The Rocky Mountain West's Changing Landscape Volume 2 Number 1 Summer 2000

Inside:

Why Montanans Come Home: Understanding Return Migration Through Interviews at Reunions Civility in Public Land Management: Building Better Relationships with the Land and Each Other

A New Vision: Collaborative Conservation

Tribal Sovereignty: Moving into the Twenty-First Century
The Global Positioning of Western Canada in the New Economy
Changing Mountain Landscapes in a Changing Climate: Looking into the Future

Changing Mountain Landscapes in a Changing Climate

Looking into the Future

by Daniel Fagre

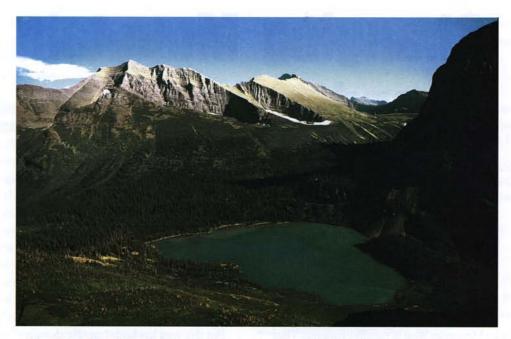
he Rocky Mountain West is rapidly changing. That much is clear when you read that half of the fastest growing counties in the country from 1990 - 1996 were in the Rocky Mountain region. Or when more people visit the llama barns at the county fair than the barn with the prizewinning steer. Or when log homes exceed 6,000 square feet, with four-car garages, but are occupied only part of the year.

But this area has been "rapidly changing" since the first Euro-American opportunists began to pour into its valleys and extract resources from its mountains. And that change has been analyzed, lamented, and promoted for just as long.

One defining characteristic of the region has *not* changed: people's perception of a grand and pristine expanse of wild landscape. Whether initially viewed by



The peaks and dramatic landscape of Glacier National Park have variously had inspirational, spiritual, and intimidating impacts on people but always have shaped the socioeconomic and cultural attributes of mountain communities. Photo by Dan Fagre, USGS.



Grinnell Lake in Glacier National Park appears to be pristine and protected by the surrounding landscape but, like many other mountain resources in the Rocky Mountain West, is increasingly affected by long-distance stressors such as air pollution and climate change. Photo by Dan Fagre, USGS.

empire builders like Louis Hill or artists like Thomas Moran, the sense of limitless and virile terrain fueled dreams and shaped the psyche of its inhabitants and others. Amazingly—despite the obvious clearcuts, interstate highways, ski areas, trophy homes, and mine tailings—this region's wild, untamed mystique still drives much of its continuing immigration. Magazines (and realtors) focus exclusively on the mythology of the mountain West, and wealthy baby boomers, dot-com millionaires, and actors can afford to buy into the Shangri-la imagery.

One obvious source for the continuing sense of an undominated landscape is the very nature of mountains. As Edwin Bernbaum points out in *Sacred Mountains* (Univ. of California Press, 1997), the contrast with awe-inspiring terrain often reminds people of their physical insignificance. The mass and verticality of peaks have inspired a sense of reverence or terror for millennia, and a majority of the world's religions view particular mountains as sacred sites. Even today it seems hard to accept that something so visually imposing could be significantly altered.

The other source for the continuing mystique is the large percentage of federal public lands in the Rocky Mountain West, particularly those in highly protected status such as national parks and wilderness areas. They create the impression that much of the landscape is set aside from private ownership and therefore cannot be

"used up" and, by inference, not degraded. This is certainly more true in the Rocky Mountain West than most other regions of the country. We have the relative luxury of controversies over bison management, grizzly bear population size, and wolf reintroductions, giving our area an exotic aura when these controversies occasionally are reported on the nightly national news. Outside of Alaska, only the Rocky Mountain West is rich enough in natural landscapes to make such issues possible.

Protected Areas in the Changing Landscape

It is also clear that the large, wild landscapes that characterize the Rocky Mountain West are under threat. Despite the fact that only 5 percent of the U.S. population lives in the Mountain Time Zone, we increasingly perceive the area's network of natural landscapes as under strain. The transformation of the landscape was well-chronicled in the Center of the American West's Atlas of the New West: Portrait of a Changing Region (W.W. Norton & Co., 1997), which described extensive development of the riparian areas that hold landscapes together, conversion of agricultural lands to other uses, and debate over roadless areas and public access to national forests. The proposal to save an intact corridor linking the Yellowstone and Yukon ecosystems (a plan known as "Yellowstone-to-Yukon," or

Y2Y) is a bold remedy for keeping intact the core landscapes that underlie the region's character and underscore the degree to which regional landscape fragmentation has entered our public dialogue about the Rocky Mountain West's future.

Buried in the debates about Superfund sites and blue-ribbon trout streams, cappuccino cowboys and loggers, and tourism-based vs. resource-extraction economies is the assumption that our core natural areas—our national parks and wilderness areas—are doing fine. That is because they are protected, set aside, and not part of the debates over land-use plans; they are fundamentally intact. Our main concern for them is external, looking only at their relationship with other parts of the landscape that are changing.

Certainly we recognize that there are local impacts of overused campsites and trails in wilderness areas and more visible issues such as snowmobile use in Yellowstone National Park. But we commonly assume that these internal impacts can be addressed by management, and we expect that the resource will recover after the right decisions are made, and things will go back to the way they were over time. This expectation is somewhat more problematic with the drive to restore natural fire frequency to our expansive mountain protected areas because of the time and logistics required to restore "fire ecology," but it still can be done if our convictions remain strong.

Long-distance Threats to Protected Areas

In perhaps the most significant changes from the past, today our protected areas are feeling stresses from sources located far beyond the Rocky Mountain West region. We recently discovered, for example, that air pollution from as far away as Southeast Asia is having a measurable impact on ostensibly pristine mountain lakes nestled below the Continental Divide in Canada. Pollutants called volatile organochlorine compounds (VOCs) are of such light molecular weight that they are transported across the Pacific Ocean in upper atmospheric currents and descend onto our landscapes in minute quantities. When they drift onto glaciers, snowfields, and cold lakes they tend to stay. But during the summer's heat, the VOCs are revolatilized from other parts of the landscape and float around until trapped by the cold elements of the landscape, which functionally act as VOC magnets. Thus, through time, cold glaciers and lakes accumulate these VOCs in sufficient concentrations that the pollutants begin to show up in fish tissue samples that exceed standards for safe human consumption.

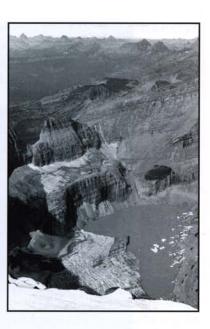


Dead whitebark pine in Glacier National Park, killed by an accidentally introduced pathogen. Photo courtesy of National Park Service archives.

Another example of distant impacts to our Rocky Mountain West is the demise of whitebark pine. This tree is considered to be a "keystone" species in alpine communities near mountain summits. Lone whitebark pine trees can act as a nucleus for colonization by subalpine fir and other plants in the windswept upper reaches above treeline. These pines play a hydrologic role: their broad crowns accumulate snow during winter's tempests; their snowmelt then provides critical moisture for other plants during summer's short growing season because the poorly developed alpine soils cannot hold adequate moisture. Perhaps most significantly, the whitebark pine produces a relatively large and nutritious crop of seed utilized by Clark's nutcracker, squirrels, grizzly bears, and, in the past, Native Americans. Early this century, however, plants imported from Europe introduced a fungus called the white pine







Changes in Grinnell Glacier revealed by a series of photographs taken near the summit of Mt. Gould, Glacier National Park. From left to right: 1938 (National Park Service archives), 1981 (Carl Key, USGS), and 1998 (Dan Fagre, USGS).

blister rust, which has since then inexorably infected and killed a large portion of the whitebark pine in the western U.S. In its northern range and Glacier National Park, researcher Katherine Kendall and collaborators have found that over 90 percent of the whitebark pine are dead, leaving stark tree skeletons dotting the alpine slopes and ridges. Thus, a fundamental ecological change in our mountain plant communities has occurred even in the remotest parts of our protected areas, with its source on the other side of the globe.

A more visible change has occurred throughout the Rocky Mountain West in the gradual disappearance of glaciers from the hanging valleys and serrated ridges they carved over thousands of years. Much of the glacial recession has occurred in the years since mountainous protected areas were created. In Glacier National Park, for instance, there are at most 37 glaciers remaining from the 150 estimated to have existed in 1850. Furthermore, Carl Key and others have estimated that the largest remaining glaciers cover, on average, less than one-third their previous area. Additionally, the current ice surfaces of these glaciers are hundreds of feet lower than they were previously, indicating that they are dramatically thinner. This glacial shrinkage continues and, at the increasing rate of melting, one computer analysis projects the complete disappearance of functioning glaciers in Glacier National Park just thirty years from now.

Because there have not been significant long-term changes in local precipitation, Myrna Hall concluded that the increase in the average summer temperature over the past 100 years was the main driver of change. Glaciers are excellent barometers of climate change because, unlike biological organisms, they do not adapt to change, but merely reflect it.

What does this mean for Glacier National Park? Superficially, it means that a charismatic geologic feature will be missing from the park. Although the impetus for naming the park was the world-class glacially carved terrain as much as the existing glaciers, the public still associates glaciers with the park, and seeing one is as important as seeing Old Faithful in action in Yellowstone. Even George Bird Grinnell, who was an early and influential champion of establishing the park, expressed dismay when he visited "his" glacier (Grinnell Glacier in the Many Glacier Valley) in 1927 as an old man and found it to be much smaller than when he first explored it in the nineteenth century.

As glaciers disappear from the headwaters of valleys and seasonal snowpacks melt earlier, the existing coldwater streams will have little or no baseflow in late summer. Stream temperatures will rise and alter the distribution and abundance of thermally sensitive aquatic organisms, and such changes will cascade throughout the food web.

Most importantly, the disappearance of glaciers as a

response to regional warming strongly indicates that other pervasive ecosystem changes have occurred and may accelerate in the future. Clearly, global-scale environmental changes, such as long-distance chemical transport, introduction of exotic diseases, and climate shifts, can influence even those mountain sanctuaries protected within a relatively natural regional landscape.

Understanding Mountain Ecosystem Change

How, then, can we assess and understand the impacts of such external stressors on our protected areas if we want to manage our natural landscape networks in the Rocky Mountain West? Mountain ecosystems are particularly difficult to evaluate because they have steep environmental gradients and complex topography, meaning that ecological processes, species, and relationships can change quickly over relatively short distances.

This problem confronted the National Park Service (NPS) in 1990 when it joined the U.S. Global Change Research Program's mission to understand the impacts of climate change on our nation's resources. In the national program, the NPS played an unique role for several reasons. First, the relatively unaltered national park ecosystems could act as benchmarks against which the condition of other systems could be compared. Second, inclusion of protected landscapes could help differentiate between effects of global-scale environmental change to ecosystems from those changes occurring locally and regionally. Despite the impacts to Glacier National Park's ecosystem described earlier, such systems represent some of our best opportunities to understand the intricacies of ecosystem structure and function and to use this knowledge to address ecosystems which have undergone more extensive alteration.

The NPS had its own concerns, too. The agency's mandate to provide for public enjoyment of parks while keeping their resources intact in perpetuity is a near-impossible task to begin with, but it is made doubly difficult by coping with climate-driven changes beyond park managers' control.

In 1991, Glacier National Park began an ecosystemscale program to assess the potential impacts of climatic and global environmental change on its resources. Given the daunting complexity of ecosystem structure and function, and responses to multiple sources of stresses, the only manageable approach to dealing with this task was to employ advances in simulation modeling, computing technology, and new data sources from satellites. This technology-intensive modeling of ecosystem dynamics allowed researchers to estimate the complex interplay of factors; computers can store and organize large amounts of information and simulate quantified ecosystem responses by which different levels of climate change or other disturbances can be measured. This "cyber-symbiosis" between ecologists (who provide the established ecological relationships reduced to computer code) and computers (with vast memory and ability to process multiple relationships simultaneously) gives us unprecedented opportunities for understanding ecosystems in an integrative manner.

Dr. Steven Running and his staff and colleagues at the Numerical Terradynamics Simulation Group at the University of Montana, Missoula, further developed and applied a simulation modeling program known as Regional

Hydro-Ecological Simulation System (RHESSys) so that it specifically estimated ecosystem processes and changes in Glacier National Park.

This powerful program combines remote sensing, ecological modeling, and geographic information system technologies to produce and map estimates of forest evapotranspiration, amount of annual carbon stored, and other processes for each slope, aspect, and

...global-scale
environmental changes,
such as long-distance
chemical transport,
introduction of exotic
diseases, and climate
shifts, can influence even
those mountain sanctuaries protected within a
relatively natural
regional landscape.

elevation. Satellite-based sensors (such as those on NASA's Landsat Thematic Mapper) provide estimates of Leaf Area Index (a measure of plant community photosynthetic capability) for each spatial unit throughout the mountain topography of Glacier National Park. Applied to each spatial unit is an estimate of daily climatic conditions derived from a mountain climate program and weather stations scattered throughout the park. The simulation program applies equations describing tree physiological responses to water and light to estimate how much growth a forest will undergo each day for each unit. RHESSys also can calculate the daily water balance for a drainage, estimate the distribution and moisture content of the snowpack, and provide daily discharge estimates for all streams.

Most critically, perhaps, RHESSys can visualize and



Smoke from the 1999 Anaconda Fire in Glacier National Park. Future fire frequency will have implications for air quality within national parks and mountain protected areas as well as nearby communities. Photo by Dan Fagre, USGS.

graphically portray ecosystem processes and attributes that cannot be seen and may seem abstract, yet are critical to an ecosystem's responses and its future. This visualization provides an entirely new dimension for scientists and ecosystem managers thinking about these areas and is, perhaps, the equivalent of a CAT scan in portraying important but previously inaccessible information. It opens up the ecosystem's underlying physiology, so to speak, and makes it part of our intuitive understanding.

While RHESSys was targeted at understanding ecosystem processes, another model called FIREBGC was developed by Drs. Robert Keane and Kevin Ryan of the U.S. Forest Service's Intermountain Fire Sciences Laboratory. This model aimed to estimate the structure of the ecosystem by combining the bio-geochemical drivers of RHESSys with a forest succession model to estimate standlevel dynamics such as rates of tree regeneration, growth, and mortality. This allowed FIREBGC to estimate the forest stand's stem density, amount of coarse woody debris, duff depth, and other structural characteristics that are important for accurately assessing potential forest fire frequency. It also could estimate the dominant tree species

present in each spatial unit given the life histories, competitive relationships, and typical responses to long-term climate for all this region's trees.

In short, FIREBGC can provide unprecedented detail about an extensive forested system from these calculations. A map of these forest characteristics is an invaluable tool for guiding decisions about Glacier National Park, but it is important to realize that these are simulations and therefore only hypotheses about what is out there until the model's results are verified by data from the real ecosystem. This verification required more than eight years of coordinated field studies to monitor mountain climatology, snow distribution, glacier activity, stream hydrology, aquatic biota, forest demographics, and soil respiration in Glacier Park and to compare the acquired data with the ecosystem estimates from the models.

Here are some examples of the information revealed by U.S.G.S. field research and by Dr. Richard Hauer of the University of Montana's Flathead Lake Biological Station. Over 4,500 snow measurements, taken from a variety of slopes and aspects in two topographically diverse mountain watersheds, correlated well with model estimates. Similarly,

the daily flows in seven streams continuously monitored during the eight years compared well with the flows predicted by the models for that period. In watersheds with remnant glaciers, however, higher observed flows during late summer underscored the contributions of glacial meltwater to streamflow and the need to include this source in future models of mountain hydrology. Modeled stream temperatures closely reflected observed temperatures from temperature loggers placed in the streams at various elevations, but it became clear that floodplains were areas of great thermal complexity and thus not easily modeled.

Frequent monitoring of stream insects clearly showed that predictable species replacement along different sections of the streams was tied to water temperature rather than other variables such as substrate particle size. This suggests that general warming of stream water temperatures due to earlier snowmelt and loss of glaciers will cause an upslope migration of those macroinvertebrates with narrow thermal tolerances.

Numerous forest plots throughout both study watersheds were selected to represent various combinations of
slope, aspect, and elevation. Measurements of stand
characteristics, such as stem density, were made at each
plot and compared to FIREBGC's estimates for the same
area. The computer model accurately estimated most
forest attributes, but it underpredicted net primary
productivity and evapotranspiration in early seral forest
stands because the program does not simulate undergrowth
ecosystem processes at the detail provided for tree species.
Overall, however, RHESSys and FIREBGC reasonably
predicted the structure and composition of mountain forest
communities and the daily rates of ecosystem processes at
various spatial scales.

Applying New Research Tools to Protected Area Management

So now we have a gee-whiz tool capable of simulating an ecosystem's processes in intimate detail, map its daily dynamic, and produce compelling graphics that help us intuitively understand its gestalt. What is its practical use? The modeling program is particularly helpful in guiding the questions we ask about the future. Here are a few that come to mind:

- Where will changes in the ecosystem be greatest with continued climate change?
 - Which plant communities benefit and which don't?
- Does increased climatic variability cause more change than gradual increases in average temperatures?
 As a proxy for the real ecosystem, we can subject our

virtual ecosystem to many conditions we wouldn't want to impose on Glacier National Park or the other protected areas in the Rocky Mountain West. From such "experiments" we can learn what to expect in the future and how our local and regional management decisions will interact with global changes in shaping that future.

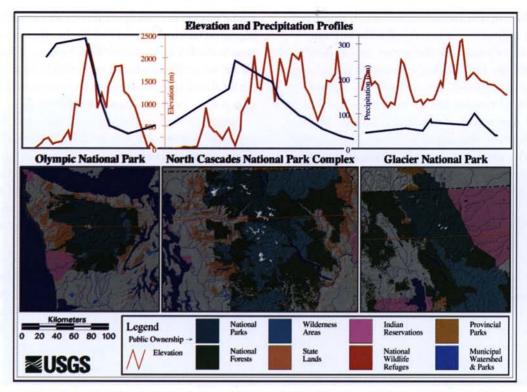
Several examples will clarify this latter point. We envisioned future conditions at Glacier National Park by applying a climatic scenario with a 30 percent increase in precipitation and 0.5-degrees Celcius increase in annual temperature for the next 200 years. (Global-scale models developed by the federal agencies NASA and NOAA tell us that this is one of the most likely scenarios for west of the Continental Divide in Montana.)

The model predicted that many mesic tree species, such as western red cedar and western hemlock, will begin to expand their ranges in the valley bottoms on the west side of Glacier, more closely resembling parts of the Pacific Northwest. However, overall increased forest productivity means increased fuel loads and potential for greater fire intensity, size, and frequency. It also means greater evapotranspiration, and, with snowpacks melting earlier in the year, the greater overall precipitation does not prevent the larger forests from depleting soil moisture and reducing streamflows in late summer. Ironically, then, increased annual precipitation doesn't prevent some permanent streams from becoming ephemeral in this future scenario, with obvious negative consequences for the aquatic organisms that live in those streams.

Some climate change scientists suggest that more variability in our annual weather patterns has already occurred and will become more extreme in future years. We looked at the impacts of such a scenario on Glacier National Park by simulating a climate regime in which average temperatures remained constant but the year-toyear variability increased markedly. The eastern side of the park generally responded more dramatically than did the area west of the Continental Divide, but high-elevation subalpine tree communities on either side of the divide became nitrogen stressed. Significant reductions in net primary productivity occurred on the eastern side as trees were stressed during more frequent droughts, leading to an upward shift of both upper and lower treelines. Some variability scenarios indicated an eventual conversion of Glacier's east side to a grassland-dominated environment.

Clearly, climatic variability has great potential to transform Glacier's ecosystem, particularly east of the divide, and the ecosystem modeling provided a means to alert us to this possible future.

Finally we looked at the consequences of different



A transect of mountain-dominated national parks from the Pacific Ocean to the Great Plains will be used to further examine the role of climatic variability and regional landscape fragmentation as agents of long-term change. Graphic by Rob Norheim and David Peterson, University of Washington and USGS-GFS.

combinations of future climate change and different management responses. For instance, we mapped the perimeter and intensity of likely future forest fires using the current climate and historic policies of fire suppression. Not surprisingly, fire intensity and size increased. However, even with future climates providing additional forest growth, long-term restoration of a policy favoring natural fire frequency counteracts much of the potential increased fuel loads.

The model showed overall increased net primary productivity and available nitrogen after natural fire frequencies were in place. However, this management shift also generated negative consequences for local air quality, with increased smoke emissions. Various air pollution measures of probable future smoke emissions, such as PM2.5 (particulate matter 2.5 microns and smaller), were estimated under a future climate scenario and natural fire frequency, with the resulting estimates suggesting that standards for human health will be exceeded.

On the other hand, the successional response of the landscape to these simulated forest fires predicts more diverse mosaics of vegetation which, in turn, will influence future ecosystem processes in quantifiable ways. These mosaics reflect greater levels of overall species biodiversity,

and the model output could be reconfigured to estimate the future extent of specific wildlife habitat as well.

Such tools provide the ability to evaluate different combinations of climate change and landscape management for specific purposes as well as the general state of Glacier's future ecosystem. Managers can "practice" with a simulated ecosystem and evaluate many options before being faced with some of the real challenges that seem likely to occur.

In addition to evaluating the impacts of management and future climate on Rocky Mountain West core areas, ecosystem modeling can be used to improve current management programs. For instance, monitoring will be more efficient by focusing on resources or areas that models suggest are most vulnerable to change. Using the same climate scenario described above, we found that one subdrainage of the McDonald watershed will likely experience water temperature increases four to five times greater than others. This area would be a candidate for detecting early and pronounced change, and would indicate more pervasive changes to come. Similarly, the vegetation on the park's eastern side represents a more vulnerable resource under the climatic variability scenario and may warrant additional monitoring and management attention.

The Future: Expanding Our Vision

The ecosystem modeling capabilities described in this article, when complemented by monitoring in the field, provide us with a multifaceted approach to assessing the present structure and function of the core protected areas such as Glacier National Park in our Rocky Mountain West landscape. This approach can be applied to other mountain ecosystems throughout this region.

As we've seen, the assumption that these protected areas are entirely intact is unwarranted, although they do represent the best examples of naturally functioning ecosystems available to study and to enjoy. The predictive tools described here suggest and graphically portray that future changes will be more profound as global-scale environmental changes weigh more heavily on these protected areas.

These core protected areas anchor our strategies, plans, and expectations for the regional natural landscapes that continue to define the Rocky Mountain West. As they are undergoing rapid change, we must use ecosystem modeling capabilities to examine mountain ecosystem issues at the regional scale. In fact, just such a program has begun.

A regional study is looking at a transect of mountain bioregions to examine the differences in ecosystem dynamics between core areas and the rest of the regional landscape, to examine how the core areas provide ecosystem services to surrounding landscapes, and to project future changes to these relationships under conditions of increasing landscape fragmentation, disturbance, and climatic change. This study-entitled CLIMET (for Climate-Landscape Interactions, a Mountain Ecosystem Transect)—is a U.S.G.S. partnership with Dr. Dave Peterson, and builds on his existing global change research. The mountain regions are the Olympic Peninsula, with Olympic National Park at its core; the North Cascades region, with North Cascades National Park at its core; and the Northern Rocky Mountains region, with Glacier National Park at its core.

This transect of three separate mountain systems represents a gradient of climatic regimes from maritime to continental, and a disturbance gradient from extensive landscape fragmentation outside the park to relatively intact natural landscapes surrounding the park. The complementary strategy is to establish a mountain transect along the axis of the continental divide where there are north-south gradients in climatic regimes and disturbance levels but there is a measure of ecological connectivity along the cordillera.

These regional-scale ecosystem studies will enrich our public dialogue about what we want the Rocky Mountain

West to be and how to ensure we can get there. Regionalscale simulations can provide us with alternative futures, and judicious use of the visualization tools will help to communicate and clarify the future in which we all will eventually live. **CL**

References

-Blais, J.M.; D.W. Schindler, D.C. Muir, L.E. Kimpe, D.B. Donald, and B. Rosenberg, Accumulation of persistent organochlorine compounds in mountains of western Canada," *Nature*, 395:585-588 (1998).

-CLIMET Website: http://www.cfr.washington.edu/usgs/cascadia/climet/index.htm

-Fagre, D.B., P.L. Comanor, J.D. White, F.R. Hauer, and S.W. Running, "Watershed responses to climate change at Glacier National Park," *Journal of the American Water Resources* Association, 33:755-765 (1997).

-Hall, M.H.P., Predicting the impact of climate change on glaciers and vegetation distribution in Glacier National Park to the year 2100. M.S. Thesis, State University of New York, Syracuse (1994).

-Keane, R.E., K.C. Ryan, and S.W. Running, "Simulating effects of fire on northern Rocky Mountain landscapes with the ecological process model FIRE-BGC," *Tree Physiology*, 16:319-331 (1996).

-Keane, R.E., C.C. Hardy, K.C. Ryan, and M.A. Finney, "Simulating effects of fire on gaseous emissions and atmospheric carbon fluxes from coniferous forest landscapes," *World Resource Review*, 9:177-205 (1997).

-Kendall, K.C. "Whitebark Pine: Ecosystem in Peril," in LaRoe, E. T., ed., *Our Living Resources*, U.S. Dept. of Interior, National Biological Service, Washington, D.C.: 228-230 (1995).

-Key, C.H., D.B. Fagre, and R.K. Menicke, "Glacier recession in Glacier National Park, Montana," in R.S. Williams and J. Ferrigno, eds., Satellite Image Atlas of Glaciers of the World. U.S. Geological Survey Professional Paper 1386-J. U.S. Government Printing Office, Washington D.C. (in press).

-White, J. D., S.W. Running, P.E. Thornton, R.E. Keane, K.C. Ryan, D.B. Fagre, and C.H. Key, "Assessing regional ecosystem simulations of carbon and water budgets for climate change research at Glacier National Park, USA," *Ecological Applications*, 8:805-823 (1998).

Dan Fagre has been working for nine years with many partners and collaborators in the Northern Rocky Mountains to understand how global-scale environmental changes will affect our collective backyards in this region. He is an ecologist at Glacier National Park, working for the U.S. Geological Survey's Northern Rocky Mountain Science Center. He received his Ph.D. from the University of California, Davis, and acknowledges his talented and dedicated staff's contributions to the research described in this article.