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Moose Population History on the Northern Yellowstone Winter Range

Plants Exposed to High Levels of Carbon Dioxide

Economics of Wolf Recovery in Yellowstone

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Silhouette of moose in pond.
Photo by Dan Tyers.



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Plants Exposed to
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in Yellowstone National Park

A Glimpse into the Future?

Michael T. Tercek, Thamir S. Al-Niemi, and Richard G. Stout



MICHAEL TERCEK

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 (CO₂) 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 CO₂ 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 CO₂ 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-CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ in Yellowstone National Park (YNP). Our results show that Yellowstone offers rare, natural environments for scientists to investigate the long-term effects of increased CO₂ and high temperatures (both separately and in tandem) on plants.

Background: Responses of Plant Communities to CO₂ 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 CO₂ levels of 500 to 800 parts per million (ppm) compared to the current "background" CO₂ concentration (about 380 ppm). Most of these investigations have used either small-scale growth chambers or free air CO₂ enrichment (FACE) facilities that pump CO₂ 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 CO₂ 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-CO₂ 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 (Körner 2000). In summary, the growth chamber studies tend to indicate that higher levels of CO₂ increase crop production. However, outdoor experiments using FACE facilities tend to show that the benefits of high CO₂ on plant productivity have been overestimated and may be only short term (Long et al. 2006). At the physiological level, elevated CO₂ 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 CO₂ 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 CO₂ 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 CO₂) 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 CO₂ environment may allow plants to use nitrogen more efficiently. FACE studies have shown that plants often respond to extended CO₂ enrichment by reducing the concentration of their main photosynthetic enzyme, ribulose biphosphate carboxylase (RuBisCo) (Ellsworth et al. 2004). RuBisCo captures CO₂ 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-CO₂ 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 CO₂ would likely have a negative impact on grazing animals, such as the bison and elk in YNP (Wilsey, Coleman, and McNaughton 1997).

Finally, increased CO₂ 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 CO₂ levels increase. When opened, the stomates allow CO₂ to enter the leaf and water to escape. Land plants try to conserve water by closing their stomates if CO₂ 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 CO₂. 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 CO₂ 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 CO₂. But in the long term (decades, centuries) will these conditions exert pressures through natural selection that result in genetic adaptations to elevated CO₂? And if so, what will likely be the nature of these adaptations?

Studies Using Environments Naturally High in CO₂

In attempts to answer these questions, scientists have examined plants growing near natural CO₂ 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-CO₂ environments often occur in areas of volcanic activity and are manifested as "mofettes" (carbon dioxide springs), CO₂ vents, or elevated CO₂ gas flux from the soil. Though not as controllable as greenhouse or FACE experiments, these natural high-CO₂ environments provide opportunities to examine relatively long-term adaptations of plants to high CO₂. 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 CO₂ 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-CO₂ 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 CO₂ (95–99%) (Kharaka, Sorey, and Thordsen 2000; Werner and Brantley 2003). Despite this, there have been only a few reports of the effects of CO₂ 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 CO₂ in YNP.

Methodology

CO₂ Measurements. To measure carbon dioxide in the field, we used several different portable CO₂ 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) CO₂ 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-CO₂ locations were identified, more measurements were periodically made at some locations to better establish average long-term CO₂ levels. Leaf tissue specimens were collected from hot springs panic grass (*Dichanthelium lanuginosum*) and other species at some of these high-CO₂ locations and at background-CO₂ locations nearby for subsequent laboratory analyses to test the presumption that plants in these areas were indeed chronically exposed to elevated CO₂. Two indicators of plant exposure to elevated levels of CO₂ 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 CO₂, 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 CO₂, 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-CO₂ Areas in Yellowstone. We found 15 sites in YNP that had consistently elevated CO₂ concentrations (Fig. 1). Fourteen of these sites contained several high-CO₂ plant communities, ranging in surface area from 1 m² to greater than 10 m². The fifteenth site, Death Gulch, also had very high CO₂ emissions, but its famously lethal crevices (Haines 1996) did not contain vegetation in the areas nearest to the CO₂ 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 CO₂: 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 CO₂ measurements, and lists of the plant species present at each site.

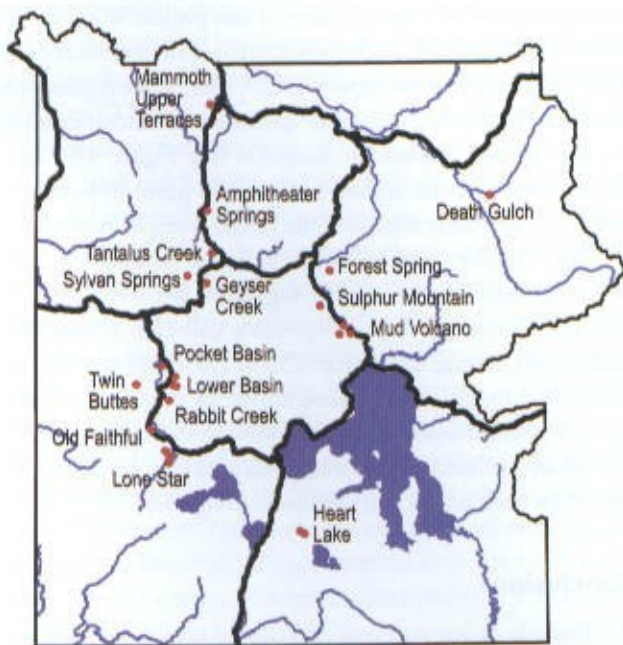


Figure 1. Each location marked on the map contains from 2 to 30 plant communities growing in above-normal CO₂ concentrations.

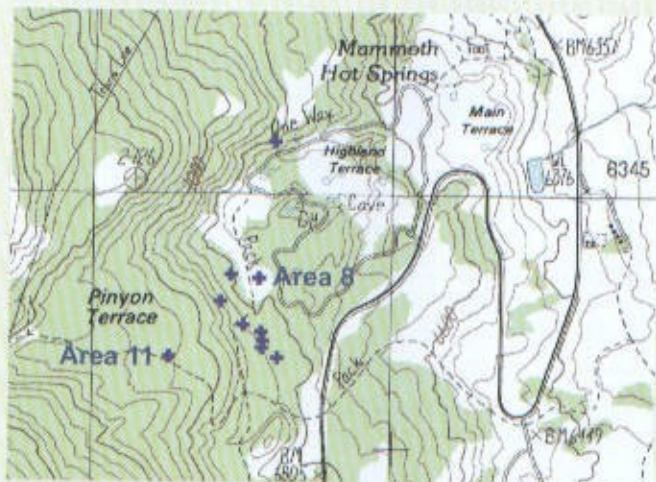
GLOSSARY

CO₂ 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 CO₂ 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 CO₂. The more CO₂ 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.)

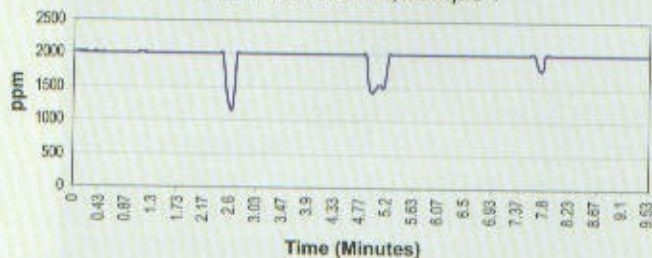
Immunoassay. An immunoassay is a biochemical test that measures the level of a substance using the reaction of an antibody to its antigen. In this case the antigen is RuBisCo. To make antibodies against this protein, it is first purified from plant tissue. A solution containing the purified RuBisCo is 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



MICHAEL TENCER

Mammoth Area 11, Sample 1



Soil Temperature = 14°C

pH = 7.0

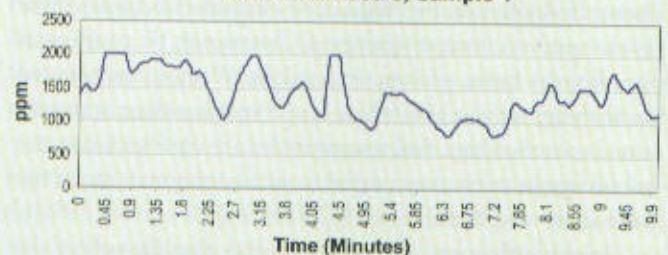
Plant Species: lodgepole pine, juniper, strawberry, barberry, grasses

Figure 2. Crosses on the map indicate locations of high-CO₂ 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 CO₂ parts per million sampled every 16 seconds.



MICHAEL TENCER

Mammoth Area 8, Sample 1



Soil Temperature = 35°C

pH = 7.0

Plant Species: sedges, asters, dalmatian toadflax

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-CO₂ study sites compared to those in control plants collected from background-CO₂ 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 CO₂ 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 CO₂ 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 CO₂ levels at ≥600 ppm than from plants at background CO₂ sites.

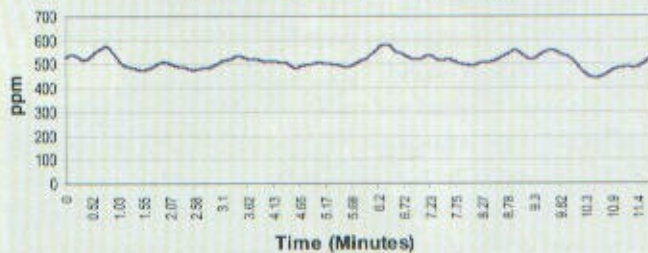
Conclusions

Using portable CO₂ infrared gas analyzers, we have measured the soil-surface CO₂ concentrations at dozens of vegetated geothermal areas within Yellowstone. Many of these sites displayed high-CO₂ values, ranging from 450 to more than



MICHAEL TERCKER

Mud Volcano Area 1, Sample 3

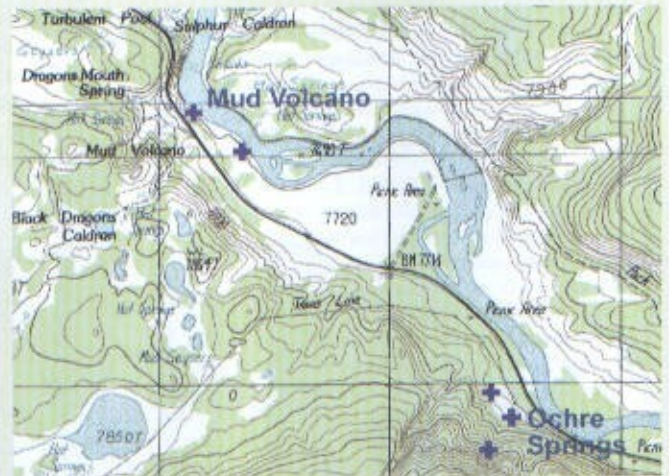


Soil Temperature = 14°C
 pH = 4.5
 Plant Species: sedges, grasses, including *Agrostis scabra*

2,000 ppm. A few of the sites are greater than 10 m² and almost all are far removed from human disturbance. Also in contrast to most previous studies of high-CO₂ environments, our surveys of Yellowstone have identified numerous high-CO₂ sites that can be paired with control sites that have background levels of CO₂ and comparable vegetation, soil type, and environmental characteristics.

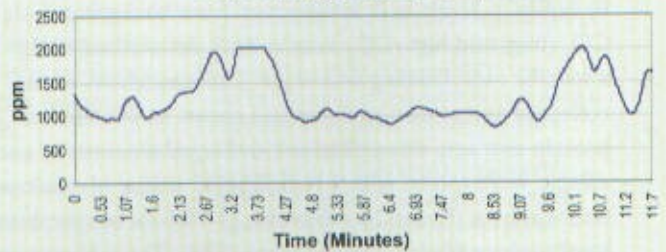
At both our background- and high-CO₂ sites, leaves were collected primarily from hot springs panic grass (*D. lanuginosum*), which is often the dominant plant species in YNP geothermal soils. We found that leaves from the high-CO₂ sites consistently had less RuBisCo, the primary photosynthetic enzyme, than similar leaves collected from plants growing at background CO₂ sites. Using HPLC analysis of leaf extracts, we also found that leaves collected at high-CO₂ sites typically had higher levels of sucrose, a photosynthetic end-product. These findings support the hypothesis that plants growing in high-CO₂ areas of YNP make physiological adjustments similar to those observed in experimental Free Air CO₂ Enrichment (FACE) studies. However, unlike plants in FACE experiments, YNP plants have likely been exposed to elevated CO₂ concentrations for many generations and, in some cases, may have also had to cope with high temperatures.

Mud Volcano Area



MICHAEL TERCKER

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-CO₂ 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 CO₂ parts per million sampled every 16 seconds.

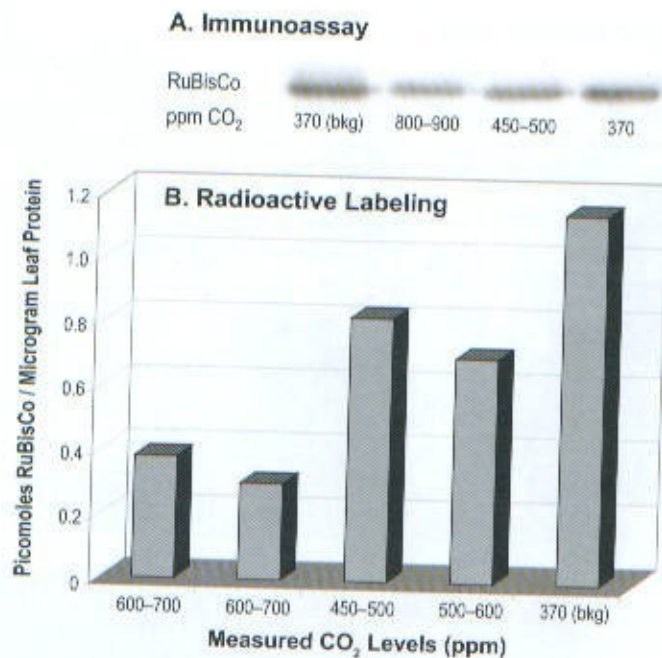


Figure 4. A) RuBisCo levels in *D. lanuginosum* from background-CO₂ (bkg) and high-CO₂ sites in YNP determined using immunoassay technique. Leaf specimens were collected from plants exposed to the field-measured CO₂ levels indicated below, wrapped in aluminum foil, and immediately frozen in liquid nitrogen. 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).

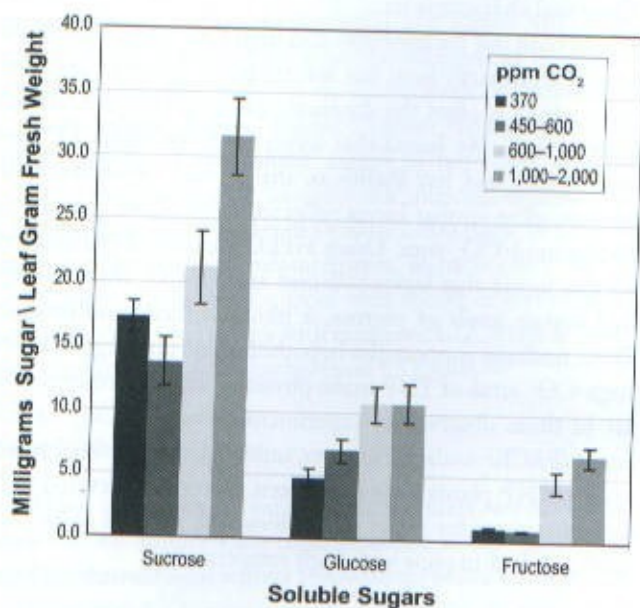
B) RuBisCo levels in *D. lanuginosum* from background-CO₂ (bkg) and high-CO₂ sites in YNP determined using a specific radiolabeling technique. Leaf specimens were collected and stored as described above. In the lab, leaf protein extracts were obtained and equal amounts of each sample were mixed with a radiolabeled analog of ribulose biphosphate (RuBisCo substrate) [2-¹⁴C]-carboxyarabitol biphosphate (Evans and Seemann 1984). The proteins were then precipitated and collected using microfiltration. 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-CO₂ 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 CO₂ (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 CO₂ 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 CO₂. 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-CO₂ world.

Since we initiated our studies in 2004, at least three other researchers have begun to investigate high-CO₂ 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 CO₂ 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 CO₂.

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.



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COURTESY OF MICHAEL TERCEK

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.



COURTESY OF THAMIR S. AL-NIEMI

Dr. Thamir S. Al-Niemi is an Assistant Research Professor in the Department of Plant Sciences and Plant Pathology, Montana

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COURTESY OF RICHARD STOUT

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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