Plants Exposed to High Levels of Carbon Dioxide in Yellowstone National Park

A Glimpse into the Future?

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Ross' bentgrass (*Agrostis rossiae*), which is endemic to Yellowstone, often grows in areas with very high carbon dioxide concentrations.

HUMANS ARE CURRENTLY conducting a biology experiment on a planetary scale. Earth's ecosystems are being altered to such a degree by our collective activities that scientists have recently coined the term "anthropocene" to describe the current geologic age (Crutzen and Stoermer 2000) because human impacts such as land use and industrial pollution have grown to become significant geological forces, frequently overwhelming natural processes.

The burning of fossil fuels is often cited as a prime example of how we are exerting major effects on the environment. This, along with deforestation, has resulted in a 50% increase in atmospheric carbon dioxide (CO_2) since 1800. The latest estimates are that the level of this atmospheric "greenhouse gas" will more than double within the next 100 years (Solomon et al. 2007). Although the link between increasing atmospheric CO_2 and global warming has long been controversial, the vast majority of scientific evidence now strongly supports this connection (see the most recent reports from the Intergovernmental Panel on Climate Change at http://www.ipcc.ch). The general conclusions from these reports are that significant increases in both Earth's atmospheric CO_2 concentration and average air temperature will occur within this century, at historically unprecedented rates.

Such environmental changes will be extremely rapid from the perspective of biological evolution. For example, it is unclear how individual plant species and plant communities will adapt to an abruptly warmer, high-CO_2 world. These are critical questions since we depend on plants for food, fiber, and fuel, and since plants usually provide the foundation for biotic communities. Recent studies show that natural ecosystems are already responding to human-caused environmental changes (see Cleland et al. 2007 for example). But how will natural ecosystems respond to the predicted higher CO_2 levels and warmer temperatures compared to today? Plant communities that already exist under such conditions may help provide answers.

Areas with surface geothermal activity, such as Yellowstone, offer environments that often contain high CO_2 because of volcanic gas vents, and they have high temperatures due to geothermal heat. Until recently, virtually nothing was known about the magnitude of Yellowstone's CO_2 emissions, how widespread they were, or which plant species grew near them. Here we report on the first concerted effort to study and characterize plant communities exposed to high levels of CO_2 in Yellowstone National Park (YNP). Our results show that Yellowstone offers rare, natural environments for scientists to investigate the long-term effects of increased CO_2 and high temperatures (both separately and in tandem) on plants.

Background: Responses of Plant Communities to CO_2 Enrichment

In the past 20 years, scientists have been conducting both greenhouse and field experiments in order to predict how plants will respond to elevated CO_2 levels of 500 to 800 parts per million (ppm) compared to the current "background" CO_2 concentration (about 380 ppm). Most of these investigations have used either small-scale growth chambers or free air CO_2 enrichment (FACE) facilities that pump CO_2 into several acres of crops, natural grassland, or forest (Long et al. 2005; Long et al. 2006). To a much lesser extent, studies have been conducted using natural CO_2 springs (see below). It is important to realize that the physiological responses observed in plants during these experiments help us predict how productive our food crops will be and how nutritious forage species will be for grazing animals in a high-CO_2 future. These physiological changes might also determine whether some plant species survive in their current natural habitats or are marginalized or eliminated by invading plant species.

The growth chamber and FACE studies have produced somewhat complex results, but they agree in many generalities (Korner 2000). In summary, the growth chamber studies tend to indicate that higher levels of CO_2 increase crop production. However, outdoor experiments using FACE facilities tend to show that the benefits of high CO_2 on plant productivity have been overestimated and may be only short term (Long et al. 2006). At the physiological level, elevated CO_2 usually produces an increase in leaf biomass, a decrease in nitrogen content per unit of biomass, and higher water use efficiency, which is the amount of water used per unit of biomass production. We discuss these findings in more detail below.

The influence of elevated CO_2 on plant productivity is not consistent, and it partly depends on whether there are enough resources available to support a higher photosynthetic rate. Carbon dioxide is the fuel for photosynthesis, and it is in relatively short supply in our atmosphere (less than 0.04%). Therefore, it is easy to understand why increasing CO_2 availability to plants might increase photosynthesis and boost biomass production. However, plants need a variety of nutrients in order to maintain their metabolism, and carbon is only one of them. If increased carbon availability (increased atmospheric CO_2) is not accompanied by an adequate supply of other resources, particularly nitrogen, then there will be little change in plant growth rate.

Even though adequate nitrogen supply is crucial to maintaining productivity gains in the long term, an enriched CO_2 environment may allow plants to use nitrogen more efficiently. FACE studies have shown that plants often respond to extended CO_2 enrichment by reducing the concentration of their main photosynthetic enzyme, ribulose bisphosphate carboxylase (RuBisCo) (Ellsworth et al. 2004). RuBisCo captures CO_2 and begins the process of photosynthetic conversion of this gas into sugars. Usually RuBisCo is by far the most abundant protein in leaves. Plants make less RuBisCo under high-CO_2 conditions, presumably because they do not need as much of this enzyme for photosynthesis and because it allows them to conserve nitrogen. Consequently, the plant material may have less protein content per amount of biomass and, thus, less nutritional value as forage. For this reason, some think that increased atmospheric CO_2 would likely have a negative impact on grazing animals, such as the bison and elk in YNP (Wilsey, Coleman, and McNaughton 1997).

Finally, increased CO_2 supply usually increases water use efficiency in plants. This is chiefly because stomates (the cellular pores in leaves that allow for gas exchange) tend to close when CO_2 levels increase. When opened, the stomates allow CO_2 to enter the leaf and water to escape. Land plants try to conserve water by closing their stomates if CO_2 concentration increases. This could affect the species composition of many plant communities as plants invade drier areas in which they could not grow previously and other species are eliminated.

These are only a few of the ways in which plants respond to increased CO_2. We have not addressed the issue of increased temperatures due to global warming. It's easy to see why reliably predicting the botanical effects of increased atmospheric CO_2 is highly problematic at the whole-plant level and even more so at the plant community level.

So far, we've mainly discussed how plants can acclimate to sudden increases in atmospheric CO_2. But in the long term (decades, centuries) will these conditions exert pressures through natural selection that result in genetic adaptations to elevated CO_2? And if so, what will likely be the nature of these adaptations?

Studies Using Environments Naturally High in CO_2

In attempts to answer these questions, scientists have examined plants growing near natural CO_2 springs and, to a much more limited extent, plants around seams of burning coal deposits (Raschi et al. 1997; Badiani et al. 2000; Pfanz et al. 2004). High-CO_2 environments often occur in areas of volcanic activity and are manifested as "mofettes" (carbon dioxide springs), CO_2 vents, or elevated CO_2 gas flux from the soil. Though not as controllable as greenhouse or FACE experiments, these natural high-CO_2 environments provide opportunities to examine relatively long-term adaptations of plants to high CO_2. Most studies of this kind have been from sites in Europe, primarily Italy (Raschi et al. 1997); few have been from North America. As with the above greenhouse and FACE experiments, some consistent patterns emerge, including increased biomass production and higher water use efficiency.

Even though they have contributed useful information, previous studies conducted near natural sources of CO_2 have significant drawbacks. Typically, they are limited in geographic scope, are often located in regions disturbed by human populations, and are usually not directly comparable with similar, background-CO_2 sites. Because YNP encompasses one of the largest surface geothermal areas on Earth, and since it has been relatively undisturbed by humans, most of these drawbacks may be avoided.

Like other large volcanic and hydrothermal areas on Earth, Yellowstone emits a large volume of gases, predominantly CO_2 (95–99%) (Kharaka, Sorey, and Thordsen 2000; Werner and Brantley 2003). Despite this, there have been only a few reports of the effects of CO_2 on photosynthetic algae found in Yellowstone hot springs (e.g., Rothschild 1994) and none, to our knowledge, involving plants. Therefore, we set out to explore the possibility that plants and plant communities are chronically exposed to high levels of CO_2 in YNP.

Methodology

CO_2 Measurements. To measure carbon dioxide in the field, we used several different portable CO_2 gas analyzers (see glossary). Since our initial work was largely exploratory in nature, these instruments were used to make relatively short-term (15 to 30 minutes) CO_2 measurements at multiple locations within selected study areas. At each location we measured soil temperature and pH, and noted the predominant plant species. Once high-CO_2 locations were identified, more measurements were periodically made at some locations to better establish average long-term CO_2 levels. Leaf tissue specimens were collected from hot springs panic grass (*Dichanthelium lanuginosum*) and other species at some of these high-CO_2 locations and at background-CO_2 locations nearby for subsequent laboratory analyses to test the presumption that plants in these areas were indeed chronically exposed to elevated CO_2. Two indicators of plant exposure to elevated levels of CO_2 are (1) a decrease in the key photosynthetic enzyme RuBisCo and (2) an increase in the soluble sugar sucrose. Sucrose (along with starch) is a major metabolic end-product of photosynthesis.

RuBisCo Measurements. As previously mentioned, plants typically make less RuBisCo when exposed to high levels of CO_2, presumably to conserve nitrogen. We used two independent methods to determine the relative amounts of RuBisCo in leaf specimens collected in YNP. In the first technique, we used commercially available antibodies that specifically bind to RuBisCo. Such antibodies can be used in immunoassays (see glossary) in order to identify and quantify proteins, even in complex mixtures. In the second technique, we specifically tagged all the RuBisCo proteins in our leaf extracts with a radioactively labeled substance (Evans and Seeman 1984) and then determined the radioactivity of each sample. The higher the radioactivity in the sample, the more RuBisCo was present. Though a bit more involved, this method is much more accurate than the antibody method.

Soluble Sugar Analysis. At elevated levels of CO_2, leaves typically contain more sugars, mainly sucrose, presumably because of higher photosynthetic rates. We extracted soluble sugars from our leaf tissue specimens and used a technique called high performance liquid chromatography (HPLC; see glossary) to identify and measure each sugar.

Results

Surveys of Suspected High-CO_2 Areas in Yellowstone. We found 15 sites in YNP that had consistently elevated CO_2 concentrations (Fig. 1). Fourteen of these sites contained several high-CO_2 plant communities, ranging in surface area from 1 m^2 to greater than 10 m^2. The fifteenth site, Death Gulch, also had very high CO_2 emissions, but its famously lethal crevices (Haines 1996) did not contain vegetation in the areas nearest to the CO_2 vents.

Most of the sites contained vegetation that is typical of thermal areas, such as hot springs panic grass, Ross' bentgrass (*Agrostis rossiae*), and the moss *Racomitrium canescens.* However, several plant communities near Mammoth, Mud Volcano (Ochre Springs), Geyser Creek, and Sylvan Springs that were distant from obvious thermal activity included lodgepole pine (*Pinus contorta*), juniper (*Juniperus communis*), or a variety of non-thermal forbs, grasses, and sedges. Without an infrared gas analyzer, we would not have suspected that these areas contained volcanic vents. Soil temperatures a few inches below the soil surface in our survey ranged from non-thermal (about the same as air temperature) to 45°C (113°F).

In this article we offer representative data for two of the areas that we have identified with above-normal CO_2: Mammoth Upper Terraces and Mud Volcano (Figs. 2 and 3). An interactive version of our entire survey is available online at http://www.YellowstoneEcology.com/research/co2/index.html. It includes photographs, graphs of our CO_2 measurements, and lists of the plant species present at each site.

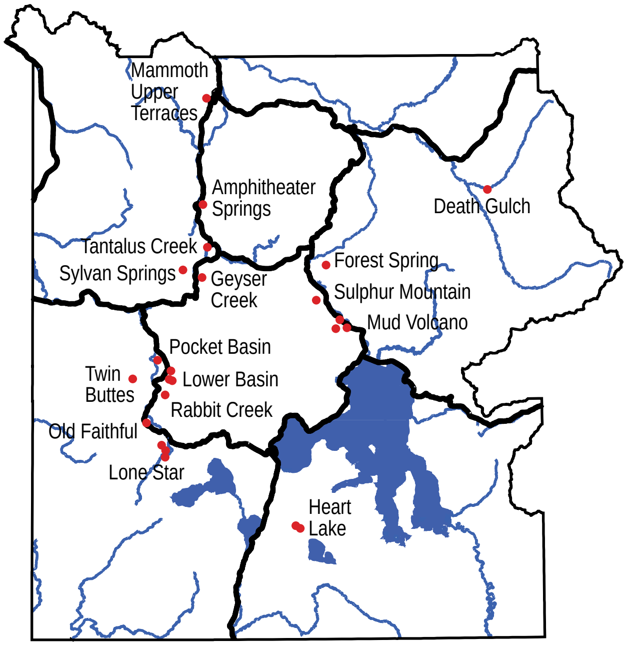


Figure 1. Each location marked on the map contains from 2 to 30 plant communities growing in above-normal CO_2 concentrations.

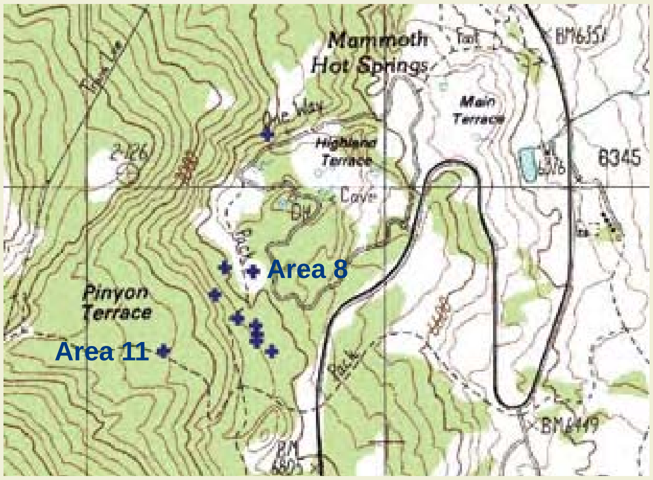
GLOSSARY

CO_2 Gas Analyzers. Because the IR (infrared) light spectrum absorbed by a particular chemical compound is unique, it can serve as a signature or fingerprint to identify that molecule. An infrared CO_2 gas analyzer consists of a light bulb that generates an IR light beam that is passed through the sample and an IR light detector set to the precise IR spectrum of CO_2. The more CO_2 present in the sample, the more IR light in this spectrum is absorbed, and the lower the amount of IR light detected.

HPLC. High-performance liquid chromatography (HPLC) is used frequently in biochemistry and analytical chemistry. Chromatography is a general term for laboratory techniques used to separate mixtures of substances. Typically, it involves passing a mixture (the "mobile phase") through a so-called "stationary phase," often packed into a small tube or column. The stationary phase may consist, for example, of cellulosic beads or of synthetic resins that separate substances on the basis of size, charge, etc. In our case, a mixture of sugars in an aqueous solution is slowly pumped through a chromatography column, and the sugars are separated on the basis of size, with the larger molecules emerging from the column faster than the smaller ones. (The column is calibrated by first running through known sugars, each of a known quantity.)

Immunoassay. An immunoassay is a biochemical test that measures the level of a substance using the reaction of an antibody to its antigen. In this case the antigen is RuBisCo. To make antibodies against this protein, it is first purified from plant tissue. A solution containing the purified RuBisCo is then injected into a mouse or a rabbit, for example. Mammals make antibodies (proteins called immunoglobulins) to this foreign protein as part of their normal immune response. After a few days, blood is drawn from the animals and the antibodies are collected from the serum. The immunoassay takes advantage of the extremely specific binding of an antibody to its antigen. The presence of the antibodies can be detected and measured using a number of biochemical techniques.

Mammoth Area

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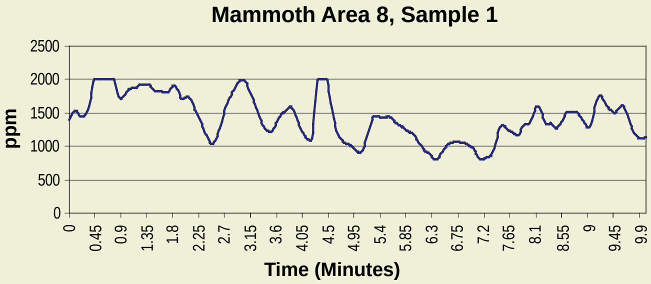

Soil Temperature = 35°C
pH = 7.0
Plant Species: sedges, asters, dalmatian toadflax


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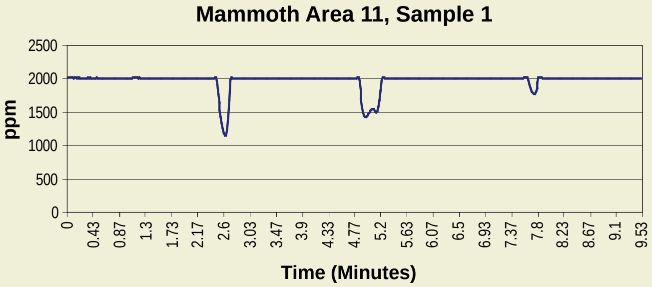

Soil Temperature = 14°C
pH = 7.0
Plant Species: lodgepole pine, juniper, strawberry, barberry, grasses

Figure 2. Crosses on the map indicate locations of high-CO_2 plant communities in the Mammoth Upper Terraces area. The location of the two representative communities are shown in the photographs and summarized in the graphs showing CO_2 parts per million sampled every 16 seconds.

RuBisCo in Leaf Extracts. As shown in Figure 4A, immunoassays aimed at quantifying RuBisCo in our leaf specimens detected relatively lower amounts of this protein in *D. lanuginosum* from high-CO_2 study sites compared to those in control plants collected from background-CO_2 sites. These results were supported by similar, but more quantitative, outcomes using the radiolabeled marker for RuBisCo (see Figure 4B). Also, plants growing at the highest levels (>600 ppm) of field-measured CO_2 generally displayed the lowest levels of RuBisCo.

Leaf Soluble Sugars. Figure 5 shows typical results of HPLC analysis of the soluble sugars in hot-water extracts from leaf specimens of *D. lanuginosum* collected at sites with background or with high levels (450 to 2,000 ppm) of CO_2 as determined by our field measurements. In most cases, significantly higher amounts of sucrose were found in leaf extracts from plants collected at sites with measured CO_2 levels at ≥600 ppm than from plants at background CO_2 sites.

Conclusions

Using portable CO_2 infrared gas analyzers, we have measured the soil-surface CO_2 concentrations at dozens of vegetated geothermal areas within Yellowstone. Many of these sites displayed high-CO_2 values, ranging from 450 to more than

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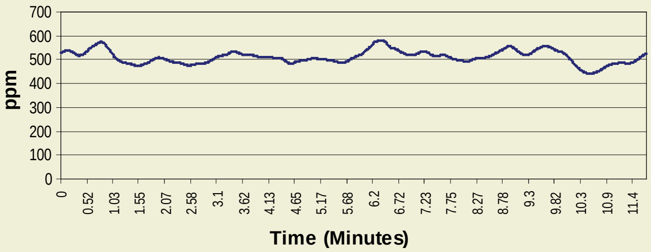
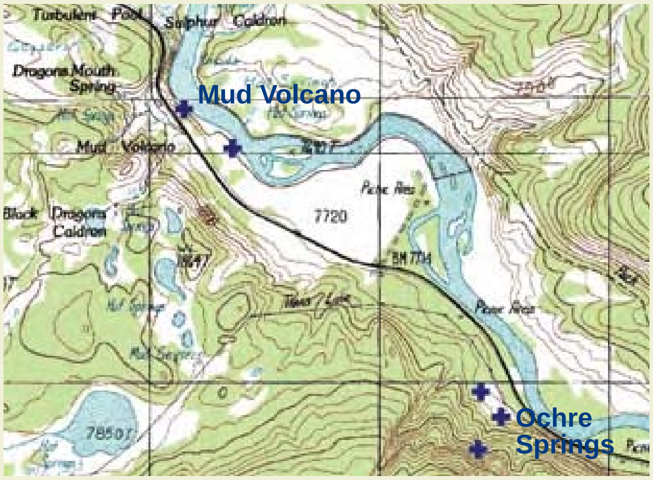


Mud Volcano Area 1, Sample 3

Soil Temperature = 14°C
pH = 4.5
Plant Species: sedges, grasses, including
Agrostis scabra

Mud Volcano Area



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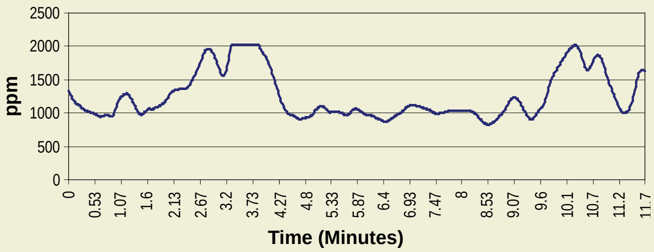

Ochre Springs Area 2, Sample 3

Soil Temperature = 6°C
pH = 4.0
Plant Species: lodgepole pine, spruce seedlings,
sedges

Figure 3. Crosses on the map indicate locations of high-CO_2 plant communities in the Mud Volcano area. The location of the two representative communities are shown in the photographs and summarized in the graphs of CO_2 parts per million sampled every 16 seconds.

2,000 ppm. A few of the sites are greater than 10 m^2 and almost all are far removed from human disturbance. Also in contrast to most previous studies of high-CO_2 environments, our surveys of Yellowstone have identified numerous high-CO_2 sites that can be paired with control sites that have background levels of CO_2 and comparable vegetation, soil type, and environmental characteristics.

At both our background- and high-CO_2 sites, leaves were collected primarily from hot springs panic grass (*D. lanuginosum*), which is often the dominant plant species in YNP geothermal soils. We found that leaves from the high-CO_2 sites consistently had less RuBisCo, the primary photosynthetic enzyme, than similar leaves collected from plants growing at background CO_2 sites. Using HPLC analysis of leaf extracts, we also found that leaves collected at high-CO_2 sites typically had higher levels of sucrose, a photosynthetic end-product. These findings support the hypothesis that plants growing in high-CO_2 areas of YNP make physiological adjustments similar to those observed in experimental Free Air CO_2 Enrichment (FACE) studies. However, unlike plants in FACE experiments, YNP plants have likely been exposed to elevated CO_2 concentrations for many generations and, in some cases, may have also had to cope with high temperatures.

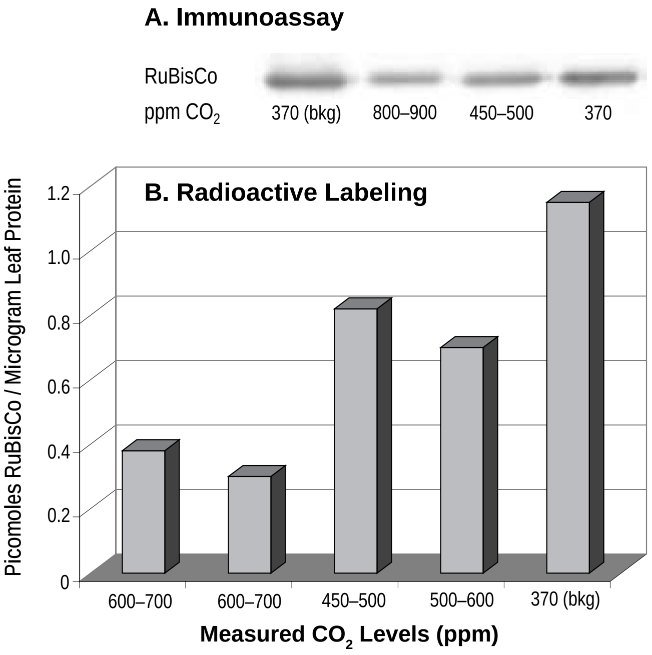

Figure 4. A) RuBisCo levels in *D. lanuginosum* from background-CO_2 (bkg) and high-CO_2 sites in YNP determined using immunoassay technique. Leaf specimens were collected from plants exposed to the field-measured CO_2 levels indicated below, wrapped in aluminum foil, and immediately frozen in liquid nitrogen. They were stored at –80°C at Montana State University until proteins were extracted from the leaf tissue in the lab. Equal amounts of the extracted proteins were fractionated, and the RuBisCo proteins (large subunit) were labeled with specific antibodies and visualized using a chemiluminescent technique (Stout and Al-Niemi 2002).
B) RuBisCo levels in *D. lanuginosum* from background-CO_2 (bkg) and high-CO_2 sites in YNP determined using a specific radiolabeling technique. Leaf specimens were collected and stored as described above. In the lab, leaf protein extracts were obtained and equal amounts of each sample were mixed with a radiolabeled analog of ribulose bisphosphate (RuBisCo substrate) [2-^{14}C]-carboxyarabinatol bisphosphate (Evans and Seemann 1984). The proteins were then precipitated and collected using microfiltraton. These filter disks were thoroughly washed to remove unbound radiolabel, and then the amounts of radioactivity on the filter disks were determined.

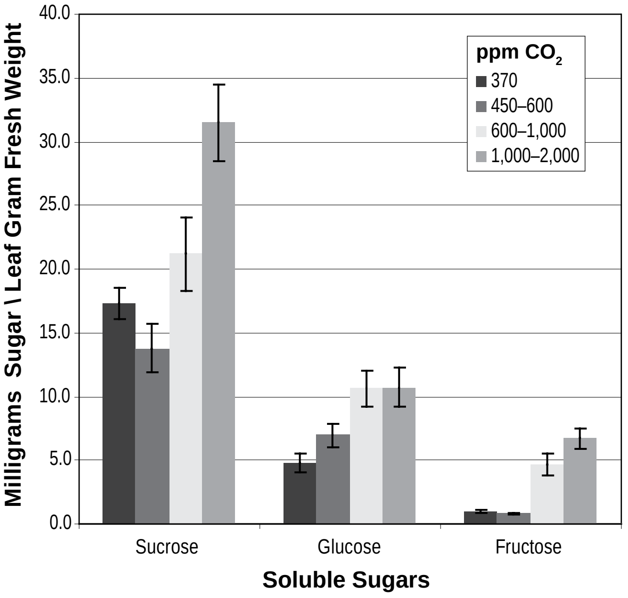

Figure 5 (*right*). The chief soluble sugars in hot-water extracts from *D. lanuginosum* collected from both background- and high-CO_2 sites in YNP. Each column represents the average (with standard error bar) of four replicate leaf samples from the same plant. Plants were collected from four sites, each with different amounts of measured CO_2 (as indicated in the legend).

Our findings support the idea that Yellowstone National Park is a valuable resource for studying the long-term effects of the impending global climate change on plants and plant communities. We plan to more thoroughly study some of these geothermal sites through long-term CO_2 and temperature measurements, more detailed plant laboratory analyses, and more attention to plant community structure. Such relatively undisturbed environments, which may have existed for tens of thousands of years, may contain plants that display biochemical, cellular, or developmental adaptations to chronic high temperatures and high CO_2. These plants may offer us a botanical glimpse of things to come. For example, they may provide plant ecologists and rangeland and forest managers information with which to make more accurate projections of future changes to plant communities. Such plants may also represent potential genetic resources for crop breeders and plant genetic engineers preparing for what will likely be a warmer, high-CO_2 world.

Since we initiated our studies in 2004, at least three other researchers have begun to investigate high-CO_2 environments in Yellowstone. Dr. Cathy Zabinski at Montana State University has been investigating how a ubiquitous root/fungus symbiosis, arbuscular mycorrhiza, functions in varying temperature and CO_2 environments. Drs. Shikha Sharma and David Williams at the University of Wyoming are using both radioactive and stable isotopes of carbon and oxygen in leaves to assess how the photosynthetic properties of vegetation are changing in response to elevated CO_2.

It is now generally accepted that human activity is making rapid, dramatic changes to the global environment. How will these environmental changes affect life on Earth? The experiment is already underway, but it's very difficult to predict the outcomes. Some clues may be provided by plants growing in Yellowstone National Park.

Acknowledgements

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Dr. Michael T. Tercek is the chief scientist and founder of Walking Shadow Ecology in Gardiner, Montana (http://www.YellowstoneEcology.com). He wrote his PhD dissertation on rare plants that grow in Yellowstone's thermal areas and has since collaborated on Yellowstone research projects with Montana State University, the University of Wyoming, Colorado State University, Rutgers University, USGS, and NPS. He has lived and worked in Yellowstone for more than 17 years.


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Dr. Thamir S. Al-Niemi is an Assistant Research Professor in the Department of Plant Sciences and Plant Pathology, Montana State University–Bozeman. His research interests include the physiology, biochemistry, and molecular biology of plants under abiotic stress conditions, especially cellular mechanisms of stress physiology in plants adapted to extreme environments in Yellowstone (see http://plantsciences.montana.edu/facultyorstaff/faculty/alniemi/alniemi.html).


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Dr. Richard G. Stout is an Associate Professor in the Department of Plant Sciences and Plant Pathology, Montana State University–Bozeman. He has been studying plants growing in geothermal environments in North America, including both Yellowstone and Lassen Volcanic National Park, for more than 10 years. His research on the cellular mechanisms of heat tolerance in hot springs panic grass (*D. lanuginosum*) has been published in several scientific journals (see http://www.plant-stuff.net/hotplants). He has also collaborated with scientists studying fungi that form symbiotic relationships with this plant (see *Yellowstone Science* 13(4), Fall 2005, p. 25).

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The U.S. Fish and Wildlife Service (USFWS) began reintroducing the endangered gray wolf to the Greater Yellowstone Area (GYA) and central Idaho in 1995. The restoration of wolves to the GYA has become one of the most successful wildlife conservation programs in the history of endangered species conservation. Yellowstone is now considered one of the best places in the world to watch wild wolves. The visibility of wolves within the park and public interest in wolves and wolf-based education programs have far exceeded initial expectations. But questions have persisted about the economic impact of wolf restoration that we have sought to answer.

During preparation of the Environmental Impact Statement (EIS) that was completed by the National Park Service prior to wolf restoration (USFWS 1994), one of the main concerns of wolf-reintroduction opponents was the expenditure of public federal funds for the restoration effort and the potential for negative effects on the regional economy. These assumed negative effects included the costs of wolf depredation on livestock and reduced big game populations resulting in lower economic returns to agencies and businesses that derive revenue from big game hunting. Proponents, on the other hand, predicted increased regional visitation and positive regional economic impacts as a result of wolf restoration.

Based on a 1991 park visitor survey, wolf recovery in Yellowstone was predicted to have a positive impact of $19 million annually in the regional economy due to increased wolf-related visitation to the park. If true, that would more than offset the negative economic impacts on the livestock industry and big game hunting that were expected to result from wolf restoration.

To test the economic projections that were made as part of the EIS analysis, in 2005 we surveyed park visitors about their expenditures and reasons for visiting the park. This paper focuses on two primary results from the 2005 survey: preferences for wildlife viewing among Yellowstone visitors and the regional economic impacts attributable to wolf presence in the park.

Data Collection

The Yellowstone National Park 2005 Visitor Survey was designed to collect a broad spectrum of information and opinions from park visitors. For purposes of the regional economic analysis, information was collected on visitor attitudes toward wolf recovery and wildlife and on visitor expenditures. From spring through fall, visitors at all five park entrance stations were asked to participate in the survey. Winter visitors traveling by car were contacted at the North Entrance. A separate sample of visitors was contacted at parking areas in the Lamar Valley where people specifically interested in seeing wolves tend to congregate. Because the Lamar Valley sample is not representative of park visitors as a whole, their survey responses are not included in the data represented here unless otherwise stated.

A total of 2,992 surveys were distributed from December 2004 to February 2006; 1,943 were completed and returned for an overall response rate of 66.4%: 1,431 from the park entrance sample (64.4% response rate) and 521 from the Lamar sample (74.2%). The resulting responses were weighted appropriately to reflect the actual distribution of 2005 park visitation by entrance and season. The survey procedure followed a standard Dillman (2000) mail survey methodology using initial contact and repeat follow-ups.

Visitor Wildlife Viewing Preferences

Visitors were asked to list the three animals from a list of 16 that they would most like to see while in the park (Table 1 compares the 2005 study results from summer visitors to

Wolf Recovery in Yellowstone

Park Visitor Attitudes, Expenditures, and Economic Impacts

John W. Duffield,
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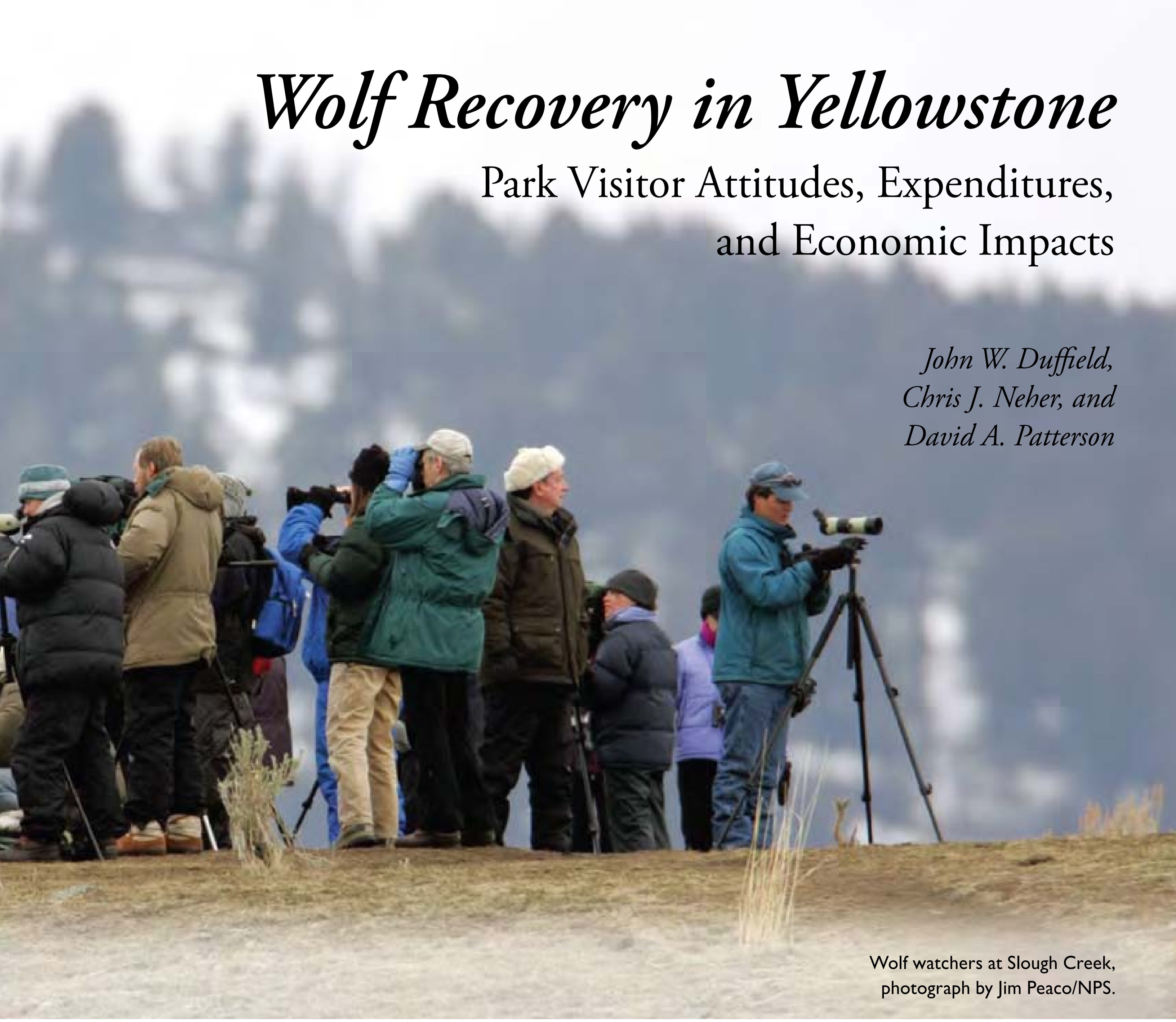

Wolf watchers at Slough Creek, photograph by Jim Peaco/NPS.

similar surveys conducted in 1991 and 1999). The "charismatic megafauna," including large carnivores and ungulates, rank highest on the lists. The large carnivores are consistently among the top five ranked species. In the 1991 study, wolves ranked ninth in popularity; 15% of park visitors listed them as one of the three species they would most like to see even though wolves were not present in the park. In the 1999 study, following wolf reintroduction, wolves were ranked second after grizzly bears and the percentage of visitors who chose wolves had increased to 36%. In the 2005 study, 44% of visitors listed wolves as a species they would most like to see, again ranking it second after grizzlies.

When asked to indicate which species they saw on their trip to the park, nearly all respondents reported seeing bison (93% to 98%), and a large share reported seeing elk (85% to 92%). As expected, very few visitors (1.8% or less) reported seeing the rarely viewed mountain lion and wolverine. Table 2 shows the percentage of entrance sample respondents who reported seeing wolves, coyotes, and both wolves and coyotes. For purposes of analyzing the impact of wolf presence in Yellowstone, we reduced the chance of counting visitors who misidentified coyotes as wolves by using the percentage of visitors who reported seeing both coyotes and wolves.

Table 2 shows that, depending on the season (spring, summer, or fall) from 9% to 19% of visitors reported seeing both wolves and coyotes. In winter, about 37% of North Entrance visitors reported seeing wolves and coyotes. Applying these percentages to the actual 2005 recreational visitation levels yields an estimate of 326,000 visitors who saw wolves in 2005. Although this is a conservative estimate because it excludes winter visitors who came through the West, East, and South entrances on over-snow vehicles, it is substantially higher than previous estimates. For example, according to field counts of wolf-watching visitors by Yellowstone National Park personnel (Smith 2005), about 20,000 visitors per year were viewing wolves. Given the size of the park, the widespread distribution of wolves (Smith 2005), and the limited presence of park personnel in the field, this method may have under-estimated the number of wolf observers by more than an order of magnitude.

Yellowstone Visitor Trip Expenditures

A key measure of the economic significance of a resource such as Yellowstone to the local economy is the amount of money visitors from outside the three-state area of Montana, Idaho, and Wyoming spend during their trips. To obtain an estimate of this, the survey questionnaire asked visitors to indicate the total amount they spent on their trip, as well as the amount they spent in these three states. Table 3 compares the reported average trip spending by season for residents of the three states to the spending of nonresidents.

Net Recreation Impacts of Wolf Recovery on the Regional Economy

Survey respondents were also asked if the possibility of seeing or hearing wolves had been a reason for their visiting the park and, if so, whether they would have come if wolves had not been present. Based on the responses to this question by both residents and nonresidents we estimated that the percentage of annual Yellowstone visitation attributable to wolves is 3.7%, ranging from 1.5% in the spring to nearly 5% in the fall. The percent for nonresidents only is similar, ranging from around 2% of spring visitors to almost 5% of summer visitors (Table 4). Table 4 shows the derivation of our estimate of the economic impact to the three-state region.

We estimate that approximately 94,000 visitors from outside the three-state region came to the park specifically to see or hear wolves in 2005, and that they spent an average of $375 per person, or a total of $35.5 million in the three states (Table 4). Prior to reintroduction, Duffield (1992) estimated that a recovered wolf population would lead to increased visitation from outside the three-state region resulting in an additional $19.35 million in direct visitor spending in the three states. Adjusted for inflation this would be $27.74 million per year in 2005—less than the $35.5 million estimate based on the data from our 2005 study, but well within the 95% confidence interval ($22.4 to $48.6 million).

Wolf Impacts on Livestock and Big Game Hunting

The EIS economic analysis provided estimates of the impacts of a recovered wolf population on livestock predation and big game populations in the three-state area. The estimated

Rank	1991 Study		1999 Summer Study		2005 Summer Study	
	Species	%	Species	%	Species	%
1	Grizzly	0.550	Grizzly	0.58	Grizzly	0.55
2	Black Bear	0.332	Wolf	0.36	Wolf	0.44
3	Moose	0.332	Moose	0.35	Moose	0.41
4	Elk	0.239	Lion	0.31	Black Bear	0.26
5	Lion	0.229	Black Bear	0.29	Lion	0.25
6	Sheep	0.219	Sheep	0.23	Sheep	0.21
7	Eagle	0.187	Eagle	0.21	Eagle	0.21
8	Bison	0.160	Bison	0.19	Bison	0.21
9	Wolf	0.154	Elk	0.14	Elk	0.14
10	Wolverine	0.047	Wolverine	0.06	Wolverine	0.06

The 2005 study also included six other species that were selected as preferred by some respondents: trumpeter swan (3%), deer (2%), fox (1.8%), coyote (0.6%), antelope (0.3%), and goose (0.1%).

Table 1. Comparison of Yellowstone National Park visitor ratings of the animals they most would like to see on their trips to Yellowstone.

Left, sample page from the 1991 survey; *below*, Female wolf pup #17 of the Rose Creek pack in Rose Creek pen, Barry O'Neill, 1995.

livestock losses of $1,900 to $30,500 per year (mostly for cattle and sheep) were based on assumptions of a recovered population of 100 wolves. During the period when wolf numbers were near 100 (1997–2000), annual losses averaged $11,300 (based on actual payments at market prices for wolf kills verified by Defenders of Wildlife, www.defenders.org). When wolves numbered more than 300 in 2004 and 2005, losses averaged $63,818 per year, twice the high-end estimate predicted in the EIS. Even if payments by Defenders of Wildlife understated livestock losses by a factor of two due to the difficulty of verifying all actual kills, recent direct losses would still be less than $130,000 per year. Other livestock industry costs resulting from wolf reintroduction have not been quantified, but could include increased fencing and management costs associated with reducing wolf predation on a given ranch.

Based on biologists' projections of the impact of wolf predation on big game populations, the EIS projected a decline of 2,439 to 6,157 hunter days for elk, deer, and moose on the northern range and for Jackson and North Fork Shoshone elk. The associated foregone annual hunter expenditure was projected to be $207,000 to $538,000, based on approximately $85 hunter expenditure per day for those species. In 2005 dollars, this would be a loss of $342,000 to $890,000. Three of the species examined in the EIS (deer, moose, and bison) either have seen no reduction in population levels (as was predicted in the EIS) or, in the case of moose, have inadequate data to evaluate current population levels (White et al 2005). There have been no reductions for permits, animals harvested, or hunter success for mule deer or moose on the northern range as a result of wolf restoration (White et al. 2005).

The other key game species, elk , has provoked substantial concern in recent years because some herd sizes have dropped dramatically as wolf numbers have risen. While a substantial body of recent literature on wolf-prey modeling in the Yellowstone ecosystem exists, most of it focuses on the northern range elk. A review of the wildlife biology literature on the northern range elk population shows a divergence of views on the extent to which wolf predation has been responsible for its decline. However, two peer-reviewed papers (Varley and Boyce 2006, Vucetich et al. 2005) show that the impact of wolves on elk numbers has been consistent with or below the EIS prediction, which was for a long-range reduction of 5% to 30% in the hunter elk harvest. If one accepts the Varley and Boyce (2006) estimates, which also include impacts on the Jackson and North Fork Shoshone elk herds, actual declines in big game populations as a result of wolf predation and associated hunter impact are in the range predicted by the EIS ($342,000 to $890,000 in 2005 dollars). A caveat to these estimates is that they do not account for substitution behavior in response to changes in elk hunting opportunities in the GYA. This may result in an overstatement of hunter impacts. It was assumed in

Statistic	**Spring N=495**	**Summer N=477**	**Fall N=322**	**Winter N=221**
% Report seeing wolves	25.4%	15.2%	18.5%	42.4%
% Report seeing coyotes	45.3%	38.9%	40.4%	71.2%
% Report seeing both	19.2%	9.1%	12.8%	36.7%
Recreational visitation (2005)	382,598	1,819,798	547,777	43,933
Number of visitors seeing wolves and coyotes	73,382	166,330	70,335	16,123
Total estimated visitors sighting wolves and coyotes (spring-fall)	310,046 (95% C.I. 257,210 to 362,882)			
Total estimated visitors sighting wolves and coyotes (year-round)	326,170 (95% C.I. 273,277 to 379,097)			
Note: winter estimate includes only North Entrance visitation.				

Table 2. Estimated number of Yellowstone visitors seeing wolves and coyotes in the park in 2005.

Season/residency	Average amount spent in ID, MT, WY	Average total trip spending	Sample Size
Spring–nonresident	$361.89	$795.14	260
Spring–3-state resident	$86.19	$112.37	101
Summer–nonresident	$369.12	$757.31	291
Summer–3-state resident	$142.06	$142.06	45
Fall–nonresident	$425.50	$855.00	149
Fall–3-state resident	$152.67	$198.64	72

Note: winter results are only representative of wheeled access and are not presented.

Table 3. Comparison of park visitor spending in Idaho, Montana, and Wyoming by season and residency based on visitors responding to 2005 entrance station surveys.

the EIS that hunters who did not receive an elk hunting permit in the GYA would not hunt elsewhere in the three-state area for elk or increase hunting effort on other species.

Conclusions

Overall, it appears that the economic predictions made in the 1994 EIS analysis were relatively accurate. Our estimated increase in park visitation (3.7%) due to wolf presence is lower than was predicted in the EIS (4.93%). However, the EIS prediction was based on a survey of only summer visitors; our 2005 study estimated a 4.78% increase in summer visitation due to wolf presence. Regarding increases in visitor spending in the three-state area due to wolf presence, the estimate of $35.5 million (confidence interval of $22.4 to $48.6 million) based on our 2005 study is consistent with the EIS estimate of $27.7 million (2005 dollars).

Projected costs of wolf predation (based on the market value of cattle and sheep taken by wolves) have been in the range predicted by the EIS, and were on the order of about $65,000 per year in 2004 and 2005. The impact of wolves on actual observed hunter harvest in the first 10 years after reintroduction was negligible, in that average hunter harvest and permits issued for big game species were either higher or unchanged compared to pre-wolf averages. However, reflecting in part the influence of a long-term drought, the presence of wolves, and aggressive management policies to reduce elk populations through hunting on the Northern Range, there

Statistic	Spring	Summer	Fall	Winter [1]
Total recreational visitation to Yellowstone	382,598	1,819,798	547,777	85,478
% of visitors from outside the three-state area	70.5%	83.68%	67.59%	82.2%
(A) Recreational visitors from out of the three states	269,770	1,522,807	370,242	70,289
(B) % of visitors who would not have visited without the presence of wolves	1.93%	4.78%	3.45%	3.66%
(C) Average spending per visitor within the three states by visitors from outside the area [2]	$361.89	$369.12	$425.50	$510.84
(A) * (B) * (C) Total estimated annual three-state visitor spending attributable to wolves [3]	$1,885,178	$26,889,668	$5,431,916	$1,314,167
Total estimated annual visitor spending in the three states attributable to wolves	$35,520,929			
95% Confidence interval	$22,404,274 to $48,637,585			

[1] Based on 1999 winter visitor survey estimates (Duffield and Neher 2000).
[2] Average spending for those who specifically came to see wolves was nearly identical, but due to a much smaller sample size, had a much higher variance.
[3] Sample size, by season for the 2005 sample was: 495 for spring, 477 for summer, and 322 for fall. The winter sample from 1998–1999 was 221.

Table 4. Estimated three-state (MT, ID, and WY) direct expenditure impact associated with wolf presence in Yellowstone National Park based on visitors responding to entrance station surveys.

has been recently a substantial reduction in elk permits. There is not a consensus among biologists on the actual impact of wolves on elk populations, but modeling supports the view that the long-term economic impact on big game hunting will be within the range projected by the EIS, of $342,000 to $890,000 per year (2005 dollars).

Weighing the economic impacts of increased tourism against reductions in livestock production and big game hunting participation, one can conclude that the net impact of wolf recovery is positive and on the order of $34 million in direct expenditures. An input-output model of the three state economy (Minnesota Implan Group, 2007) can be used to estimate the effect on economic output, by accounting for indirect and induced expenditures throughout the three-state economy. Including this multiplier effect leads to an estimated total economic impact in the three-state area of about $58 million in 2005 (range of $34 to $80 million).

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