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.

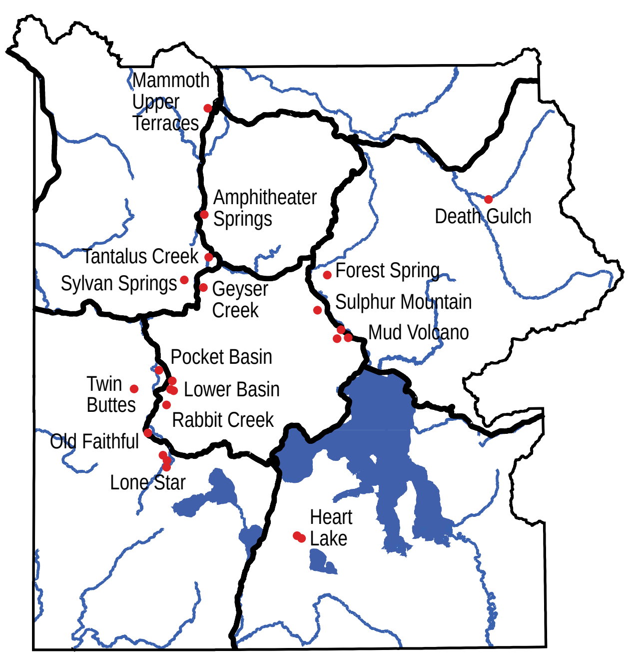


Figure 1. Each location marked on the map contains from 2 to 30 plant communities growing in above-normal CO_2 concentrations.

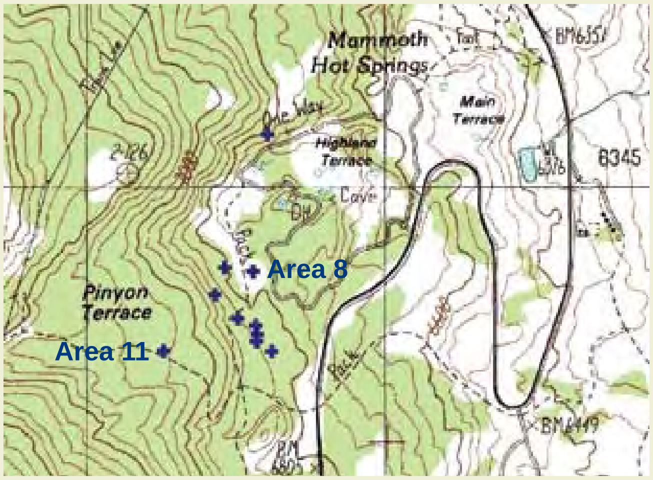
GLOSSARY

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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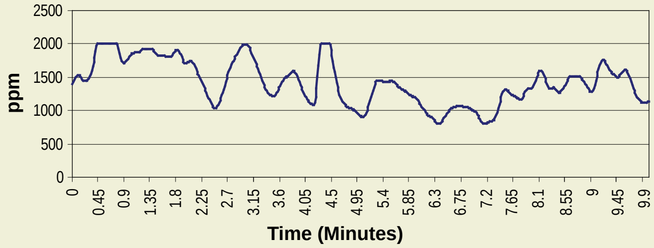
Mammoth Area 8, Sample 1



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

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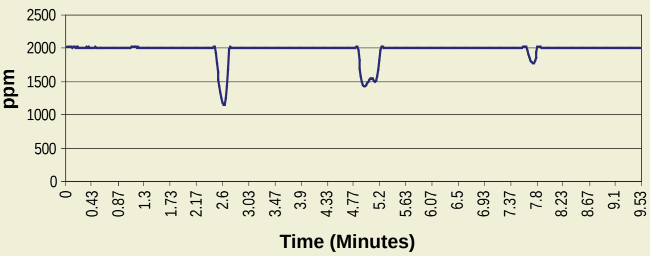
Mammoth Area 11, Sample 1



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-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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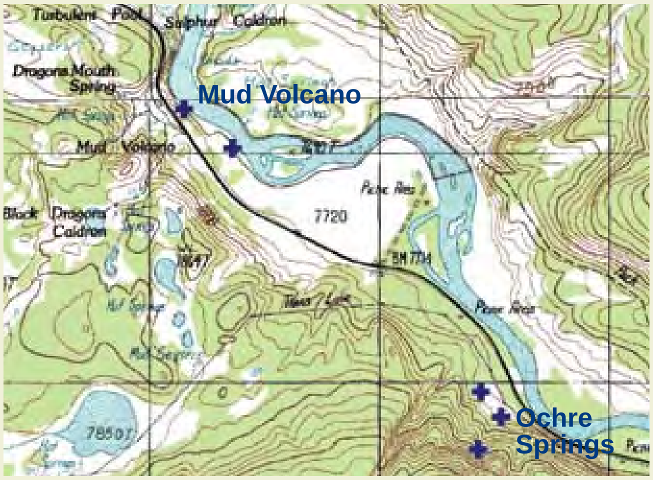
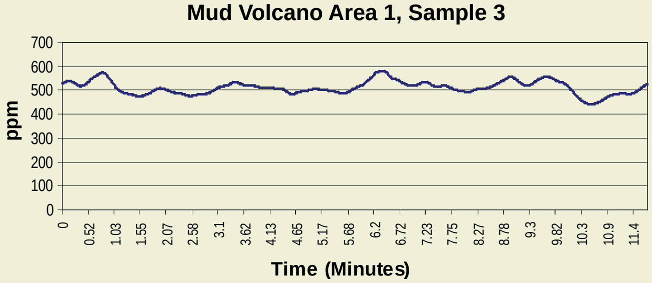
Mud Volcano Area





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

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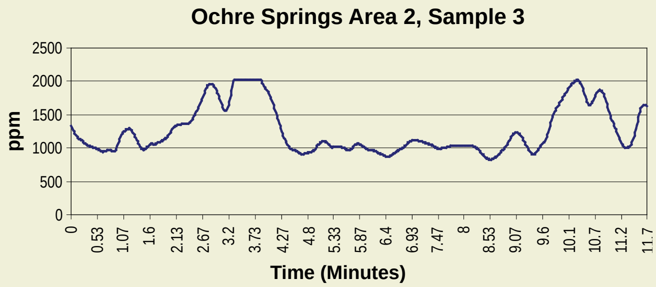

Soil Temperature = 6°C
pH = 4.0
Plant Species: lodgepole pine, spruce seedlings, sedges

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.

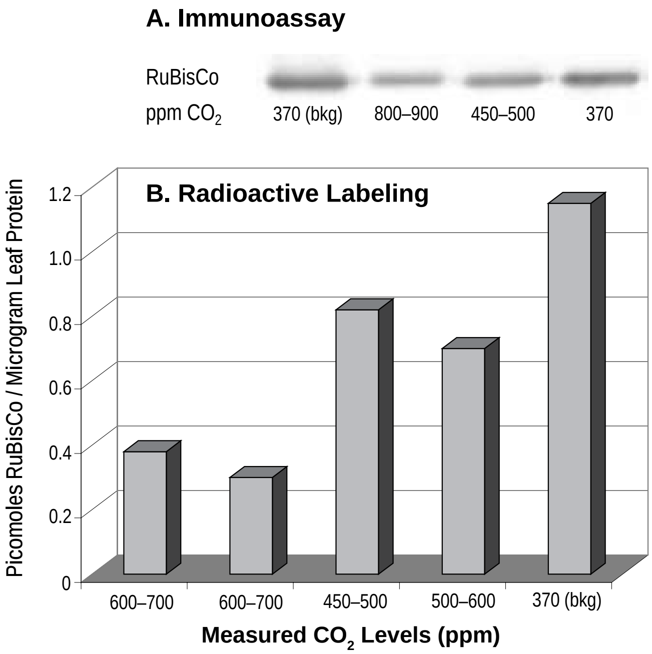

Figure 4. A) RuBisCo levels in *D. lanuginosum* from background-CO_2 (bkg) and high-CO_2 sites in YNP determined using immunoassay technique. Leaf specimens were collected from plants exposed to the field-measured CO_2 levels indicated below, wrapped in aluminum foil, and immediately frozen in liquid 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.

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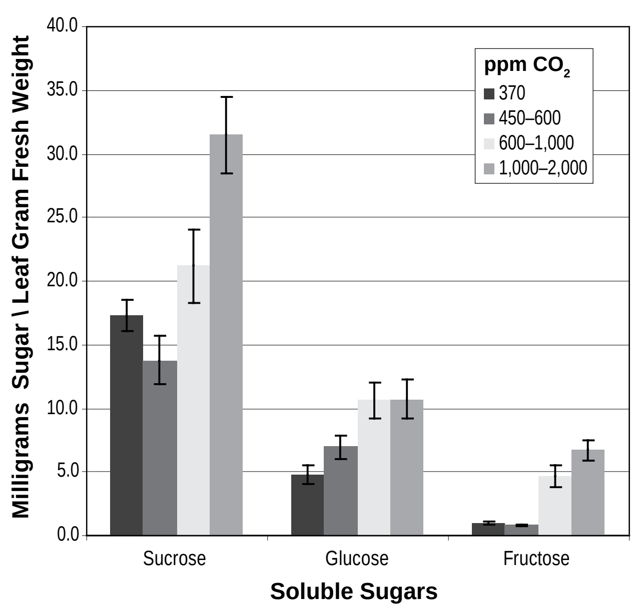

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Dr. Michael T. Tercek is the chief scientist and founder of Walking Shadow Ecology in Gardiner, Montana (http://www.YellowstoneEcology.com). He wrote his PhD dissertation on rare plants that grow in Yellowstone's thermal areas and has since collaborated 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).

References

Badiani, M., A. Raschi, A.R. Paolacci, and F. Miglietta. 2000. Plants responses to elevated CO_2; a perspective from natural CO_2 springs. *In* Environmental and Plant Response, S.B. Agrawal and M. Agrawal (eds.), Lewis, pp. 45–81.

Cleland, E.E., N.R. Chiariello, S.R. Loarie, H.A. Mooney, and C.B. Field. 2007. Diverse responses of phenology to global change in a grassland ecosystem. *Proceedings of the National Academy of Sciences (USA)* 103:13740–13744.

Crutzen, P.J., and E.F. Stoermer. 2000. The "Anthropocene". *Global Change Newsletter.* 41:12–13.

Ellsworth, D.S., P.B. Reich, E.S. Naumburg, G.W. Koch, M.E. Kubiske, and S.D. Smith. 2004. Photosynthesis, carboxylation, and leaf nitrogen responses of 16 species to elevated pCO_2 across four free-air CO_2 enrichment experiments in forest, grassland, and desert. *Global Change Biology* 10:2121–2138.

Evans, J.R., and J.F. Seemann. 1984. Differences between wheat genotypes in specific activity of ribulose-1,5-bisphosphate carboxylase and the relationship to photosynthesis. *Plant Physiology* 74:759–765.

Haines, A.L. 1996. *The Yellowstone Story: A History of Our First National Park.* Volume Two. Revised Edition. The Yellowstone Association, in cooperation with University Press of Colorado. Niwot, Colorado.

Kharaka, Y.K., M.L. Sorey, and J.J. Thordsen. 2000. Large-scale hydrothermal discharges in the Norris-Mammoth corridor, Yellowstone National Park, USA. *Journal of Geochemical Exploration* 69–70:201–205.

Korner, C. 2000. Biosphere responses to CO_2 enrichment. *Ecological Applications* 10:1590–1619.

Long, S.P., E.A. Ainsworth, A.D.B. Leakey, and P.B. Morgan. 2005. Global food insecurity. Treatment of major food crops with elevated carbon dioxide, or ozone under large-scale fully open-air conditions suggests recent models may have overestimated future yields. *Philosophical Transactions of the Royal Society B* 360:2011–2020.

Long, S.P., E.A. Ainsworth, J. Nosberger, and D.R. Ort. 2006. Food for thought: lower-than-expected crop yield stimulation with rising CO_2 concentrations. *Science* 312:1918–1921.

Pfanz, H., D. Vodnik, C. Wittman, G. Aschan, and A. Raschi. 2004. Plants and geothermal CO_2 exhalations – survival in and adaptation to a high CO_2 environment. *In* Progress in Botany, vol. 65, K. Esser, U. Luttge, W. Beyschlag, and J. Murata (eds.), Springer, pp. 499–538.

Raschi, A., F. Miglietta, R. Tognetti, and P.R. van Gardingen. (eds.) 1997. *Plant Responses to Elevated CO_2: Evidence from Natural Springs.* Cambridge University Press, 272 pp.

Rothschild, L.J. 1994. Elevated CO_2: impacts on diurnal patterns of photosynthesis in natural microbial ecosystems. *Advances in Space Research* 14(11):285–289.

Solomon, S., et al. (eds.) 2007. Climate Change 2007: The Physical Science Basis: contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. (Available online at http://www.ipcc.ch)

Stout, R.G., and T.S. Al-Niemi. 2002. Heat-tolerant flowering plants of active geothermal areas in Yellowstone National Park. *Annals of Botany* 90:259–267.

Werner, C., and S. Brantley. 2003. CO_2 emissions from the Yellowstone volcanic system, *Geochem. Geophys. Geosyst.* 4(7), 1061,doi:10.1029/2002GC000473.

Wilsey, B.J., J.S. Coleman, and S.J. McNaughton. 1997. Effects of elevated CO_2 and defoliation on grasses: a comparative ecosystem approach. *Ecological Applications* 7:844–853.