end.

Jerry developed his love for and passion to protect all that is wild at a very early age. Born to Emma and Gerald Mernin in Sacramento, California, Jerry spent his formative years in Yosemite National Park where his father was District Ranger. Raised on National Park Service lore, Jerry had a deep understanding and a unique perspective of Park Service operations that would serve him well during his long, distinguished career.

Jerry began as a seasonal Fire Lookout at Pelican Cone in Yellowstone in 1952 and spent other summers at Glacier and Yosemite national parks. His first permanent position was at Bryce Canyon National Park. After a brief time at Grand Canyon National Park, he returned to Yellowstone in 1964. Turning down promotion after promotion, Jerry remained in Yellowstone until his retirement in 1996. His commitment to Yellowstone didn't end with retirement, however; he continued to volunteer and spend summers patrolling and protecting the park's backcountry until his health no longer permitted it. Throughout the remainder of his life, he would continue to be a strong advocate for Yellowstone's wilderness and preservation, sharing his thoughts and expertise with park management and others. He leaves a legacy in several generations of younger park rangers inspired by his example.

Jerry is survived by his wife of nearly 40 years, Cindy; sister, Lynn Salley of Ashville, North Carolina; nieces and nephews, and by many extended family and friends.

YS

Shorts

Monitoring Yellowstone's Bumble Bees

Cameron, S.A., J.D. Lozier, J.P. Strange, J.B. Koch, N. Cordes, L.F. Solter, and T.L. Griswold. 2011. Patterns of widespread decline in North American bumble bees. *Proceedings of the National Academy of Sciences: PNAS Early Edition*. Available at: www.pnas.org/cgi/doi/10.1073/pnas.1014743108.

Bumble bees are important pollinators of wild plants and agricultural crops. Recent observations suggest that populations of some North American bee species are declining and that a national assessment of bee populations and exploration of possible causes of population declines are needed. A group of researchers from the University of Illinois, the US Department of Agriculture, Agricultural Research Service Pollinating Insects Research Unit, and Utah State University initiated a three-year interdisciplinary study of changing distributions, population genetic structure, and levels of pathogen infection in bumble bee populations across the United States. Two sites in Yellowstone National Park were included in the 382 locations sampled for this study.

The authors compared current and historical distributions of eight historically abundant bumble bee species using museum records and data from nationwide surveys. They also tested the presence of a pathogen infection and each population's genetic diversity and structure. The results show that the relative nationwide abundance of four species declined by up to 96% and that their surveyed geographic ranges contracted by 23%–87%, some within the last 20 years. The results also show that declining populations have significantly higher infection levels of a parasitic pathogen and lower genetic diversity compared with nearby stable populations of the same species. Given these results, higher pathogen prevalence and reduced genetic diversity can be used as predictors of declining abundance and range in North America, although the cause and effect remain unknown.

Two of the targeted species are native to the Greater Yellowstone Ecosystem and were studied at sites within and near the park. The authors targeted the western bumble bee (*Bombus occidentalis*) and the bifarious bumble bee (*Bombus bifarius*) in their inventory of Yellowstone bees. Yellowstone is one of the few locations in this nationwide study where the authors found healthy western bumble bee populations, which are dramatically declining in other parts of the lower 48 and Canada. Why populations in the park and other locations in the Rocky Mountains remain healthy while populations further west have disappeared is still unclear. The bifarious bumble bee was found to have healthy populations throughout its range, including Yellowstone. Continued monitoring will study the decline or stability of western bumble bee populations in the park and the genetic diversity of those populations. The authors intend to continue monitoring bumble bees in Yellowstone and other study areas as funding is available.


JOYCE KNOBLETT

Western bumble bee (*Bombus occidentalis*).

—*James P. Strange, Utah State University*

Microbial Diversity in Non-sulfur and Iron Geothermal Steam Vents

Benson, C.A., R.W. Bizzoco, D.A. Lipson, and S.T. Kelley. 2011. Microbial diversity in nonsulfur and iron geothermal steam vents. *FEMS Microbiology Ecology* 76:74–88.

Fumaroles, or steam vents, are breaks in the Earth's surface where steam and other gases emerge. As the steam emerges from the vent, it cools and leaves deposits around the opening. Microorganisms are found in the condensed steam and often become embedded within the steam deposit matrix to survive. In doing this, they can sustain themselves with gases like ammonia for nitrogen and minerals like sulfur, iron, and other cofactors brought up from the subsurface. These deposits concentrate on the cooler cave ceilings and deposit sites by condensation, oxidation, precipitation, or evaporation, making this a rich source of nutrients in an otherwise sparse habitat.

The authors of this study developed new approaches to isolate DNA and analyze the microbial community found in fumarole deposits, which has been difficult to do with existing approaches. Samples of deposits were collected from steam vents and caves in Yellowstone National Park (Amphitheater Springs, Norris Geyser Basin, and Roaring Mountain), Hawaii Volcanoes National Park, and Lassen Volcanic National Park. Whenever possible, caves were selected with physical characteristics that minimize or eliminate contamination from the air, such as the Roaring Mountain non-sulfur steam cave. Only a shallow scraping (usually less than a centimeter) of the inside of the cave was sampled, collecting material that was deposited by the steam and not the underlying soil. Using this approach, the authors extracted DNA or grew cultures from the deposits of organisms residing in or carried from the near subsurface into the steam deposits. Each sample was analyzed using X-ray microanalysis and classified as a non-sulfur, sulfur, or iron-dominated steam deposit. Obtaining high-yield, high-quality DNA from the samples for cloning was difficult and only half of all the samples yielded sequences. Analysis of archaeal 16S ribosomal RNA gene sequences showed that sulfur steam deposits were dominated by *Sulfolobus* and *Acidianus*, while non-sulfur deposits contained mainly unknown *Crenarchaeota*. Several of these novel *Crenarchaeota* lineages were related to chemoautotrophic ammonia oxidizers, indicating that fumaroles represent a likely habitat for ammonia-oxidizing Archaea. Archaeal and bacterial enrichment cultures were grown from the majority of the deposits and members of the *Sulfolobales* were isolated. These results provide the first evidence of Archaea in geothermal steam deposits and show that fumaroles harbor diverse and novel microbial lineages.

—Courtney A. Benson, Richard W. Bizzoco, and Scott T. Kelley
Department of Biology, San Diego State University

C. BENSON

Roaring Mountain steam vents and fumaroles include both non-sulfur and sulfur depositing caves and vents.

C. BENSON

The reddish deposits in this fumarole (measuring 93°C, pH 5.5) located in Norris Geyser Basin are from iron precipitated from rising fumarolic steam by oxygen in the air surrounding the vent.

Thermophile Converts Biomass to Fuel

Scott D. Hamilton-Brehm, Jennifer J. Mosher, Tatiana Vishnivetskaya, Mircea Podar, Sue Carroll, Steve Allman, Tommy J. Phelps, Martin Keller, and James G. Elkins. 2010. *Caldicellulosiruptor obsidiansis* sp. nov., an anaerobic, extremely thermophilic, cellulolytic bacterium isolated from Obsidian Pool, Yellowstone National Park. *Applied and Environmental Microbiology* 76(4):1014–1020.

Cellulosic biomass will likely serve as an important source of stored renewable energy in the future, but efficiently converting it to liquid fuels will require overcoming the recalcitrance of lignocellulosic materials to enzymatic hydrolysis. Members of the genera *Caldicellulosiruptor* are anaerobic, extreme thermophiles known to express heat-stable extracellular enzyme systems for breaking down biomass and to use both hexose and pentose sugars for fermentation. Given these properties, recent studies have focused on their use for converting biomass to fuel.

Strains of *Caldicellulosiruptor* had been isolated from thermal features in Iceland, Kamchatka, and New Zealand, and solar-heated ponds in Owens Valley, California, but the authors of this paper were the first to characterize a species from Yellowstone, where cellulolytic organisms were known to be abundant in hot springs in the Mud Volcano area. From samples collected at the edge of Obsidian Pool, they isolated a bacterium that they have proposed designating *C. obsidiansis*. Heat-tolerant grasses at the pool likely provide a source of lignocellulosic biomass for the organism, as could leaf litter and animal dung. With optimal growth at 78°C (and growing at a maximum of 85°C), *C. obsidiansis* is near the upper temperature limit of extremely thermophilic, cellulose-hydrolyzing organisms. In the laboratory, *C. obsidiansis* produced ethanol when metabolizing switchgrass and Avicel (the trade name for a cellulose that has been reduced to a fine powder). Although the quantities of ethanol produced in this way are low, recent progress has been made in genetically modifying thermophilic anaerobes to produce knockout mutants capable of fermentation resulting wholly or principally in a single end product, in this case ethanol.

Aquatic Plant Inventory

C.E. Hellquist and C.B. Hellquist. 2011. Aquatic Plant Inventory of Yellowstone National Park, 2008 and 2010.

In addition to spanning moisture and elevation gradients, Yellowstone's aquatic habitats are influenced by geothermal features, creating a variety of water chemistry conditions for aquatic plants. This inventory combined fieldwork, taxonomic research (morphological and molecular), use of herbarium collections, contributions from US and European botanists, and ecological sampling to better understand the diversity, abundance, and ecology of the park's aquatic vascular flora.

During the summers of 2008 and 2010, the Hellquists surveyed 224 sites in the park, documented 102 species and hybrids of vascular aquatic plants in over 25 families, and found rare aquatic species in more than 140 locations. Of special note were new records for the rare pondweeds *Potamogeton strictifolius* (new to Montana), and *P. obtusifolius* and *P. zosteriformis*, which have not been found in Wyoming since the early 1960s. They found no exotic aquatic plant species in the park. They believe that the Yellowstone herbarium may now have the most comprehensive scientific collection of native aquatic vascular plant specimens in the western United States.

C. E. HELLQUIST

C. Barre Hellquist stands among hybrid *Potamogeton* and hybrid *Stuckenia* in the Firehole River. The large pondweed with broad, brownish green foliage is the "Firehole hybrid." Previously misidentified as *P. illinoensis* or *P. nodosus,* it is actually a cross between one of those species and *P. natans*.

Managing Yellowstone Bison

White, P.J., R.L. Wallen, C. Geremia, J.J. Treanor, and D.W. Blanton. 2011. Management of Yellowstone bison and brucellosis transmission risk—Implications for conservation and restoration. *Biological Conservation* 144(5):1322–1334.

Yellowstone bison herds are managed to reduce the risk of brucellosis transmission to cattle while allowing some migration out of the park to winter ranges in Montana. This migration enables bison to access forage that is more readily available in areas with less snow and it releases portions of bison range in the park from intensive use for part of the year. Although about 1,800 cattle are released onto public and private lands north and west of the park during mid-June and July, no transmission from bison to cattle has occurred. The transmission risk is considered extremely low by June 15 because of management which maintains separation between cattle and bison, the concentration of bison births in a short period, the occurrence of bison births away from cattle ranges, the bison's thorough cleaning of birth sites, scavenger removal of potentially infectious birth tissues, and the short persistence of *Brucella abortus* in late spring weather conditions.

Brucellosis exposure in female bison has increased or remained constant at about 60% since at least 2000. This could be because the Interagency Bison Management Plan was not fully implemented. For example, bison leaving the park were not consistently captured and tested for brucellosis, and no bison were vaccinated. Interagency managers committed to increased vaccination in the 2008 adaptive management plan and the National Park Service has initiated environmental review to explore remote-delivery vaccination of bison in the park.

Hazing operations to move bison back into the park from low-elevation ranges with new grasses in mid-May must often be repeated because the bison are still undernourished from the winter, they have newborn calves, and their higher-elevation summer ranges usually still have substantial snow. From 2000 to 2010, a total of 3,207 bison were sent to slaughter or were shot because hazing became ineffective and capture was not feasible; a further 216 bison were sent to a quarantine program run by the state of Montana and the US Department of Agriculture.

There is no evidence that culling has threatened the long-term genetic viability or persistence of the population, or substantially altered the migratory behavior of bison. However, the culls differentially affected the northern and central herds, reduced female cohorts, and dampened productivity in the central herd. Sporadic, nonrandom, large-scale culls of bison have the potential to perpetuate large population fluctuations by altering the herds' age structure and increasing the variability of associated vital rates. The authors therefore conclude that long-term bison conservation would benefit from management practices that maintain more population stability and productivity, and they recommend several adaptive management adjustments that could be implemented to enhance bison conservation and reduce brucellosis infection. YS

What Do We Know about Fungi in Yellowstone National Park?

Cathy L. Cripps and Leslie Eddington

Agaricus species in grassland.

Fungi are the fabric that holds most ecosystems together, yet they are often forgotten, ignored, underestimated, or even reviled. Still it is the fungi in all their diverse roles that weave organisms, organic matter, soil, and rocks together. The Kingdom Fungi includes an estimated 1.5 million species worldwide (Hawksworth 2001)—molds, yeasts, plant pathogens, aquatic fungi, coral fungi, teeth fungi, bird's nest fungi, stinkhorns, cup fungi, morels, truffles mushrooms, boletes and more. Fungi were once thought to be related to plants but they lack chlorophyll and cellulose cell walls. Instead, fungi have chitin cell walls, a key fungal characteristic. DNA reveals that fungi are most closely related to animals. Like animals they are heterotrophs and must obtain food from an outside source; in fungi this is accomplished by absorption. Unlike bacteria, fungi have a nucleus and are multicellular (except for yeasts).

Fungi facilitate the establishment and survival of forbs, grasses, and forest trees in numerous ways and, in essence, are a link between the biotic and abiotic. Fungi may be saprophytic (decomposing dead plants and returning nutrients to the soil), mycorrhizal (attached to roots where they provide nutrient conduits for plants, shrubs, and trees), and/or pathogenic (thinning weak plants and allowing the strong to survive). Once in a while, a human-introduced fungus wreaks havoc as an invasive species that can devastate forests. The pathogenic white pine blister rust (*Cronartium ribicola*), accidentally imported from Europe in the early 1900s, is currently decimating whitebark pine forests.

The bodies of all fungi except yeasts are comprised of hyphae, tiny microscopic threads that permeate soil, roots, leaves, and wood, feeding off the richness of forests and meadows. The mycelium (a mass of hyphal threads) can exist out-of-sight almost indefinitely. The fleshy fruiting bodies (i.e., mushrooms) are the reproductive part of the fungus, ephemeral structures designed to lift the fungus out of the soil or wood in order to disseminate its reproductive propagules as spores.

How many fungi species occur in Yellowstone National Park? How are they distributed? What is their importance in ecosystem processes? Our goal was to synthesize information about Yellowstone fungi from collection records and to make recommendations for expanding the knowledge of fungi in the park. Delving into the literature and fungal herbaria in the United States and Europe, we compiled reports and records of fungi from the park over the last 130 years. Our findings were interesting not only for their historical value, but because they provide valuable baseline data to guide future research efforts. Management decisions often depend on this kind of basic knowledge.

COURTESY NEW YORK BOTANICAL GARDEN HERBARIUM

The first recorded fungus for Yellowstone National Park is *Hymenochaete* (now *Veluticeps*) *fimbriata*, a crust fungus collected on wood by Frank Tweedy in 1885 and deposited in the New York Botanical Garden Herbarium.

The History of Fungi Collecting in Yellowstone

The first fungus recorded from Yellowstone, *Hymenochaete fimbriata* (now in the genus *Veluticeps*), was collected in 1885 by botanist Frank Tweedy, who wrote the park's first botanical guide, *Flora of the Yellowstone National Park,* in 1886. It is a tough leathery bracket or crust fungus found on dead pine. This is one of the few Type specimens from Yellowstone, it was described for the first time from a collection which is now in the New York Botanical Garden's Fungal Herbarium.

Mycological priorities have changed over time. Until the mid-1970s, most of the fungi collected in the park were plant pathogens; more than 90% were rusts. Around 1900, Wyoming botanist Aven Nelson made numerous collections of plants and fungi, most of which are rust fungi. Nelson's specimen from Yellowstone is *Puccinia annulata*, a rust found on *Epilobii* species. Other collectors who contributed to our knowledge of rusts in the park include Hedgecock (1902–1909), Bartholomew (1913), Conard (1924-1926), Overholts (1926), Pady (1941), and Sprague (1941). Overholts was one of the few to collect small Ascomycota in the park.

Rusts were of interest not only for their pathogenic nature, but because species and strains often associate with a particular plant species. Rusts and other pathogens could be easily pressed flat along with plant leaves, and many fungal herbaria got their start this way. It was only later that large fleshy fungi (mushrooms) were dried and stored, at first pressed flat like plants, then later dried whole and stored in packets or boxes.

Large fleshy fungi (mostly Basidiomycota) were not seriously collected in the park until the 1960s, perhaps because of a lack of interested mycologists, but access and the ability to dry fungi quickly were still problematic. Fungal fruiting bodies are ephemeral and appear only after rainfall or in high humidity and, unless special techniques are used, that is the only time the fruiting bodies can be collected. Special drying methods are necessary to preserve the fleshy fungi, otherwise they quickly melt into a slimy mass. Portable dehydrators for specimens did not exist early on and were not common until the 1950s, and even then many field camps lacked the electricity to run them. Although adventurous backcountry mycologists know it is possible to dry fungi over campfires, even using dried herbivore dung as fuel in woodless areas, larger fungi collected far from roads are more likely to be lost to decay. Today fungi are described and photographed when fresh, then dried on electric dehydrators before being packaged for posterity.

About 100 fungi were collected every 25 years until 1976, when the number increased dramatically (fig. 1). Dr. Kent McKnight of Brigham Young University, Utah was an important collector of fungi in Yellowstone from the 1960s through the 1980s. He was sometimes accompanied by Prof. Meinhard Moser of the University of Innsbruck (Austria) and Dr. Joseph Ammirati of the University of Washington. Their collecting trips produced the spike in records after 1976 and culminated in the publication of "A Checklist of Mushrooms and Other Fungi in Grand Teton and Yellowstone National Parks," published in 1982. This list, while valuable, unfortunately does not indicate which fungi were found in which park, although many likely occur in both parks. Today, some of the collections (vouchers) from McKnight's checklist are in Yellowstone's Heritage and Research Center, but others have been deposited elsewhere. Many of McKnight's collections, housed at Brigham Young, are currently inaccessible. Moser's numerous collections at the University in Innsbruck are housed in the herbarium there.

A large portion of the mushroom flora in the Rocky Mountains, including most of the fungi likely to be fruiting in Yellowstone in autumn, are from the large and difficult

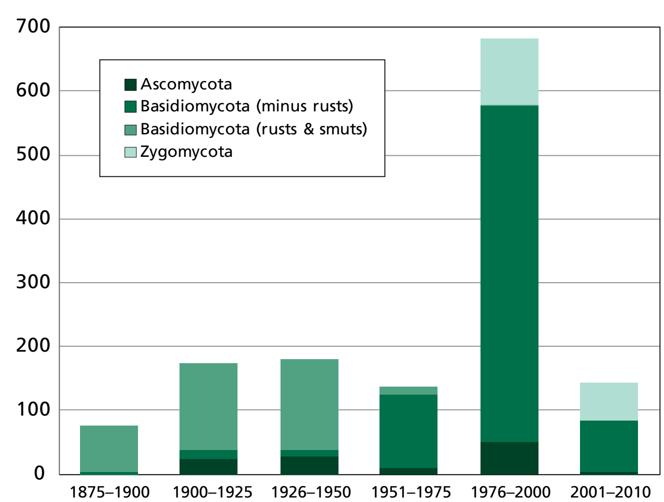


Figure 1. Number of fungi collected in Yellowstone National Park from 1875 to 2010. Zyggomycota collections are all of *Pilobolus*. Yellowstone's bioblitz in 2009 netted at least 82 species of macrofungi.

Mycology crew for Yellowstone National Park's first bioblitz in August 2009.

The first record of *Tricholoma cingulatum* for the region was found during Yellowstone's first bioblitz.

genus *Cortinarius*—rusty, brown-spored mushrooms with a cobweb-like veil. There are few specialists for this genus, but fortunately the three men noted above pooled their expertise for the benefit of the park. Their checklist contains more than 64 taxa of *Cortinarius*, and our database extends this to 103 species (McKnight 1982, 1986; Moser and McKnight 1984; Moser et al. 1999).

The lichenologist Sharon Eversman of Montana State University made a major contribution by collecting lichens in the park over many years (Eversman 2004). While lichens are often called dual organisms and not traditionally included in fungal databases, in recent years they have been classified as fungi because they are comprised mostly of ascomycete fungal hyphae with a layer of algal cells that produce food for the symbiotic partners. Eversman deposited 524 well-referenced specimens in 81 genera and as 255 species—a sufficiently extensive collection to suggest the range of a species within the park.


Figure 2. Most sites where fungi have been collected and recorded from 1885 to 2010 are near park roads.

In August 2009, when 125 researchers came from all over the country to collect as many different specimens as possible during Yellowstone's first "bioblitz." Dr. Cripps led the mycology crew from Montana State University and the Southwest Montana Mycological Association in Bozeman. Despite the dry conditions at that time of year, the crew netted more than 80 species of fungi during the 24-hour period, including two which were previously unreported in the park and one which was new for both Montana and Idaho. This was the first report of *Tricholoma cingulatum*, which occurs only with willows, in the Rocky Mountain region.

Fungi Sites in Yellowstone

Fungi have been collected at about 80 sites in the park, often near lakes, creeks, rivers and falls (fig. 2). This may be because fungi often fruit in moist habitats and Yellowstone is seasonally dry in many areas, or it might reflect the larger diversity of plants and microhabitats in these areas; a significant portion of Yellowstone's plant diversity is found in riparian areas (*Yellowstone Science* 2004). Perhaps this pattern merely reflects the propensity of mycologists, like tourists, to stop near these refreshing locations.

All forest trees in Yellowstone depend on mycorrhizal fungi (literally "fungus root") in one way or another. The presence of appropriate mycorrhizal fungi appears critical to forest health and sustainability. While some mycorrhizal fungi will attach to the roots of any woody plant, many have co-evolved with a particular tree species over thousands of years. Certain species of *Suillus* (slippery jacks) are restricted to five-needle pines, which in Yellowstone means whitebark and limber pine (Mohatt et al. 2008). An example would be the Siberian suillus (*S. sibiricus*) found on whitebark pine at

Suillus sibiricus (below) is mycorrhizal with five-needle pine species such as these whitebark pine on Dunraven Pass.

All forest trees in Yellowstone depend on mycorrhizal fungi in one way or another. The presence of appropriate mycorrhizal fungi appears critical to forest health and sustainability.

Dunraven Pass as well as on stone pines in Europe and Asia. Researchers have found that some ectomycorrhizal fungi prefer young trees and others mature forests. This means that when fire resets the successional clock for plants, it does the same for fungi. The records of many fungi from the park list them simply as "with pines," although specialized habitats such as whitebark pine forests (Mohatt et al. 2008; Cripps and Trusty 2007), thermal areas (Redman et al. 1999), and subalpine conifer forests (Cullings et al. 2000) have been the focus of some research.

Yellowstone is well known for its geothermal areas and the unique forms of life that thrive at high temperatures. The bacteria *Thermus aquaticus*, discovered in Yellowstone's lower geyser basin, contains an enzyme stable at high temperatures (Brock 1985) that has been used in molecular research and in determining fungal relationships. What about thermophilic (heat-loving) fungi? Brock, who discovered *Thermus aquaticus*, reported a few thermophilic and thermotolerant fungi from Yellowstone (Tansey and Brock 1971, 1972), and more recent researchers have discovered others in the park (Sheehan et al. 2005). Two thermotolerant and 16 thermophilic fungi have been reported from Amphitheater Springs (Redman et al. 1999; Hensen et al. 2005). *Curvularia protuberata*, a fungus that lives in the roots of *Dichanthelium lanuginosum* (hot springs panic grass), appears to give the grass its tolerance to hot soils (Redman et al. 2002). At least this is true when a virus first infects the fungus (Marquez et al. 2007) which then infects the plant.

Other researchers have found arbuscular mycorrhizal fungi (Glomeromycota) that can exist on plant roots in geothermal soils in the park (Bunn and Zabinski 2003; Appoloni et al. 2008). A few ectomycorrhizal fungi are recorded with conifers near thermal features (Cullings and Makhija 2001). There are likely other fungi yet to be discovered that thrive in and around the park's hot springs, geysers, fumaroles and geothermal areas.

In Yellowstone, fungi are mostly observed as mushrooms, puffballs, or bracket fungi on trees during certain parts of the year. Mushrooms and puffballs are of special interest because some are edible. Although park rules prohibit people from collecting and removing any mushrooms from the park without a permit, deer, elk, bear, squirrels, voles and insects are among the many animals that eat the fruiting bodies. Edible fungi documented in the park include king boletes (*Boletus edulis*), black morels (*Morchella elata*), golden chanterelles (*Cantharellus cibarius*), slippery jacks (*Suillus* species), oyster mushrooms (*Pleurotus* species), orange milky cap (*Lactarius deliciosus*), shrimp russula (*Russula xerampelina*), shaggy manes (*Coprinus comatus*), meadow mushroom (*Agaricus campestris*) and giant western puffball (*Calvatia booniana*). Toxic species include those in genus *Amanita*, such as *A. muscaria* (yellow variety of fly agaric) and *A. pantherina* (brown panther)

This giant western puffball (*Calvatia booniana*) is about one foot in diameter, edible, and a decomposer of grass.

Meadow mushroom (*Agaricus campestris*) occurs in open grasslands.

(McKnight 1982). Others, such as *Psilocybe merdaria* (non-psychoactive) are found on substrates such as bison dung.

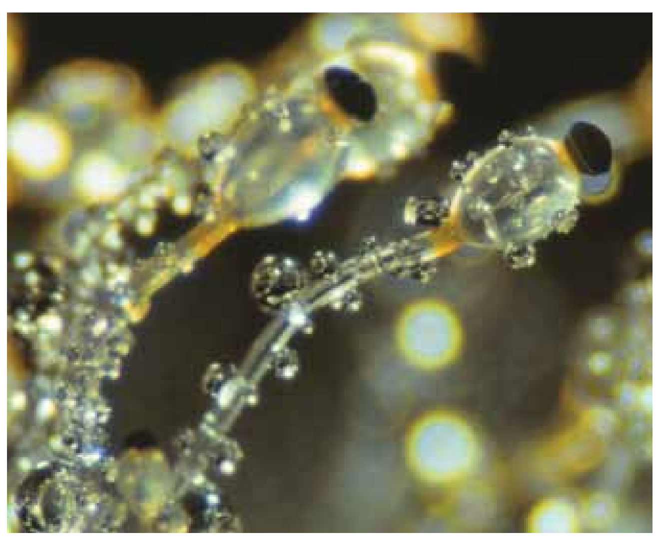
In addition to the mushrooms that sprout out of bison dung in the park are tiny, dung-loving fungi that go unnoticed by most people. On hands and knees, the researcher Michael Foos found *Pilobolus*, the only fungus in Zygomycota recorded in the park, on herbivore dung everywhere in Yellowstone (Foos 1989). This fungus, whose name literally means "hat thrower," shoots its spore packet out of the "zone of repugnance" (a scientific term for a bison paddy or elk duds) onto vegetation at a g-force of 20,000 to 180,000, one of the fastest flights in nature (Yafetto et al. 2008). If eaten by a grazing ungulate, the spores travel through the animal's digestive tract and land back in the manure, ready to do their job of reducing the pile. While *Pilobolus* itself appears to be an innocuous decomposer, Foos (1987) discovered that lungworms can infect elk by hitching a ride on the spore packets.

Gaps in Our Knowledge of Fungi

Our investigative work revealed more than 1,489 records of fungi (not including lichens) collected in the park that are now deposited in various herbaria or mentioned in scientific papers. This translates into 520 species (186 genera) (table 1). The total number of recorded fungi appears minimal given that mycologists estimate that there are typically six times more fungi than plants in most areas (Hawksworth 2001). This suggests that at least 7,680 species of fungi would be expected in the park in proportion to Yellowstone's plant flora of 1,280 known species (*Yellowstone Science* 2004). That leaves a great deal more for us to discover.

Although subsequent identification of fungi sites is sometimes difficult, especially for fungi recorded before GPS, most of the recorded sites are near roads—the pattern typical of other fungal surveys in which mycologists have taken advantage of easy collecting before undertaking

The inedible and non-psychoactive *Psilocybe merdaria* is a decomposer of bison dung.



Pilobolus (highly magnified) fruits on dung and decomposes it. Note the dark spore packets which are shot off.

time-consuming hikes and expeditions. Other areas of the park remain as mycological blank spots. According to the database we developed, the most studied groups of fungi in Yellowstone are the rusts (Uredinales), mushrooms to some extent (particularly the genus *Cortinarius*), the dung fungus *Pilobolus* (Zygomycota), and lichens (Cripps 2011). These are basically researcher-driven results, dependent on the interests of specific collectors in the park. Most of the collecting has been of fungal fruiting bodies, with no major efforts to culture fungi from particular substrates except dung and thermal pools.

In some cases, fungal presence has been detected on roots (as mycorrhizae) and in thermal areas using molecular techniques and the data are catalogued as DNA sequences in Genbank (Cullings et al. 2001). But little to nothing is known of microfungi within other substrates, e.g., soil fungi, endophytes (inside plants), and little is known of the micro-ascomycota as pathogens or decomposers. Most of the fungal species recorded for Yellowstone are known from a single recorded specimen in the database and therefore, except for lichens and perhaps *Pilobolus*, accurate distributions are not known, even for the more well-studied groups.

NPS/H. KREDIT 1974

Wolf lichen (*Letharia vulpina*) is among the more studied fungi that occur in Yellowstone.

Table 1. Genera and number of species of fungi reported in Yellowstone National Park from 1885 to 2010.

		Genera			
Absida-1	Chrysomphalina-2	Galerina-2	Leccinum-3	Peziza-1	Sarcodon-1
Acaulospora-4	Chrysomyxa-4	Gastropila-1	Lentinellus-1	Phaeogalera-1	Sarcosphaera-1
Acremonium-2	Cintractia-1	Gautieria-2	Lepiota-2	Phaeolus-1	Scolecobasidium-2
Aecidium-4	Clavaria-1	Geastrum-2	Lepista-3	Phaeomarasmius-2	Scutellinia-1
Agaricus-7	Clavariadelphus-2	Gigaspora-2	Leptoporus-1	Phanerochaete-1	Scutellospora-1
Agrocybe-2	Claviceps-1	Gloeophyllum-4	Leratiomyces-1	Phellinus-1	Septoria-1
Albatrellus-2	Clitocybe-7	Glomus-9	Leucopaxillus-1	Phialophora-1	Sporothrix-1
Albugo-1	Clitocybula-1	Golovinomyces-3	Lindbladia-1	Pholiota-5	Steccherinum-1
Amanita-7	Coleosporium-2	Gomphidius-2	Loreleia-1	Phragmidium-11	Strobilurus-1
Amylocystis-1	Coltricia-2	Guepiniopsis-1	Lycoperdon-4	Phyllachora-2	Stropharia-1
Anthracobia-2	Coprinopsis-1	Gymnomyces-1	Lyophyllum-1	Pilobolus-4	Suillus-15
Antrodia-1	Cortinarius-103	Gymnopilus-3	Marssonina-1	Piloderma-1	Syncarpella-1
Armillaria-1	Cronartium-5	Gymnopus-1	Megacollybia-1	Plectania-1	Taphrina-1
Ascobolus-1	Cryptoporus-1	Gymnosporangium-7	Melampsora-10	Pluteus-1	Tarzetta-1
Aspergillus-2	Cumminsiella-1	Gyromitra-3	Melampsorella-2	Podosphaera-1	Tephrocybe-2
Astreus-1	Cunninghamella-1	Hebeloma-5	Melanoleuca-3	Psathyrella-3	Thelebolus-1
Auricularia-1	Curvularia-1	Helvella-1	Morchella-4	Pseudeurotium-1	Thelephora-1
Bankera-1	Cylindrosporium-1	Herpotrichia-1	Mycena-5	Psilocybe-1	Thermomyces-1
Blumaria-1	Cyptotrama-1	Hyaloperonospora-1	Naohidemyces-2	Puccinia-52	Tilletia-3
Boletopsis-1	Cystodermella-1	Hydnellum-4	Naucoria-1	Pucciniastrum-2	Torula-1
Boletus-1	Dilophospora-1	Hydnum-1	Neolecta-1	Pycnoporellus-2	Tranzschelia-1
Botryobasidium-1	Discina-1	Hygrocybe-2	Neolentinus-1	Ramaria-2	Tranzscheliella-1
Bovista-1	Endocronartium-1	Hygrophorus-12	Nidula-1	Ramularia-4	Trichaptum-1
Brauniellula-1	Entoloma-4	Hypholoma-4	Onnia-2	Rhizina-1	Tricholoma-10
Calvatia-5	Entyloma-3	Hypocrea-1	Orbilia-1	Rhizogene-1	Tricholomopsis-2
Calyptospora-1	Erysiphe-3	Inocybe-7	Otidia-1	Rhizophagus-3	Truncocolumella-1
Cantharellus-1	Flammulaster-1	Kuehneromyces-2	Pachylepyrium-1	Rhizopogon-7	Tyromyces-1
Cenococcum-1	Floccularia-4	Laccaria-2	Paraglomus-2	Rhodocollybia-2	Uromyces-9
Cercosporella-2	Fomitopsis-1	Lachnellula-1	Penicillium-1	Rhodocybe-2	Ustilago-3
Chaetomium-1	Fuligo-2	Lachnum-1	Peniophora-1	Royoporus-1	Veluticeps-2
Chroogomphus-2	Funneliformis-2	Lactarius-13	Peridermium-3	Russula-16	Wilcoxina-1

C. CRIPPS

Caloscyphe fulgens is a spring cup fungus that can be pathogenic on spruce seeds.

Only 5% of the estimated 1.5 million species of fungus in the world have been named, making the description of unknown species time-consuming and creating bottlenecks in species identification.

Most collections of Yellowstone fungi are in the New York Botanical Garden, the US Department of Agriculture, National Fungus Collection in Beltsville, Maryland, and Yellowstone's herbarium at the Heritage and Research Center in Gardiner, Montana. Although Hawksworth emphasized the importance of fungal culture collections in his 2004 article, "Fungal diversity and its implications for genetic resource collections," much of what he says translates to the importance of dried herbarium collections. For example, the DNA of rusts in the park is available in chronological order. Have the genetics of rusts changed over time? What is the epidemiology of fungal pathogens in the park? Have some fungal species declined or disappeared as they have in Europe? These are some of the many questions that can be answered with herbarium specimens. The herbarium represents an important aspect of our natural history: in human terms (the collectors), in genetic terms (DNA repositories), in chemical terms (record of pollutants) and in fungal terms (biodiversity past and present). Without knowledge of our fungal history, we go blindly forward into the ecological future.

Recommendations for Field-Based Inventory

How can we learn more about fungi in Yellowstone National Park? Mycologists are testing new survey methods, combining bioblitzes that invite the public with the expertise of specialists. This has added to our knowledge of fungi in Point Reyes, Rocky Mountain, and Great Smoky Mountains national parks. In the latter, an "all taxa survey" of fungi was attempted (Hughes and Peterson 2007) during which fungi were collected by many means, including culturing and detection with DNA probes (Rossman 1994; Mueller et al. 2004). These methods can reveal the fungi in soil, inside plants, on roots, and in the air, adding greatly to the diversity count, but they do not always provide reference material for herbaria and they are time-consuming, resource exacting, and often expensive.

The exhaustive all taxa survey is a "holy grail" for fungi, but usually needs to be tempered because of limited financial resources and the availability of mycologists. Only 5% of the estimated 1.5 million species of fungus in the world have been named, making the description of unknown species time-consuming and creating bottlenecks in species identification. In addition, the character of the particular park to be surveyed is an important consideration. While fungi may fruit nearly year round and be easily accessible in some parks, dry and/or cold conditions limit fungal fruiting to particular seasons in each elevation zone, resulting in small windows of opportunity for collection in Yellowstone. Many areas of the park are inaccessible because of difficult terrain or wildlife habitat (grizzly bear, moose, wolves, bison), and trampling by large herbivore herds is detrimental to fruiting structures. Repository and curation needs are also a consideration. Yellowstone's Heritage and Research Center in is an excellent facility for this purpose given sufficient resources for curation. These factors need to be taken into account in future fungal surveys in the park.

A survey of the park's fungi might be accomplished most effectively using a stratified sampling strategy that takes into consideration habitat type (including elevation), age class of over-story vegetation, and disturbance (fire) along with spatial, seasonal, and climatic factors. With lodgepole pine

C. CRIPPS

Guepiniopsis alpinus (lemon drops) is a wood decomposer that relies on moisture from spring snow for fruiting.

C. CRIPPS

Pholiota molesta fruits prolifically on burned soil a few years after a forest fire. It is a decomposer only found in this specialized habitat.

covering 80% of the park, these forests should be stratified into age classes and into burned/unburned areas for sampling. Riparian areas, which account for 38% of the park's plant species diversity, may be of special interest for fungi, especially during the dry season.

We recommend three sampling strategies for fungus collection, two of which require significant resources. One method is for collection of fruiting fungi, the second for isolation of fungi from substrates, and the third includes the use of molecular techniques to detect and identify fungi (Rossman 1994; Mueller 1994). Collection should be timed to correlate efficiently with high seasonal precipitation or rain events (generally a few days after), and the fruiting period for each group or species. The seasonal progression of fruiting generally starts with grass saprophytes in open grasslands at low elevations followed by fungi on burns and around remnant snowbanks in June (Cripps 2009). Forest fungi begin fruiting at the lower elevations and progress upward from Douglas fir to lodgepole, spruce-fir, whitebark pine, and finally alpine tundra (table 2). Droughts or low rainfall in July can seriously reduce fruiting at lower elevations. In years when fall precipitation is minimal, it can be difficult to find fungi fruiting at all.

Instead of relying on fungi fruiting in nature, fungal surveys can be accomplished or enhanced by culturing fungi from substrates (Rossman 1994; Mueller 1994). Although a significant portion of fungi will not grow on petri dishes in the laboratory, this method can be used to isolate some micro-fungi, pathogens, soil fungi, endophytes, mycorrhizal fungi, and aquatic fungi from substrates such as woody material, leaves, needles, soil, roots, algae, and dung. While this method takes significant resources and needs to be applied or supervised by experts, it has the potential to increase the diversity of fungi recorded in an area.

Molecular methods, which are particularly applicable to fungi that do not fruit or grow in culture, are currently being used for soil fungi, mycorrhizal fungi, and thermal fungi (Mueller et al. 1994). Molecular methods can be used to identify population level diversity in fungi, to delineate fungal "individuals", determine relationships, and identify unique organisms or sequences for patent purposes (Varley 2005). This method is time and resource consuming and can only be applied by experts. However, it holds the promise of discovering some of Earth's more unique and cryptic organisms.

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Table 2. A generalized model showing where and when fungi are likely to fruit in Yellowstone National Park (Cripps 2011) with monthly precipitation averages for Mammoth Hot Springs, 1971–2000.

Habitat type	Ecological group	Apr 1.17"	May 1.96"	June 1.99"	July 1.56"	Aug 1.47"	Sept 1.35"	Oct 0.96"
Low elevation sage & grasslands	grass saprophytes	x	x	x				
Douglas fir & limber pine forests	saprophytes, mycorrhizal			x		x		
Low & mid elevation burns	burn fungi		x	x				
Lodgepole pine forests with remnant snowbanks	snowbank fungi			x	x			
Riparian areas before flood stage	willow fungi		x	x	x	x	x	
Aspen & cottonwood cover areas	saprophytes, mycorrhizal		x	x	x	x	x	
Lodgepole pine forests	saprophytes, mycorrhizal		x	x			x	
Spruce-fir forests	saprophytes, mycorrhizal				x	x	x	x
Whitebark pine forests	saprophytes, mycorrhizal				x	x	x	x
Alpine tundra	saprophytes, mycorrhizal				x	x	x	
Geothermal areas		x	x	x	x	x	x	x

Data compiled from information on fungi in the Greater Yellowstone Area (Cripps 2001; Cripps & Antibus 2011; Cripps & Ammirati 2010; Cripps & Eddington 2005; Cripps & Horak 2008; Mohatt et al. 2008).

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Endemic Plants of Yellowstone

Jennifer J. Whipple



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Left to right: Yellowstone sulfur buckwheat (*Eriogonum umbellatum* var. *cladophorum*), Yellowstone sand verbena (*Abronia ammophila*), and Ross' bentgrass (*Agrostis rossiae*).

Hidden among the steaming geysers, running rivers, and the miles and miles of lodgepole pines in the Yellowstone caldera are three surprising vascular plants that are found nowhere else in the world: Ross' bentgrass (*Agrostis rossiae*), Yellowstone sand verbena (*Abronia ammophila*), and Yellowstone sulfur buckwheat (*Eriogonum umbellatum* var. *cladophorum*). The geothermal legacy of Yellowstone is associated with the life history of each of them, but each of these endemic taxa has a particular way of surviving the rigors of the park.

Yellowstone Sulfur Buckwheat

Yellowstone sulfur buckwheat does not occur directly next to thermal features, but instead is a component of the vegetation on barren, geothermally warmed ground adjacent to thermal areas. Primarily occurring on areas of glacial till with obvious obsidian sand on the surface, it can also grow on other soil types such as soil derived from sinter. The entire world population is within the park, occurring in the Upper Geyser Basin, especially around Old Faithful, Midway Geyser Basin, the Lower Geyser Basin, and in the vicinity of Madison Junction. These plants are part of an interesting thermal plant community that is encountered in the vicinity of geyser basins. Growing on mildly influenced geothermal ground, it includes several species that are more often encountered at lower elevations or as components of the more xeric Great Basin flora. Superficially, these areas look relatively barren and have been perceived in the past as unimportant sites, but the plants have been drawn from different areas of the West, forming a unique community. Where the ground is cold and barely influenced by geothermal heat, the plants including Yellowstone sulfur buckwheat drop out of the vegetation. Perhaps they are unable to compete against other species in the area, such as the ubiquitous lodgepole pine. Lodgepole may restrict the presence of Yellowstone sulfur buckwheat due to the wild buckwheat's apparent inability to tolerate much shade. Most Yellowstone sulfur buckwheat plants are in full sunlight or in relatively open spots with only a few trees in the vicinity.

Wild buckwheats are generally tolerant of some degree of disturbance. The environment in the geyser basins supports plants that can adapt to areas being disturbed by geothermal changes such as areas heating up or cooling down. Yellowstone sulfur buckwheat is quite capable of moving with changing conditions, as clearly demonstrated by its ability to spread into disturbed sites such as along the road prism near the interchange at Old Faithful.

One of the fascinating aspects of the wild buckwheats in the thermal areas is that there are several taxa that appear superficially similar and thus it is easy to overlook the amount of diversity that is in plain view. On closer examination, all of these taxa are easily separated by typical variations in flower color, the inflorescence, and the shape and hairiness

Wild buckwheats are notoriously difficult to identify and in the thermal areas can appear superficially similar. Yellowstone sulfur wild buckwheat (*Eriogonum umbellatum* var. *cladophorum)* with bright yellow flowers (left*),* and its close relative *Eriogonum umbellatum* var. *majus* with cream yellow flowers (right) are considered members of the same species.

of the leaves, but they are also temporally separated. The other bright yellow sulfur buckwheat in the area, *Eriogonum flavum* var. *piperi*, blooms early in the summer, well before Yellowstone wild buckwheat. The close relative *Eriogonum umbellatum* var. *majus* with cream yellow flowers also blooms before Yellowstone sulfur wild buckwheat. These two taxa are considered members of the same species, but I have seen no sign of interbreeding or hybridization. The last wild buckwheat to begin blooming is Yellowstone sulfur buckwheat, mostly in July and early August, though I have seen plants in full bloom in early September, which is extraordinarily late for a native species in the park. Like many members of the genus, Yellowstone wild buckwheat has bright yellow flowers that dry on the inflorescences instead of falling off like most wildflowers, so the wild buckwheats appear colorful long after the plants have ceased to bloom.

The wild buckwheats are a notoriously difficult to identify and rapidly speciating North American group, chiefly from the western portion of the continent. Yellowstone wild buckwheat was first described scientifically from collections made by Per Axel Rydberg and Ernst A. Bessey from the Upper Geyser Basin on August 6, 1897. First identified as a specimen of *Eriogonum umbellatum* (Rydberg 1900), it was later elevated to species status by E. L. Greene, a California expert who named it *Eriogonum rydbergii* in honor of one of the two original collectors (Greene 1902). Subsequently it was presumed to be just a minor variant in the widespread and variable *Eriogonum umbellatum* complex, not sufficiently different to warrant any attention. James L. Reveal, the *Eriogonum* expert, after examination of herbarium material and seeing the plants in Yellowstone, believes that it is a distinct variety and worthy of taxonomic recognition. He published it as a recognized taxon in the treatment of *Eriogonum* in the *Flora of North America* (FNA 2005).

The recognition of Yellowstone sulfur wild buckwheat is directing attention to finding out more about it. The first mission is to find out the exact distribution of this taxon by surveying all of the known locations. Parts of the Upper Geyser Basin have already been mapped and, in summer 2011, mapping was initiated around Madison and in the geyser basins along the Firehole River. In the future, its life history needs to be elucidated along with genetic investigation of its status and relationship with other members of the *Eriogonum umbellatum* species complex.

Yellowstone sulfur buckwheat grows on barren glacial till adjacent to thermal areas, often with obvious obsidian sand on the surface.

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Yellowstone sand verbena is a short-lived perennial that sprawls on the sand, rarely rising more than two or three inches above the ground.

Yellowstone Sand Verbena

The only thing that Yellowstone sand verbena has in common with Yellowstone yellow sulfur buckwheat is that the sand verbena may also be positively influenced by the presence of the geothermal system. *Abronia* (sand verbena) is a genus that justifies its common name; most species occur exclusively on sandy substrates. Yellowstone sand verbena is known only from the sandy shoreline of Yellowstone Lake. All of the species in the genus are from the western United States except for one that occurs in Mexico. Yellowstone sand verbena is one of the most northern members of the genus and occurs at a higher elevation (7,700 ft) than most *Abronia* species.

The main occupied site is in the vicinity of areas of hot ground and minor thermal features, though the species also grows successfully outside the range of geothermal influence. Plants close to thermal features can be killed by the increasing heat as summer progresses or by an increase in thermal activity. Sometimes adjacent plants appear to become dormant during the hottest portion of the summer, but nearby plants can be the epitome of health. The frigid winter temperatures and cool summers may have necessitated the presence of geothermal heat for a sand verbena to survive and evolve to successfully inhabit the lake's shoreline.

Yellowstone sand verbena is a short-lived perennial that sprawls on the sand, rarely rising more than two or three inches above the ground. Since the plants are covered in sticky glands except for the flowers, anything that comes close may stick to the leaves and stems, including sand, feathers, and small bits of plant material, leading to a somewhat disheveled appearance. The taproot may go very deep into the sand; no excavations have been done to determine the maximum length, though plants have been partially washed out by high lake levels. It is apparent that the roots can be at least one inch thick and several feet long, probably enabling the plant to utilize moisture deep in the sand.

The most conspicuous parts of the plant are the white blossoms which occur in a head-like arrangement of up to 21 separate flowers subtended by membranous bracts. These inflorescences are held at or above the canopy level of the prostrate plant. The plants begin blooming if the temperatures are warm enough by mid-June and are known to continue blooming well into September or until there is a killing frost. During the summer the flowers may open or close at various times, though the exact triggering mechanism is not entirely understood. Possible different hypotheses include sensitivity to light levels such as clouds or time of day, temperature or temperature change, wind speed, or an interaction of several factors. After the inflorescence finishes blooming and the seeds are developing, the flowering stem bends lower so that the seeds are adjacent to the sandy ground. Seed dispersal appears to be at the base of the plant, but the windy nature of the beach probably ensures at least some wind dispersal in the vicinity. Natural seed set is high, 59%–84% (Saunders and Sipes 2006).

Yellowstone sand verbena was first known to Euroamericans by Frank Tweedy's collection in August 1885 from sandy beaches along the shoreline of Yellowstone Lake, at what he described as the "mouth of Pelican Creek." Originally the specimen was identified as *Abronia villosa* (Tweedy 1886), a common purple-flower annual species of the Southwest. In

The frigid winter temperatures and cool summers may have necessitated the presence of geothermal heat for a sand verbena to survive and evolve to successfully inhabit the lake's shoreline.

Seed dispersal appears to be at the base of the plant, but at least some wind dispersal is guaranteed along the shore.

1900 Per Axel Rydberg examined the material and decided it was sufficiently distinct to warrant description as a new species, *A. arenaria*. This name, though, was already in use for one of the maritime sand verbenas on the west coast of North America. E. L. Greene resolved the problem by proposing the name *A. ammophila* for the Yellowstone material (Greene 1900). During the first half of the twentieth century, the material continued to be recognized as distinct, but the 1964 treatment in *Vascular Plants of the Pacific Northwest* by C. Leo Hitchcock and Arthur Cronquist included *A. ammophila* within the concept of a variable *A. fragrans*. Don Despain's 1975 "Field Key to the Flora of Yellowstone National Park" also followed this treatment. Lee Galloway (1975) reexamined the entire genus and resurrected *A. ammophila* as a unique species, including material from Sublette County, Wyoming, within his concept of the taxon. Subsequent investigators have decided that the Sublette material is more properly placed within *A. mellifera* (Marriot 1993; Fertig et al. 1994). Currently, *A. ammophila* is recognized as a highly restricted endemic of Yellowstone National Park (Flora of North America 2003).

One of the first concerns when confronted with a species that may be quite rare is to determine the extent of the population. The historical distribution of Yellowstone sand verbena is uncertain, but clearly the species was previously more widely distributed along the shoreline of Yellowstone Lake. A specimen in the Yellowstone herbarium collected by H. S. Conard on 23 June 1926 was from a sandy dune "near Fishing Bridge Camp; Lake." In the 1920s the Fishing Bridge Campground was located in what is now the western portion of the Fishing Bridge Museum parking lot. Apparently, the sand verbena was present on the sandy lakeshore, probably in front of the site where the museum would be built in 1930. Aven Nelson collected Yellowstone sand verbena from "on the sandy banks, near lake hotel" in 1899. The closest extensive sand banks to the Lake Hotel would be the shoreline on both sides of the mouth of the Yellowstone River in the vicinity of the current Fishing Bridge development, though there are sandy areas closer to the hotel. While working on his monograph on *Abronia* in the summer of 1968, Galloway states in his field notes that he was a quarter of a mile west of the mouth of Pelican Creek, where there were numerous small plants in the vicinity (L. A. Galloway, personal communication). Today, there are no plants from the mouth of Pelican Creek to Bridge Bay, through the entire area of the Fishing Bridge and Lake developments.

Extensive shoreline surveys of Yellowstone, Lewis, Shoshone, and Heart lakes in the 1990s located only four sites where *A. ammophila* were present, all of them on Yellowstone Lake: the north shore (the type locality), Rock Point, on the east shore of the South Arm, and near Pumice Point. Since Yellowstone sand verbena needs fairly fine sand, it is unlikely that there are any sites away from the park's major lakes.

A grid system used to count every single plant present in 1998 arrived at a total of 8,326 plants (Whipple 2002). Many of these plants were young individuals recruited during the wet summers of 1996 and 1997 which may not have survived, so the current population is probably much lower. An estimate made after partially counting some areas in 2009 suggested that the current population is approximately

Cheryl Decker and Pat Corry sampling and plotting Yellowstone sand verbena near Storm Point in October 2004.

Yellowstone sand verbena growns in fairly fine sand, so it is unlikely to be found away from the park's major lakes.

2,600–3,100 plants (Corry 2009). The primary site is on the north shore, where 96% of the world's population occurs; most of the rest of the plants (4% of the population) are at Rock Point. The other two sites had 1 and 22 plants in 1998. These two populations fluctuate and at times there have been no plants present at one of these sites. Neither the South Arm nor the site near Pumice Point is truly viable due to low numbers so they will not help the species' long-term survival.

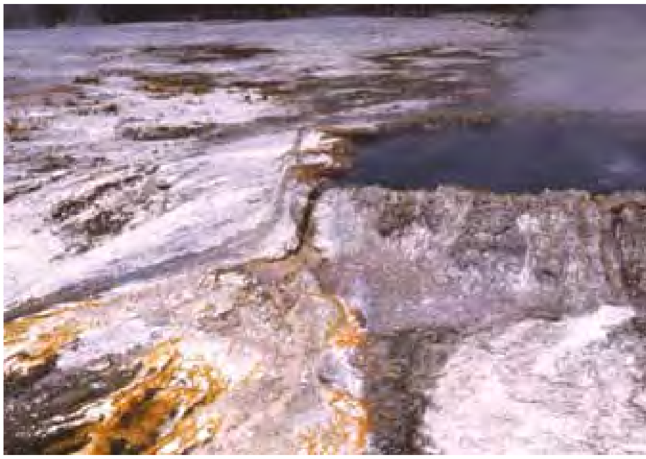
When a highly localized rare species occurs such as Yellowstone sand verbena, one of the major interests is to determine its reproduction biology. Pollinators were present at the primary site during a 2003 study, with *Noctuidae* (noctuid moths) appearing to be the flowers' most frequent visitors. Also likely transferring pollen were *Sphingidae* (hawk moths), butterflies, and bumblebees. However, rates of pollinator visits were very low, and probably adversely affected by strong and gusty winds and precipitation (Saunders and Sipes 2006). Investigation of the flowers showed that pollen viability was high on the first day of blooming but then dropped precipitously on subsequent days, while stigmas were receptive for all three days of anthesis (Saunders and Sipes 2006). Experimental hand-pollinations tests demonstrated that the flowers were capable of self pollination, probably because the floral morphology makes it possible for automatic self-pollen deposition (Saunders and Sipes 2006). The ability to produce viable seed in the absence of pollinators is fortuitous. Most of the species of *Abronia* whose reproductive biology has been investigated (*A. macrocarpa*, *A. latifolia*, *A. maritima*, and *A. umbellata*) are obligate out-crossers and therefore totally dependent on pollinators to successfully produce seed. Yellowstone sand verbena's mixed-mating system (both outcrossing and self pollination) enables it to survive even if pollinators are not present.

Survival for Yellowstone sand verbena is dependent on keeping the remaining population on the north shore viable. The habitat along the lakeshore is difficult, with cold long winters and summers that are extended dry periods punctuated by cold weather, high winds, and icy precipitation. Luckily, the plants are survivors, as demonstrated by their mixed-mating system, long blooming season, high seed set, and ability to tolerate and perhaps utilize some geothermal influence. As a group, though, sand verbenas are known to be highly susceptible to disturbance by people walking though the populations and trampling, so areas where the sand verbena persists need to be monitored to make sure that the plants are not receiving too much attention from hiking boots and sneakers.

Ross' bentgrass is a Yellowstone endemic, found only in the Upper, Midway, Lower, and Shoshone geyser basins.

Ross' Bentgrass

The unquestioned champion of endemic plants influenced by the geothermal system is Ross' bentgrass. Nestled into the warm cracks in sinter and depressed areas that in some locations almost resemble little natural greenhouse sites, it is restricted to areas of geothermal heat that are warm to the touch. As a grass, it didn't garner attention in the early years of the park. It was first collected in 1890 by Edith A. Ross of Davenport, Iowa, where she probably came into contact with and may have been mentored by one of the major botanical forces exploring the Rocky Mountains, C. C. Parry (Ewan 1950). Parry visited the park in 1873 and made disparaging remarks about the ubiquitous lodgepole pine. "Mile after mile of continuous forest may be traversed without seeing any other arborescent species, and their tall, straight, uniform trunks and scattering foliage will be always associated with the monotonous and disagreeable features of the park scenery" (Parry 1874). Whatever Parry thought of Yellowstone, it was Ross who discovered the bentgrass growing in the geyser basins along the Firehole River. The specimen eventually came to the attention of George Vasey, who described the bentgrass as a new species in 1892 and named it after Ross (Vasey 1892).



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The population of Ross' bentgrass at Punchbowl Spring was the only documented population until 1982.

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Growth of Ross' bentgrass is limited to areas of geothermal heat that are warm to the touch, usually cracks or depressions.

Ross' bentgrass remained elusive, being infrequently collected in the later nineteenth century and the first half of the twentieth century. The few specimens in herbaria (none of them in the Yellowstone Park Herbarium) were all from the Upper Geyser Basin, generally with labels that do not provide specific location information. A few specimens with more specific labels include those from near Beehive, Whistle Geyser, and Punchbowl Spring. As a consequence of the Endangered Species Act (ESA) of 1973, interest skyrocketed about the exact status of plants perceived to be rare in the United States. The Smithsonian nominated *Agrostis rossiae* for listing under the ESA in 1975. Investigations by Robert Dorn in the late 1970s and early 1980s failed to find the species at any location except Punchbowl Spring, leading to elevated concern about its status. Bob Lichvar of the Wyoming Natural Heritage Program came to Yellowstone in the spring of 1982 and visited the Punchbowl Spring population with Don Despain and myself. We determined that there was a small healthy population in the vicinity of Punchbowl and also located a patch on Geyser Hill near Anemone Geyser. During subsequent explorations I located additional occurrences in the Pine Springs area and in the Midway and Lower geyser basins. Today Ross' bentgrass is known to occur in the Lower, Midway, Upper, and Shoshone geyser basins.

Bentgrass (*Agrostis*) species are often cryptic without any obvious characteristics that enable reliable separation into the various taxa. Additionally, they are known for their ability to adapt rapidly to unusual edaphic conditions such as heavy metals associated with mining. Geothermal settings have provided another venue for the genus to demonstrate its versatility in the face of changing environmental factors. Traditionally, the two bentgrasses recognized in Yellowstone's thermal areas were *A. rossiae* and the widespread *A. scabra* (ticklegrass), which occurs throughout most of the northern portion of North America and possibly Asia. Examination of material in the geyser basins suggested that there two different entities were keyed to *A. scabra* in standard floras: an annual taxa which occurs in geothermal settings similar to where Ross' bentgrass was located, and a widespread perennial taxa that flowered later in the summer (Tercek 2003). Genetic investigations of other geothermal *Agrostis* taxa showed that *A. scabra* var. *geminata* from Lassen Volcanic National Park and *A. pauzhetica* from the Valley of the Geysers on the Kamchatka Peninsula of Russia are actually members of a widespread geothermal *Agrostis* complex and are closely related to both Ross' bentgrass and the annual *A. scabra* taxon present in Yellowstone (Tercek 2003). Ticklegrass, the perennial *A. scabra*, is not especially closely related even though it superficially resembles the thermal taxon. The thermal "*A. scabra*"

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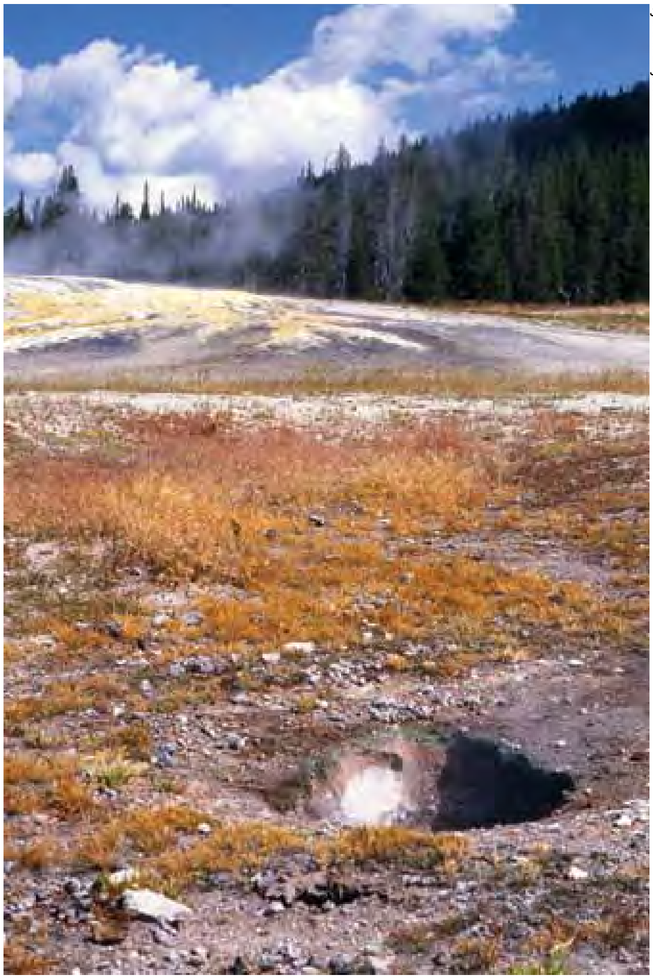
Park botanists survey the Upper Geyser Basin for Ross' bentgrass.



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Ross' bentgrass is constrained by its need for a "vapor-dominated," geothermally warmed site, like Geyser Hill.

*Geothermal settings have provided another venue for the genus [*Agrostis*] to demonstrate its versatility in the face of changing environmental factors.*

or "TAS" should be either included in a broad concept of a thermal *Agrostis* species or recognized as a variety or subspecies under this taxon. The problem, though, is what should be the correct scientific name? The oldest published name has precedence, but what is it? *A. rossiae*? Or is there a much older name that has been included within the broad concept of the perennial ticklegrass? To determine the correct scientific name for TAS, *Agrostis* specimens from all over the world need to be examined to decide which is the oldest appropriate name. Additionally, the actual distribution of TAS needs to be determined in order to determine whether this taxon is another rare species of geothermal areas, though in Yellowstone it is much more common than Ross' bentgrass.

Ross' bentgrass is easily overlooked in the geyser basins. The grass is short, usually two or three inches in height, but occasionally reaching up to 8 inches under ideal conditions. It is most conspicuous when it sprouts in December or January while non-thermal plants are covered in snow and dormant. The short green leaves attract the attention of herbivores in the geyser basins, so it is not unusual to find tufts of grass pulled out by an elk or bison trying to eat something that is barely an inch tall. Perennial grasses would withstand the grip of their teeth and remain in the ground, but Ross' bentgrass is a shallowly rooted annual so the whole plant is pulled out. Elk and bison cannot eat it without consuming a mouthful of gritty silicious soil so they spit it out and the plant dies. Luckily, most animals do not continue in this enterprise so most plants survive the winter season.

Even though Ross' bentgrass occurs in four geyser basins, its distribution is highly scattered and constrained by its requirement for a geothermally warmed site. Many locations in the thermal areas that superficially appear satisfactory are not occupied by the plants. The plants need a very precise location that usually occurs in "vapor-dominated" sites (Tercek 2004). Plants can occur on the walls of submerged thermal springs, along steaming cracks, or in thermally influenced depressions. None of these sites are normally flooded by geothermal activity, and they have a stable ground surface (loose sinter is not inhabited) and a stable, low geothermal temperature. All of the known populations are being surveyed by GPS for inclusion in the park's rare plant mapping layer. With most of the sites now surveyed, there is less than 12 acres of occupied habitat!

Besides needing the right conditions in December or January to sprout, the weather needs to be conducive for the plants to survive and then bloom in May or June, prior to being killed by the increasing soil temperature. Hot dry conditions early in the spring or changes in the thermal system

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Ross' bentgrass is easily overlooked in the geyser basins. The grass is short, usually two or three inches in height, can cause many plants to die early due to rising soil temperatures. Extreme conditions can highly restrict the number of plants that successfully produce seed in a particular year. There appears to be a good seed bank in the soil since the plants are able to migrate in response to change in the geothermal features. Casual observations during the last 20 years show that some sites have been remarkably stable, varying only in the number of individuals from year to year. In contrast, the occurrence near Whistle Geyser in Black Sand Basin has been extirpated, probably because of a change in geothermal activity and the spread of several exotic species into the one small area that could still possibly support Ross' bentgrass. Other sites have significantly expanded and contracted. At Calthos Spring, the extent of the bentgrass has been highly impacted by the height of the pool of water, being restricted to a crack system on the northwest side of the spring when the water is high and overflowing, but spreading when the pool is lower and temperatures are cool enough for plants to grow around the edges of the pool's former high water mark. The distribution of Ross' bentgrass, especially in the Upper Geyser Basin, is also affected by the presence of numerous nonnative annual species such as bluegrass, cheatgrass, speedwells, and chickweeds that can also grow in the presence of geothermal heat. The spread of nonnative species is the biggest threat to the survival of Ross' bentgrass (except for another caldera eruption!).

Ash clouds from Yellowstone volcanism may have spread remnants of previously endemic taxa from Yellowstone and permanently eradicated these unknown entities from the mark of history. Pleistocene glaciation and the icecap in the region of the park also may have contributed to the extirpation of many plant species from the immediate area. Even though a respectable number of taxa occurr within the park (about 1,440), the level of vascular plant endemism in the park is less than in many areas of the surrounding states. But the Yellowstone volcanism represented by the continuing geothermal presence on the plateau has allowed the speciation and/or survival of these three fascinating endemic taxa of Yellowstone. Hopefully, Yellowstone buckwheat, Yellowstone sand verbena, and Ross' bentgrass will survive and prosper well into the future.

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NPS/HEKTNER

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Yellowstone's Most Invaded Landscape

Vegetation Restoration in Gardiner Basin

E. William Hamilton, III and C. Eric Hellquist

COURTESY OF THE AUTHORS

Gardiner Basin as seen from rocky mudflows over former agricultural fields. The light green coloration of the flat fields is almost entirely desert alyssum, May 2007.

Located at the north entrance of Yellowstone National Park, Gardiner Basin is probably one of the most overlooked areas in Yellowstone despite its easy accessibility by car and its proximity to the town of Gardiner, Montana. Extending along the Yellowstone River from Gardiner to Yankee Jim Canyon, Gardiner Basin consists primarily of a grassland ecosystem classified as an arid to semi-arid cold desert that experiences cold winters and hot, dry summers (fig. 1). Precipitation averages about 25 cm annually, with approximately 30% of the precipitation occurring from March to June (National Park Service 2005). For the visitor with an eye for landscape features and geology, Gardiner Basin has a complex history characterized by glacial features, riverine and flood deposits, and undulating landslide hillocks at the base of Sepulcher Mountain (National Park Service 2005). Large ungulate grazers in Yellowstone spend winter months in low elevation range (Frank and McNaughton 1992) and Gardiner Basin is a migration corridor for bison, pronghorn, and elk along the park's northern border adjacent to Paradise Valley. However, the quality of winter forage in this important migration corridor has been reduced by the prominence of invasive plant communities. Gardiner Basin has the most extensively invaded expanses of grassland in Yellowstone due to its 125-year history of human use, agriculture, and disturbance (Olliff et al. 2001).

Gardiner Basin has a rich human cultural history including Native American occupation features. The railroad passed through the basin where the former town of Cinnabar was the initial terminus of the Northern Pacific Railroad. Theodore Roosevelt arrived at Cinnabar prior to entering Yellowstone during his 1903 vacation. From the late 1880s to the early 1900s, Gardiner Basin was planted and irrigated. The cultivated lands between Reese Creek and Gardiner were annexed to Yellowstone in the 1930s and this agricultural history of Gardiner Basin has contributed greatly to its current ecology (National Park Service 2005). Today invasive plant communities that provide poor quality forage dominate the former agricultural fields. This lack of quality forage is especially problematic for pronghorn, a species that has been in decline across Yellowstone, but is a regular grazer in Gardiner

The town site of Cinnabar circa 1900. Photo by Paul Hoppe, as reproduced on page 15 of *A Photo History of Aldridge: Coal camp that died a-bornin'* by Bill and Doris Whithorn. Printed by Acme Print and Stationary, Minneapolis, Minnesota, 1965.

Basin (National Park Service 2005). In recent years, Gardiner Basin has also been an area of activity related to the movement of bison across the park boundary and onto adjoining private land and national forest.

Most of Gardiner Basin is of the bluebunch wheatgrass-Sandberg's bluegrass habitat type (Despain 1990). Native plant communities that remain on rocky, uncultivated soils in Gardiner Basin are characterized by needle and thread grass (*Hesperostipa comata)*, Sandberg bluegrass (*Poa secunda*), bluebunch wheatgrass (*Pseudoroegneria spicata)*, prairie junegrass (*Koeleria macrantha)*, and plains prickly pear (*Opuntia polyacantha*). However, these native communities are increasingly colonized by a variety of invasive plants that are most abundant at the former agricultural fields, including desert alyssum (*Alyssum desertorum)*, crested wheatgrass (*Agropyron cristatum)*, cheatgrass (*Bromus tectorum)*, annual wheatgrass (*Eremopyrum triticeum)*, and prickly Russian thistle (*Salsola tragus)*. The dominance of this invasive plant community within an important ungulate corridor (~500 ha) has made understanding and restoring the ecology of Gardiner Basin a priority for both scientists and resource managers (National Park Service 2005).

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A pronghorn traversing a former agricultural field near Stephens Creek, May 2007.

Invasive Plants' Influence on Above- and Below-ground Interactions

Invasive species are considered the second most significant threat to the world's biodiversity after habitat loss (Wilcove et al. 1998). In Yellowstone, where invasive plant species represent about 15% of the flora (Whipple 2001), species invasions threaten to degrade the park's cultural, ecological, and historic resources (Olliff et al. 2001). These introduced plants may be the most significant human-initiated alteration of Yellowstone's vegetation (Despain 1990).

Phenological differences between native and invasive plants can lead to changes in succession and related community attributes (Walker and Smith 1997; Woods 1997). However, the presence of invasive plants has ecological consequences beyond the replacement of native plant communities. Invasive species can disrupt ecological relationships that are much more subtle and difficult to measure. Plants directly influence their environment and the organisms that consume their tissues through their biochemical properties (Schlesinger 1997; Bardgett 2005). Plant traits such as biomass production, litter quality, and nutrient acquisition can influence soil conditions including temperature, pH, water content, nutrient availability, and soil texture (Bardgett 2005). Simultaneously, the soil biota, including fungi, bacteria, archaea, and invertebrates, are driving nutrient cycling processes that affect plant community dynamics (Bardgett 2005). Thus, the interactions between plant characteristics and soil biota determine the conditions under which plant-soil feedbacks and their community consequences occur (Ehrenfeld 2004; Bardgett 2005; Eviner and Hawkes 2008). Feedbacks between plants and microbial communities may promote the persistence or replacement of both above- and belowground communities as well as rates of nutrient cycling (Blank and Young 2002; Bardgett 2005; Harris et al. 2005; Raich and Tufekcioglu 2000; Wardle 2005; Wolfe and Klironomos 2005). Positive feedbacks between plants and microbes play a central role in early successional communities and feedback dynamics are related to specific plant-microbe associations (Reynolds et al. 2003).

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A community of exotic plants dominated by annual wheatgrass and desert alyssum bordering a native dominated community characterized by needle and thread grass, July 2006.

As the importance of plant-soil feedbacks has gained increased recognition and research effort, the role of plant-soil feedback relationships within the context of invasion ecology has become a topic of great interest (Ehrenfeld 2003, 2004; Bardgett 2005; Reinhart and Callaway 2006). The morphological and chemical traits of invasive and native plants can be an important influence on microbial community composition and the ecosystem processes that they mediate (D'Antonio and Hobbie 2005; Wardle 2005; Wolfe and Klironomos 2005). However, an understanding of how invasive plants can alter nutrient fluxes and storage by changing physical characteristics of habitats and the composition of the soil biota is just beginning to emerge (Ehrenfeld 2004; Eviner and Hawkes 2008; Heneghan et al. 2008).

The impacts of plant invasions on above- and belowground succession are diverse. Plant invasions can facilitate further colonization by exotics (Reinhart and Callaway 2006; Jordan et al. 2008), reduce growth of native plant species (Jordan et al. 2008), change nutrient conditions (Evans et al. 2001; Scott et al. 2001; Holly et al. 2008), influence microbial community composition of soils (Kourtev et al. 2002; Duda et al. 2003; Holly et al. 2008), and may impede restoration efforts (Jordan et al. 2008). Due to habitat heterogeneity and the diversity of plant species and traits, predicting the magnitude of the effects of exotic species on soil quality is difficult (Scott et al. 2001; Eviner and Hawkes 2008). However, recent applications of molecular tools such as polymerase chain reaction (PCR) can help ecologists identify important shifts in prokaryotic community composition and function that may occur in response to changes in soil conditions influenced by plant species characteristics (Hawkes et al. 2005).

As invasive plants become more integrated into Yellowstone's plant communities, they become part of a complex ecological web that includes the soil biota and the grazers that eat or avoid the invasive plants. The confluence of historical and ecological events in Gardiner Basin is providing an exceptional opportunity to examine feedbacks between plants and nitrogen-cycling microbial communities in a context of exotic plant invasion and a major National Park Service habitat restoration effort.

Vegetation Restoration in Gardiner Basin

During the late 1940s–1950s a ranchland conversion effort occured in Gardiner Basin. The effort attempted to foster rangeland conditions and provide a winter forage base for ungulates, by planting crested wheatgrass (*Agropyron cristatum*), a species well-adapted to arid conditions. Crested wheatgrass is now recognized as an undesirable invasive species in the American West, with no real winter forage value to native ungulates. However, in the last 15–20 years an exotic mustard, desert alyssum (*Alyssum desertorum*), has greatly expanded its coverage in that area (National Park Service 2005). Desert alyssum now forms near monocultures (A and B, below) in the

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Drying desert alyssum in the foreground with green desert alyssum in the center (A). A patch of desert alyssum showing abundant seed pods (B), May 2007.

The dominance of this invasive plant community within an important ungulate corridor has made understanding and restoring the ecology of Gardiner Basin a priority for both scientists and resource managers.

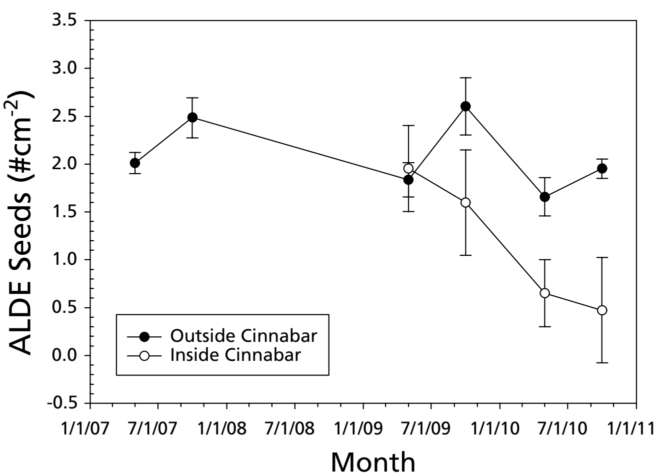


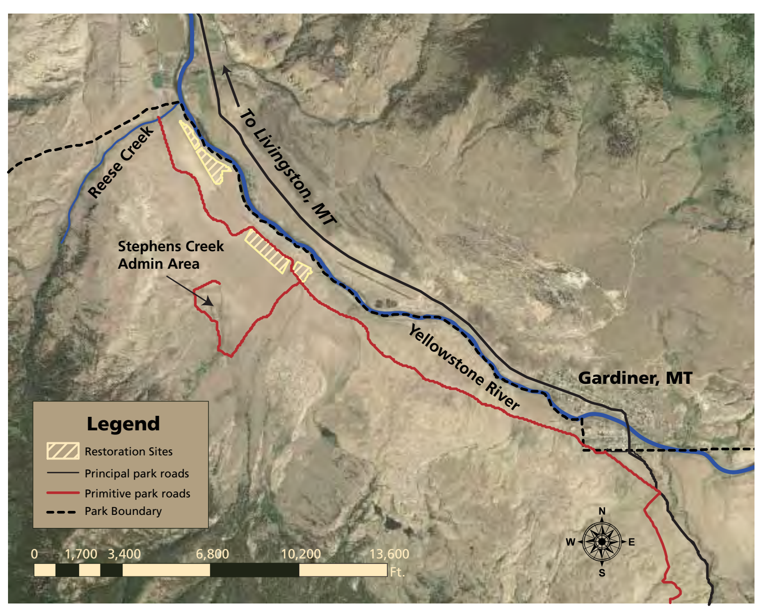
Figure 1. Mean (+/-1SE) *Alyssum desertorum* (ALDE) seed bank germination inside and outside the Cinnabar exclosure. The top 1 cm of soil was collected, stored at 4°C and germinated within 2 days of collection by moistening the soil to return water content to 50% of field capacity. Cumulative total seed counts were determined over 10 days.

former agricultural fields and produces copious seeds (fig. 1), with annual seed banks of 3.1+/-0.4 seeds cm^{-1}. It is colonizing surrounding landslides and mudflows, and becoming more abundant in the Mammoth Hot Springs vicinity as well as in dry soils across the park's northern range.

Led by vegetation specialist Mary Hektner, the Yellowstone Center for Resources convened a workshop with the Gallatin National Forest and the Montana State University Center for Invasive Plant Management to seek ideas for the restoration of Gardiner Basin (National Park Service 2005). The working group concluded that (1) the agricultural soils in the basin had been severely degraded chemically and physically, (2) restoration would be challenging due to the low precipitation, high winds, ungulate use, and the extent to which invasive plants were established in the basin, (3) obtaining native seed to restore the site would be a logistical challenge, and (4) setting restoration goals would be difficult because of a lack of similar efforts that could be used as a reference to assess progress in Gardiner Basin (National Park Service 2006).

After developing an incremental restoration agenda, in 2008 the National Park Service erected exclosures at Cinnabar (10.5 ha), Stephens Creek (3.0 ha), and Reese Creek (8.1 ha) (fig.2). These exclosures will remain in place for approximately 10 years so that researchers can test the feasibility of restoring native arid vegetation to Gardiner Basin and study how plant communities, microbial communities, and soil quality are linked. These test exclosures will also be used to help establish and revise protocols for vegetation restoration projects throughout the park (National Park Service 2006).

The first step of the pilot vegetation restoration project involved applying herbicides to kill the standing invasive plant communities. At the Cinnabar exclosure, invasive plants were killed in May of 2009 and 2010, and the soil was seeded with a cover crop of barley (*Hordeum vulgare*) and winter wheat (*Triticum aestivum*) in October 2009 to prevent soil erosion, augment organic matter in the soil, and deter recolonization by exotic species. The Stephens Creek and Reese Creek exclosures were seeded in May 2010. Following successful soil stabilization through the use of cover crops, native species will be no-till drilled into the stubble crop in the second or third year. The native grassland seed mix, collected by the US Department of Agriculture, Natural Resource Conservation Service, will approximate native plant communities near Gardiner Basin, including Sandberg bluegrass (*Poa secunda*), bluebunch wheatgrass (*Pseudoroegneria spicata*), green needlegrass (*Nassella viridula*), needle and thread grass (*Hesperostipa comata*), prairie junegrass (*Koeleria macrantha*), and western wheatgrass (*Pascopyrum smithii*).



NPS/GIS

Figure 2. National Park Service restoration exclosures.

A National Park Service restoration exclosure with rows of barley cover crops in the foreground. Barley is used to condition the soil by adding organic matter that should facilitate the establishment of native plants that will be seeded into the exclosures in the coming years, October 2010.

How are Native and Invasive Plant Communities Related to Soil Communities?

Since 2007, we have been trying to understand how the dominant invasive plant communities of Gardiner Basin have altered plant-soil feedbacks and how these feedbacks may change as exotic vegetation is replaced by native species during the restoration project. Restoration of degraded grasslands with native species can have positive effects on soil microbial communities and soil quality (McKinley et al. 2005). As plant species turn over during vegetation restoration, so will microbial communities. In a Midwest grassland where microbial communities recovered in restoration sites, the longer the restoration period, the more similar (although not identical) microbial parameters became compared to native conditions (McKinley et al. 2005).

Succession of microbial communities will initiate a change in nutrient cycling dynamics. In Gardiner Basin, enhancing the success of the vegetation restoration will require knowledge of prokaryotic community composition linked to transitions in plant communities and the related ecosystem processes mediated by plant-microbial interactions. In addition, the "ecological legacies" of long-established invasive plant communities will need to be overcome by restoration and management practices (D'Antonio and Meyerson 2002; D'Antonio and Hobbie 2005).

We have been collecting data at locations across Gardiner Basin based on the presence of invasive species in relation to native species. Our work is using a variety of ecological data to better understand the chronosequence of above- and belowground plant and prokaryotic succession as influenced by management in Gardiner Basin. We are attempting to determine whether plant species invasions in Gardiner Basin leave an ecological legacy with regard to prokaryotic abundance, community composition, and nutrient cycling. Understanding belowground consequences of plant species turnover will enhance the efficacy of National Park Service management practices and will allow for better use of time and resources during subsequent restoration efforts.

Our initial efforts focused on sampling small areas where native plants were growing in close proximity to distinct patches of invasive plants. We took soil cores from these patches and then analyzed the composition of microbial communities from soils associated with native or invasive plant colonization. Microbial communities were identified based on DNA restriction fragment patterns from universal prokaryotic 16s rRNA gene primers. We analyzed the relationship between microbial genetic diversity and plant community context by clustering samples based on their shared community characteristics (non-metric multi-dimensional scaling analysis). This analysis organizes data so that the samples with the most similar microbial community composition are grouped closely together whereas samples with dissimilar genetic markers are placed farther apart (fig. 3).

Our analysis of these genetic markers showed different microbial community composition associated with soils from native plants than in soils with invasive plants (fig. 3). Genetic marker richness was highest in native sites (26±3 markers). Samples from soils colonized by exotic grasses had marker richness of 18±4 markers; the exotic mustard desert alyssum had the least diverse microbial communities (12±5 markers). These data indicate that the community composition of microbes that live among the roots of invasive and native plants is dependent on plant neighbor identity. Not only are invasive species changing the outward appearance

Grassland community dominated by native needle and thread grass, July 2006.

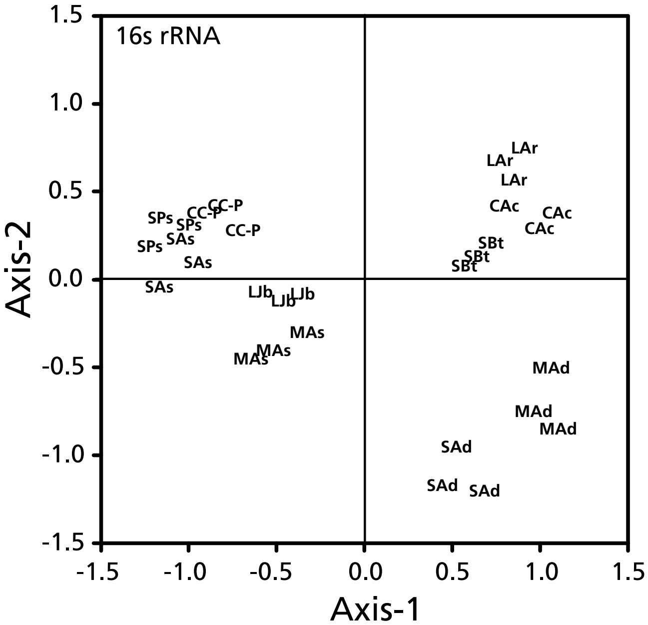


Figure 3. Ordination (NMDS) analysis of DNA restriction fragment (T-RF) patterns for a universal bacterial primer (16s rRNA gene) in four Gardiner Basin sites sampled in May 2007. Axes 1 and 2 explained 53% and 32% of the variance, respectively, and microbial biomass carbon was significantly correlated with Axis 1 (r^2=0.47).
S (Stephens Creek), C (Cinnabar), L (Landslide Creek), M (Mudslide). Ps=*Poa secunda* (native), Jb=*Juncus balticus* (native) C-P=*Carex-Poa secunda* (native), As= *Agropyron* (*Pascopyrum*) *smithii* (native), Ad=*Alyssum desertorum* (invasive) Ac=*Agropyron cristatum* (invasive), Ar=*Agropyron repens* (invasive).

and plant community composition of Gardiner Basin, but they reduce microbial diversity in the soils in which they are rooted. These data point to possible legacy effects of invasive species on the rehabilitation and restoration of ecological function of Gardiner Basin soils.

To describe potential land use legacies and plant-soil feedbacks related to invasive and native plant communities, we quantified total microbial populations using functional gene primers specific to bacteria and archaea (Dahllof et al. 2000). We extracted DNA from bare soils with no plants and DNA from soils colonized by native and invasive species of interest. Our sampling was conducted in uncultivated and formerly cultivated Gardiner Basin soils. By comparing native and invaded bare ground samples for bacterial and archaeal abundance, and subtracting bare ground gene copy numbers, we found a significant land use legacy following colonization by invasive plants (fig. 4). In general, plant species growing in native soils had greater genetic diversity than bare ground samples except for samples collected among *A. desertorum.* Thus, our data indicate that native soils have greater abundance of bacteria and archaea than invaded soils. For ecosystem restoration, it appears that microbial community composition will require continued monitoring in order to determine if plant-soil interactions have been returned to the full complexity exhibited in Gardiner Basin soils that are not colonized by invasive plant species.

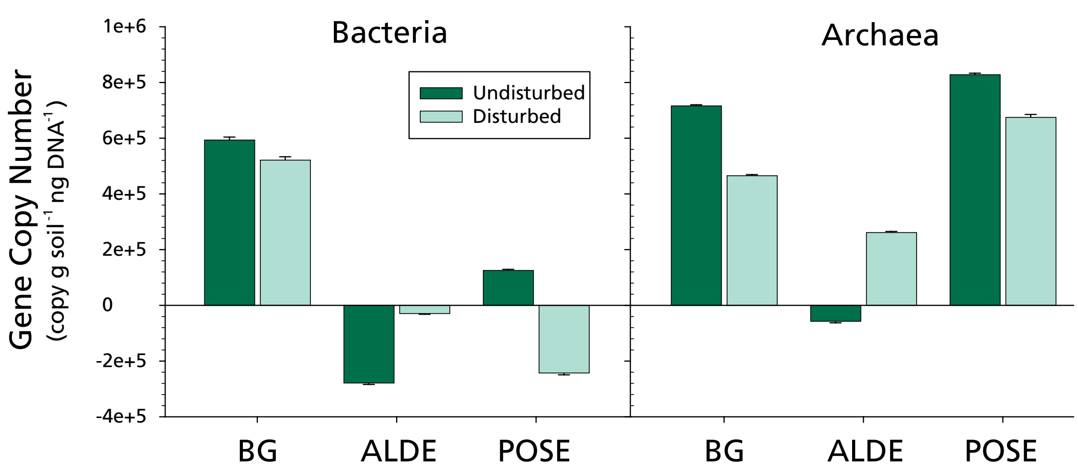


Figure 4. Mean (±1SE) gene copy number in bare ground soils (legacy effects) and from species-specific soils. The values for species-specific soils have had the gene copy number for bare ground subtracted to identify plant-soil feedbacks. Composited soil cores were collected by combining three cores for each sample (*n*=4) in April 2009. The native site is undisturbed and the invasive site is ex-arable since the 1930s. BG (bare ground), ALDE (*Alyssum desertorum*), and POSE (*Poa secunda*).

How are Microbial Patterns in Soils Related to Organic Matter?

The fertility of soils is influenced by the resident plants. As plants senesce, they donate organic matter that decomposes within soils. Plants affect the quantity and quality of organic matter in soils (Schlesinger 1997), which contributes to the composition of soil communities that determine nutrient availability (Bardgett 2005). Soil organic matter characteristics have significant effects on community composition and interactions within soils (McLauchlan et al. 2006). In a survey of 71 soils collected in the United States, organic matter (C availability) has been identified as the best predictor of bacterial abundance at the phylum level (Fierer et al. 2007). Soil organic matter also has important links to soil fertility via nitrogen cycling. To maintain high levels of grassland productivity, microbes need to take up more N than they release into the environment. This relationship is dependent on the relative mobility of C in the soils and the N content of organic matter that originates from the established plant communities. Maintaining microbially mediated soil N levels is critical for plant communities to persist or, in the case of restoration, to recover. Agricultural practices such as tilling and irrigation that took place in Gardiner Basin can reduce soil organic carbon availability (Amundson 2001), which can directly impact soil decomposition rates as well as N and C cycling. Thus, not only are the invasive plants detrimental to microbial communities, but the different organic matter quality of invasive species may serve as an impediment to habitat restoration.

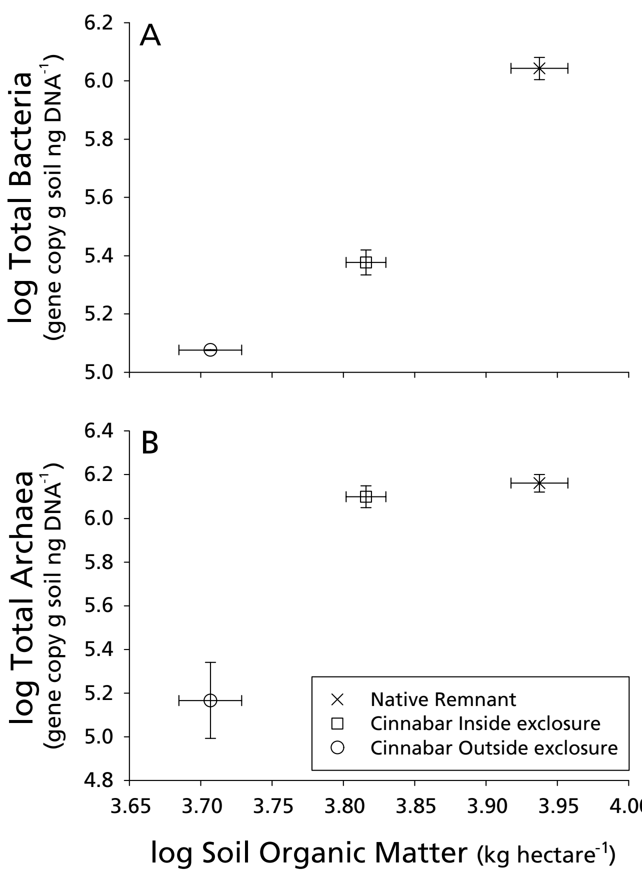


Figure 5. Mean (+/-1SE). A) log total bacterial gene copies as a function of log soil organic matter. B) log total archaeal gene copies as a function of log soil organic matter. Data collected (n=5) in April 2010 from three Gardiner Basin sites.

Evaluating microbial communities is a critical tool for determining soil quality and the progress of restoration programs (Harris 2003). In our data from three sites in Gardiner Basin and from the Cinnabar exclosure that has been planted in barley for two growing seasons, the range of soil organic matter varies up to 40% (fig. 5). One growing season of barley increased soil organic matter in the exclosure 22% compared to soils outside the exclosure. Total bacteria determined by PCR methods increased as soil organic matter increased (fig. 5A), and total archaea showed the same trend (fig. 5B). These data identify soil organic matter as a variable that can be manipulated in the field to elucidate underlying plant-microbe feedback mechanisms.

In ecologically sensitive public lands such as Yellowstone, studying plant invasions combines questions of basic ecological merit with questions of management and conservation importance (D'Antonio and Hobbie 2005). Our ongoing research describing plant-soil feedbacks, ecosystem processes (e.g., respiration and N transformations), and microbial community composition will enhance our understanding of microbial community turnover as influenced by plant community contexts in Gardiner Basin. The data collected to date shows that the early restoration efforts of herbicide treatment and growing a cover crop of barley is an effective strategy for improving soil organic matter and increasing the abundance of soil microbes, which will improve the chances of successful establishment of native plant species. We hope that our data will provide valuable insights for Yellowstone scientists, land managers, students, and individuals with an interest in the conservation and restoration of Gardiner Basin as well as similar public lands. This project represents an exciting integration of interdisciplinary techniques (field ecology, physiological ecology, and molecular biology) to answer ecological questions in a framework of community ecology, ecosystem ecology, ecological theory, and applied restoration ecology. For vegetation restoration to be successful in Gardiner Basin or anywhere else, belowground processes must be understood and promoted so that feedbacks between above- and belowground biota can flourish.

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From the Archives

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Hugo Hoppe founded the town of Cinnabar in 1883. Few images exist of the short-lived, but critical, railroad town. Looking west toward Electric Peak, we see the hotel and store captured in a glass plate negative from Norman A. Forsyth's series *Yellowstone and Wyoming,* circa 1900. The town site was abandoned in 1903, after the railroad depot moved to Gardiner, Montana—three miles closer to Yellowstone National Park.

The printing of *Yellowstone Science* is made possible through a generous annual grant from the nonprofit Yellowstone Association, which supports education and research in the park. Learn more about science in Yellowstone through courses offered by the Yellowstone Association Institute and books available by visiting *www.yellowstoneassociation.org.*

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