TAKING THE PULSE OF MOUNTAINS: ECOSYSTEM RESPONSES TO CLIMATIC VARIABILITY

DANIEL B. FAGRE[1], DAVID L. PETERSON[2] and AMY E. HESSL[3]

[1] *U.S. Geological Survey, Northern Rocky Mountain Science Center, West Glacier, MT 59936, U.S.A.*
E-mail: dan_fagre@usgs.gov

[2] *USDA Forest Service, Pacific Northwest Research Station, 400 N. 34th Street, Suite 201, Seattle, WA 98103, U.S.A.*

[3] *Department of Geology and Geography, West Virginia University, Morgantown, WV 26505, U.S.A.*

Abstract. An integrated program of ecosystem modeling and field studies in the mountains of the Pacific Northwest (U.S.A.) has quantified many of the ecological processes affected by climatic variability. Paleoecological and contemporary ecological data in forest ecosystems provided model parameterization and validation at broad spatial and temporal scales for tree growth, tree regeneration and treeline movement. For subalpine tree species, winter precipitation has a strong negative correlation with growth; this relationship is stronger at higher elevations and west-side sites (which have more precipitation). Temperature affects tree growth at some locations with respect to length of growing season (spring) and severity of drought at drier sites (summer). Furthermore, variable but predictable climate-growth relationships across elevation gradients suggest that tree species respond differently to climate at different locations, making a uniform response of these species to future climatic change unlikely. Multi-decadal variability in climate also affects ecosystem processes. Mountain hemlock growth at high-elevation sites is negatively correlated with winter snow depth and positively correlated with the winter Pacific Decadal Oscillation (PDO) index. At low elevations, the reverse is true. Glacier mass balance and fire severity are also linked to PDO. Rapid establishment of trees in subalpine ecosystems during this century is increasing forest cover and reducing meadow cover at many subalpine locations in the western U.S.A. and precipitation (snow depth) is a critical variable regulating conifer expansion. Lastly, modeling potential future ecosystem conditions suggests that increased climatic variability will result in increasing forest fire size and frequency, and reduced net primary productivity in drier, east-side forest ecosystems. As additional empirical data and modeling output become available, we will improve our ability to predict the effects of climatic change across a broad range of climates and mountain ecosystems in the northwestern U.S.A.

1. Introduction

During the past two decades, many different approaches have been used to predict the potential response of ecosystems to climatic variability and change. Typically, various general circulation models (GCM) have been used to establish scenarios that reflect the effect of increased greenhouse gases on temperature and precipitation. Modeling at various spatial scales (initially global to continental) (e.g., VEMAP members, 1995; Cramer et al., 2001) has been used to estimate changes in vegetation cover, species distribution, and carbon balance. Recently ecosystem and vegetation models have been linked explicitly with GCM scenarios to provide

Climatic Change **59:** 263–282, 2003.

a more integrated projection of how climatic trends might affect ecosystem properties (e.g., Bachelet et al., 2001) and how ecosystem processes like carbon cycling might feedback to affect atmospheric processes (Foley et al., 2000).

There is increasing interest in more accurate predictions of the effects of climatic variability and change at regional and subcontinental scales (Mote et al., 1999a; National Assessment Synthesis Team, 2000; Fagre and Peterson, 2002). It is particularly challenging to predict the effects of climatic variability in mountain ecosystems because the diverse topography, steep environmental gradients and ecological isolation of mountains result in high levels of biodiversity and endemism. This results in a complex intersection of physical and biological features that are typically beyond the capacity of existing empirical databases and models, except at very coarse spatial and temporal scales (Peterson and Parker, 1998).

To date, modeling has led the way in predicting changes in ecosystem properties perhaps to the exclusion of collecting the empirical data necessary to develop and validate robust vegetation and ecosystem models (Aber, 1997). In addition, having investigators in diverse locations and systems with different approaches and models is not conducive to integration of results across geographic locations, even if there are biophysical features in common in the systems being studied. Integrated multi-scale approaches – similar to those used at Long-Term Ecological Research sites but at a broader geographic scale – are needed to develop inferences about basic ecosystem properties across the major mountain ranges in western North America and, ultimately, across the globe. Integrated approaches that address regional ecosystem processes across elevational gradients complement projects like the Global Observation Research Initiative in Alpine Environments, GLORIA (Grabherr et al., 2000) that focus on select systems (alpine) globally.

The ongoing research program Climate-Landscape Interactions on a Mountain Ecosystem Transect (CLIMET, http://www.cfr.washington.edu/research.fme/climet) is focused on the effects of climatic variability on mountain ecosystems in northwestern North America (Fagre and Peterson, 2000). This program focuses on three basic research questions:

- What are the effects of spatial and temporal climatic variability on critical plant resources and species distributions?
- What are the effects of climatic variability on ecosystem processes (e.g., productivity) and natural resources (e.g., water supply)?
- How do different levels and types of disturbance influence landscape patterns and the sensitivity of ecosystems to climatic variability?

CLIMET uses large empirical databases of ecological, hydrological and climatological data in addition to well-established modeling approaches to answer these questions across three mountain ranges in northwestern North America (Figure 1).

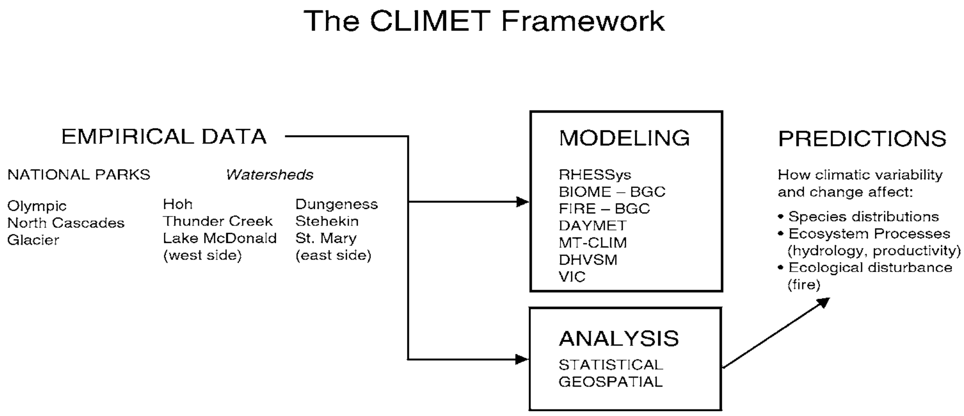

Figure 1. The CLIMET framework for quantifying the potential effects of climatic variability and change on mountain ecosystems focuses on integration of empirical data, modeling, statistical analysis and geospatial analysis.

2. CLIMET Study Area

The study area extends from the Pacific Ocean to western Montana (Figure 2), located between the mean summer (∼52° N) and winter (∼46° N) position of the polar jet stream. This boundary is vulnerable to changes in north-south gradients of precipitation and temperature as air flow patterns that control the jet stream respond to changes in forcing mechanisms. When the polar jet stream is split during winter (as in El Niño years) the frequency and intensity of storms diminish. Most weather stations in the region express linear temperature trends of +0.5 to +2.0 °C per century (mean ≈0.8 °C) since about 1900 (Mote et al., in press). Also, under many climatic-change scenarios, altered jet stream patterns could change the climatic variability of the study area at daily, monthly and interannual scales (Mote et al., 1999a).

The study area has a gradient of general climatic types, ranging from maritime (Olympic National Park [NP]) to transitional (North Cascades NP) to continental (Glacier NP). Winter temperatures are moderate in the Olympics, intermediate in the North Cascades and cold in the Northern Rockies. Precipitation varies dramatically between westside and eastside locations; for example, precipitation in the Olympics varies from >600 cm/yr (southwest, high elevation) to 40 cm/yr (northeast, low elevation), while precipitation in the Northern Rockies varies from 300 cm/yr (westside, high elevation) to 30 cm/yr (eastside, low elevation). This contrast in precipitation over small distances has a major effect on microclimate, vegetation distribution and disturbance regimes (Peterson et al., 1997). Heavy snowpack dominates all three bioregions at high elevations.

Vegetation in all bioregions is dominated by coniferous forest, with species distribution and abundance varying along altitudinal gradients and from westside to eastside. The western Olympics are dominated by temperate rainforests with

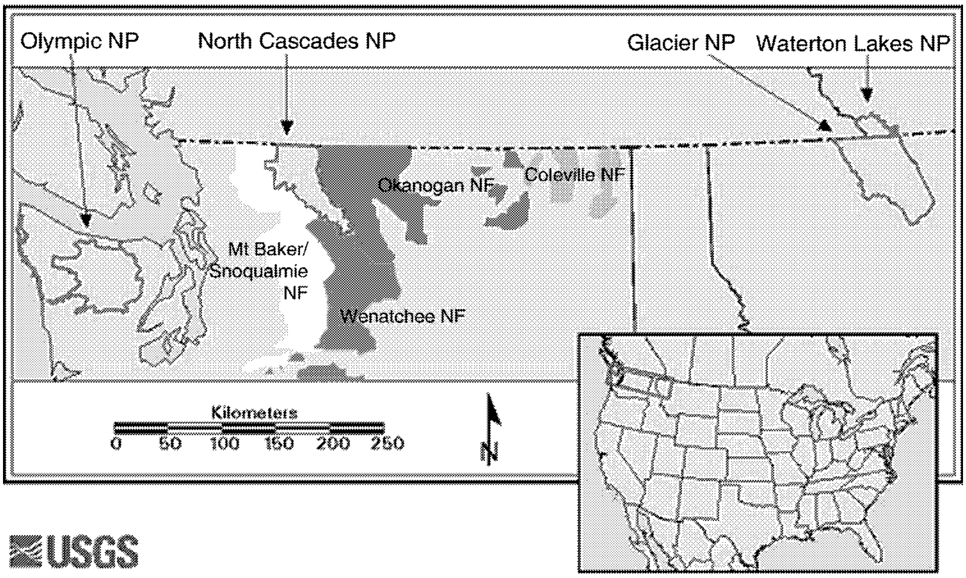

Figure 2. Location of CLIMET studies in national parks along a longitudinal gradient from marine to continental climate.

high biomass and abundant woody debris. Biomass and productivity generally are lower in the North Cascades and lowest in the Northern Rockies. There are 10 coniferous species in common among bioregions. The national parks within each bioregion are largely undisturbed by humans and are contiguous with national forest wilderness along portions of their borders. Late-successional forests are located primarily within national parks and wilderness, while most non-wilderness forests on adjacent national forest, state, tribal, and private lands have been harvested at least once during the past century.

3. Effects of Climatic Variability on Mountain Ecosystems of the Northwestern United States: What We Know

The past decade of research in the CLIMET study area and beyond (see publications at http://www.cfr.washington.edu/research.fme/climet/products.htm) clearly documented ecosystem responses that are attributable to climatic change. These results provide an impetus and basis for investigating the effects of future climatic variability on species distribution, ecosystem processes and ecological disturbance. These data have been derived through paleoecological studies, long-term monitoring and retrospective analyses of existing data.

3.1. SPECIES DISTRIBUTION

Recent paleoecological studies in the Olympic Mountains have shed some light on how climatic variability at the multi-millennial scale has affected the distribution and abundance of coniferous (Gavin et al., 2001) and alpine species (Gavin and Brubaker, 1999) in northwestern North America during the Holocene. However, relatively little is known about how recent (ca. last 150 years) climatic warming has affected regional plant species distribution. Localized changes in plant abundance and distribution suggest a response to climatic warming is occurring.

Subalpine meadows have been increasingly displaced by subalpine tree species throughout the CLIMET study region (Marr, 1977; Woodward et al., 1995; Rochefort and Peterson, 1996; Hessl and Baker, 1997), especially since the 1930s. Other areas, such as snow avalanche paths, have also experienced relatively rapid 'in-filling' (Butler and DeChano, 2001). Indeed this 'in-fill' phenomenon appears to be common throughout western North America (Rochefort et al., 1994), especially during periods of reduced snowpack in high-snowfall areas. There is no clear evidence that altitudinal treeline has moved uniformly and significantly upward in the northern Rocky Mountains during the recent climatic warming (Butler et al., 1994), but some areas have had upward forest migrations of 100–250 m since 1935, probably as a result of both climatic shifts and changes in fire suppression policy (Butler and DeChano, 2001). From the data available in the literature, altitudinal treeline in western North America has rarely moved up more than 100 m during the Holocene, even during prolonged warm periods (Rochefort et al., 1994). However, in Glacier National Park tree establishment above treeline has increased during the last 80 years (Bekker et al., 2000). Spaces between krummholz patches have filled in, the area covered at treeline has increased by 3.4%, tree density has increased within patches and there is a trend of krummholz shifting to upright tree form, all of which increase biomass and make a more abrupt transition from forest to tundra at treeline (Klasner and Fagre, 2002).

What are the drivers for these changes in Glacier National Park? Temperature records for nearby towns (e.g., Kalispell, Montana) date back as far as 1896 but records are much shorter within the park. Selkowitz et al. (2002) reported no significant increase in summer temperatures (July–September) from nearby Kalispell between 1922–2000 but Finklin (1986) reported net increases in both winter and summer temperatures of 1.1 °C using a 3-station weighted average to approximate conditions in the park from 1910–1980. A different analysis of Kalispell summer temperatures (June–August) from 1899–1995 (Fagre and Peterson, 2000) and records from other stations (e.g., Fortine) further corroborate a net increase in temperature that occurred primarily in the early part of the 1900s. This is the approximate period when tree establishment at treeline began to increase (Bekker et al., 2000). Changes in precipitation also could drive vegetation responses. Annual mean precipitation, measured at Kalispell, increased (0.09 cm/yr) during the past century (Selkowitz et al., 2002). Despite this increase, snowpacks in the Glacier

National Park region were reduced in size and melted earlier during the 1950–2000 period, suggesting a shift in the rain-to-snow ratio. This would help explain the observed treeline forest expansion and in-filling. However, this apparent snowpack decline is due to its positioning in the larger pattern of Pacific Decadal Oscillations (Selkowitz et al., 2002) that influence decadal-scale regimes of snowfall. No overall trend is evident when snow records from 1922 through the present are considered although the different phases of PDO and associated snow regimes likely influence rates of tree in-filling and meadow invasion.

3.2. ECOSYSTEM PROCESSES

3.2.1. *Hydrology and Glaciers*

Large-scale patterns of streamflow in northwestern North America are strongly associated with temporal variation in the El Niño Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO). In the Columbia River basin, which extends from the Cascade Range to the Rockies, low streamflow is positively correlated with warm, dry ENSO and with warm, dry (positive) PDO (Hamlet and Lettenmaier, 1999); extreme high flows are associated with cool, wet ENSO and with cool, wet (negative) PDO. The relationship between streamflow and PDO is beginning to make long-term predictions of water supply more accurate.

Glaciers are excellent physical indicators of climatic change because they reflect decadal or longer climatic trends more than interannual variation. Of particular interest is the emerging relationship between PDO and glacial patterns, in which the warm, dry (positive) phase of PDO results in reduced mass balance of glaciers such as the South Cascade Glacier (located in the North Cascades) (Bitz and Battisti, 1999). Directional changes in climate and in the duration of multi-decadal climatic 'cycles' will clearly affect glacial mass, streamflow and aquatic ecology of mountain ecosystems.

Glaciers in the CLIMET study area generally have receded in the past 150 years. For example, at Glacier National Park, of the 150 that existed in 1850 (Carrara, 1989), less than 37 remain. The remaining glaciers have been reduced to one-third or less of their previous surface area (Key et al., 2002), and total ice and permanent snow coverage of the park have been reduced 72%. Comparing recent photographs and historic photographs taken from the same location of 17 of the remaining glaciers makes clear that glaciers continue to recede. Thirteen of the 17 glaciers are distinctly smaller when compared to photographs taken at various times in the 1900s. Based on a precision global positioning system survey of Grinnell Glacier in 2001, over 0.17 km^2 was lost from a relatively small glacier since 1993. Finally, ground penetrating radar surveys show that glacial ice has thinned by as much as 50% during the past two decades. Because annual precipitation has increased slightly and snowpacks have had no net increase since 1922 (Selkowitz et al., 2002), continued glacier recession has been linked to summer temperature increases early in the 20th century that exceeded the equilibrium threshold for glacier maintenance. If long-term warming continues at the rate of the past century, all glaciers could disappear from the park by 2030 (Hall and Fagre, 2003). Glaciers in Olympic and North Cascades National Parks also receded considerably during the 20th century (Krimmel, 2000; Granshaw, 2001; Rasmussen and Conway, 2001). This is particularly significant because the North Cascades National Park complex contains 316 glaciers and is the most heavily glaciated area of the American west (Granshaw, 2001).

3.2.2. *Tree Growth and Productivity*

High-altitude forests at several locations in western North America, including the CLIMET study area, have experienced increased growth rates during the 20th century, a phenomenon controlled by snowpack duration in some cases but perhaps also related to increased atmospheric CO_2 or other factors (Graumlich et al., 1989; Peterson, 1998a; McKenzie et al., 2001). This pattern of increased growth, which appears to be restricted to high-elevation forests and to some maritime coniferous forests, is quite distinct from the growth patterns of lower elevation forests.

In addition, forests of northwestern North America whose growth is limited by duration of snowpack or by summer moisture stress are strongly affected by PDO variability. For example, mountain hemlock (*Tsuga mertensiana*) growth is strongly limited by number of snowpack-free days during which trees can be photosynthetically productive. PDO is strongly correlated with annual snowpack, so PDO therefore is also strongly correlated with mountain hemlock growth (Peterson and Peterson, 2001) (Figure 3). Ponderosa pine (*Pinus ponderosa*) growth is strongly limited by summer soil moisture in drier eastside Cascade and westside Rockies locations. PDO is strongly correlated with annual precipitation, so PDO therefore is strongly correlated with ponderosa pine growth (Figure 4). These types of relationships between PDO and tree growth are apparently subcontinental in nature and facilitate multi-centennial reconstructions of PDO based on tree rings (Gedalof and Smith, 2001) and other bioproxies (Gedalof et al., 2002).

3.3. ECOLOGICAL DISTURBANCE

Fire is the dominant large-scale disturbance in the study area (Peterson, 1998b; Schmoldt et al., 1998), including high-intensity (westside Olympics, westside North Cascades, most subalpine systems), moderate-intensity (some westside North Cascades, some westside Rockies) and low-intensity (eastside North Cascades, eastside Rockies, some westside Rockies) fire regimes (sensu Agee, 1993). Fuel accumulation in drier forest ecosystems during the past century has pushed many of these forests from historically low-intensity regimes to current high-intensity regimes. This poses a significant challenge for developing long-term management strategies that include fire as a component of landscape disturbance.

The timing and magnitude of extreme fire events are linked to large-scale synoptic weather patterns, and accounting for extreme fire events is a key to accurate

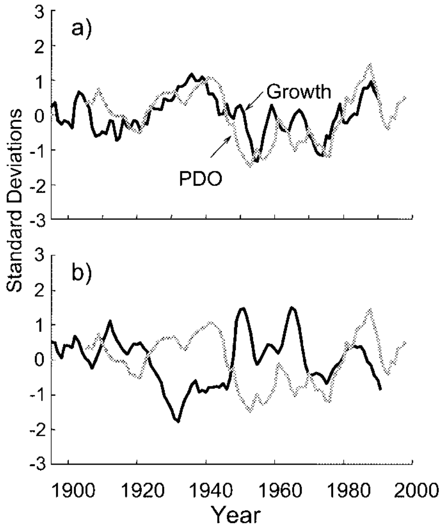

Figure 3. Time series (1900–1999) showing mountain hemlock (*Tsuga mertensiana*) radial growth (black line) from treeline sites in the Cascade Range (a) and low elevation sites (b) compared with the PDO index (grey line). Adapted from Peterson and Peterson (2001).

projections (e.g., Swetnam and Betancourt, 1990). Recent analyses have shown that the occurrence of large fires in northwestern North America is positively correlated with the warm, dry (positive) phase of PDO, which suggests a multi-decadal component to large-fire occurrence in the study area (Mote et al., 1999b). In addition, the relationship of synoptic weather patterns to fire occurrence in the CLIMET study area, including teleconnections between PDO and synoptic weather, has recently been quantified with greater accuracy.

4. Modeling the Effects of Climatic Variability on Mountain Ecosystems: A Multi-Scale Approach

CLIMET studies of the effects of climatic variability on species distributions, ecosystem processes and ecological disturbance encompass several empirical and modeling approaches. In addition, all modeling is based on a relatively large empirical database, with some data from existing records and much of it collected specifically for this research program. While some coarse-scale modeling is being conducted at large spatial scales (e.g., the scale of a national park; see below), CLIMET studies focus on key watersheds, one westside and one eastside, in each of the three parks: Olympic NP – Hoh (west), Dungeness (east); North Cascades NP – Thunder Creek (west), Stehekin (east); Glacier NP – Lake McDonald (west), St. Mary (east) (Figure 1). These watersheds were selected because they are reasonable representations of altitudinal cross-sections of the westside and eastside of

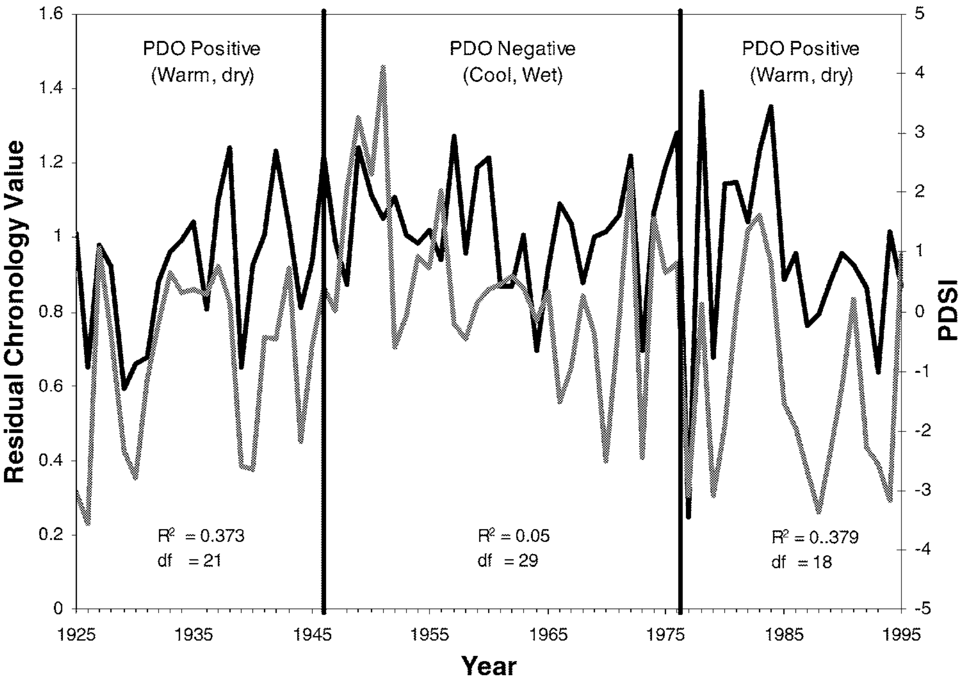

Figure 4. The relationship between drought-sensitive ponderosa pine (*Pinus ponderosa*) residual tree growth (black line) and the Palmer Drought Severity Index (PDSI) (gray line) change over time with respect to the changing phases of the Pacific Decadal Oscillation (PDO). During positive phases of the PDO (1925–1946 and 1977–1995), the adjusted R^2 ranges between 0.373–0.379, while during the negative phase of the PDO (1947–1976), the adjusted R^2 is 0.05, suggesting that PDSI is only a weak predictor of tree growth during the negative phase of the PDO.

each park, and also have sufficient long-term climatic and hydrological databases to provide input for modeling.

4.1. SPECIES DISTRIBUTION

One of the approaches CLIMET uses is statistical/empirical and, in combination with biophysical and climatic variables, it develops predictions of how dominant tree species will respond to long-term climatic change. It is based on the response of species to environmental gradients often being unimodal, with presence/absence or abundance being greatest at the center of a species range along each gradient. A multidimensional niche space of predictor variables can be estimated for a species if a nonlinear statistical model can be fit (McKenzie et al., in press). If predictor variables are spatially explicit climatic variables, then changes in geographic niches of the species can be estimated using climatic change scenarios. This approach contrasts with previous efforts focused on general vegetative associations or physiognomic types at broad spatial scales (e.g., Neilson, 1995; Iverson and

Prasad, 2001), and on the use of gap models to determine changes in tree species distribution (Urban et al., 1993; Keane et al., 1996; Zolbrod and Peterson, 1999).

Vegetation data are from 10,653 forest resource inventory plots in the Okanogan-Wenatchee National Forest (NF), Colville NF, Mt. Baker-Snoqualmie NF and North Cascades NP, occupying a longitudinal gradient from the crest of the Cascade Range to the western slope of the Rocky Mountains. This database is from the Area Ecology Program, USDA Forest Service, and for the Grizzly Bear Habitat Study (Gaines et al., 1990) and contains georeferenced information on the cover and size of dominant tree species from circular, 0.2-ha plots established across a broad range of slope, aspect and elevation combinations. Plots were in selected stands that were more than 75 years old, relatively undisturbed and relatively uniform in vegetation composition. A spatially constrained random sample of 1,000–2,000 plots is withheld from the analysis for testing the models.

The DAYMET model (Thornton et al., 1997) uses interpolation and extrapolation routines to estimate a suite of 36 daily meteorological variables for the period 1980–1997 at 1 km^2 resolution over the study region and includes a set of adjustments for elevational lapse rates and topography (Hungerford et al., 1989). Daily outputs are combined into selected monthly and annual summary coverages of climatological variables and solar radiation into ARC-INFO (ESRI, 2000) as grids, clipped to the geographic range of the vegetation plots. Vegetation plots are overlaid on the grid, and values for each of the climatic and physical variables are extracted for each plot. An additional suite of biophysical variables (e.g., seasonal, monthly and annual means of actual evapotranspiration, potential evapotranspiration, snowpack, hydrological variables and soil moisture) is obtained using MT-CLIM (Hungerford et al., 1989), a mountain microclimate simulator, in combination with coarse-scale (10 km) hydrologic simulation models such as VIC (Liang et al., 1994) that estimate water and energy balances.

Abundance measures for dominant conifer species are transformed to presence/absence and compiled into a model database with the climatic and biophysical predictors. Generalized linear models of the binomial family (McCullagh and Nelder, 1989) are used to estimate probability of occurrence for each species at each plot as a function of the predictor variables. Preliminary results indicate that for the majority of species it is possible to fit variables from both moisture and temperature categories of predictors; in all but a few cases, the models include negative quadratic terms, indicating a unimodal (concave down) response of species occurrence to a climatic or biophysical variable (McKenzie et al., in press). Climatic variables were used in the optimal models more frequently than biophysical variables, and alternative (sub-optimal) models with close to the same explanatory power always involved replacement of one predictor in the climatic category for another. Conifers, such as Douglas-fir (*Pseudotsuga menziesii*), were fairly consistent in responses at different spatial scales. Sample output is shown for Douglas-fir which is predicted to be most likely to occur where growing degree days are between 2,500 and 3,000, and soil drought days are between 100 and

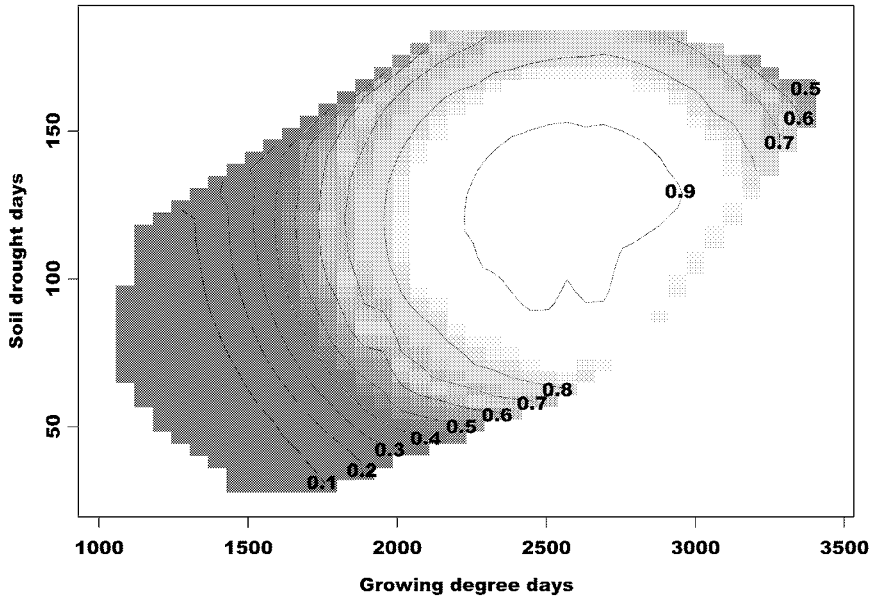

Figure 5. Predicted probability of occurrence of Douglas-fir on the Okanogan National Forest in eastern Washington, U.S.A. A generalized linear model predicts an 'environmental niche' in the two-dimensional space of growing degree days (threshold = 5 °C) and soil drought days (soil water in the top 10 cm is less than 10%). From McKenzie et al. (2003).

150 (Figure 5). Similarly, mountain hemlock (*Tsuga mertensiana*) is predicted to increase sharply where winter precipitation exceeds 80 cm (Figure 6). This predictor variable proved to be optimal at multiple scales and suggests that the models are robust across geographic gradients. Bootstrap validations suggest no loss of predictive power when applied to similar populations. Such robust models can be used with climatic change scenarios across the geographic range of the species to estimate future potential distributions and composition of Pacific Northwest forests.

We will analyze similar vegetation data available for thousands of plots in the Olympic Mountains and northern Rocky Mountains to test hypotheses developed from the North Cascades analysis and to quantify the spatial extent of biophysical relationships for species common throughout the CLIMET region. This approach, along with process-based modeling (see below), will allow us to develop inferences about the effects of climatic change on biophysical relationships, species distributions, and ecosystem dynamics at broad spatial scales in the northwestern United States.

4.2. ECOSYSTEM PROCESSES

Ecosystem processes, such as fluxes in energy, carbon, nitrogen, and water are modeled across CLIMET using a suite of models called the Regional Hydro-

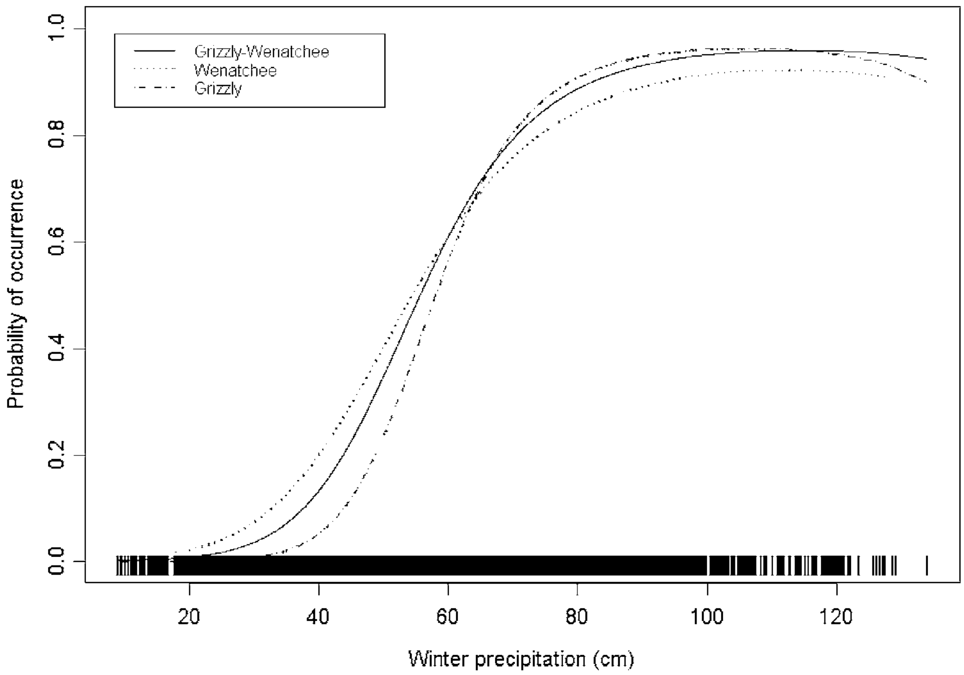

Figure 6. Estimated probability of occurrence for mountain hemlock (*Tsuga mertensiana)* as a function of winter precipitation. From McKenzie et al. (2003).

Ecological Simulation System (RHESSys) (Band et al., 1993). RHESSys is a collection of tools and interacting models that utilizes remotely sensed data to calculate metrics such as Normalized Difference Vegetation Index (NDVI) and leaf area index (LAI) for specific landscapes (Figure 7). These metrics are combined with spatially-interpolated daily climatic data from MT-CLIM for all slope, aspect and elevation combinations (Running and Gower, 1991). Simulated daily climatic data, coupled with soils and vegetation information are then used by RHESSys (White and Running, 1994) to estimate hydrological discharge as well as many other ecophysiological outputs.

Considerable hydrological modeling has already been completed for the Lake McDonald and St. Mary watersheds in Glacier NP and are underway for all other focus watersheds. Using monitoring data available since 1992, including streamflow, local weather measurements and over 7,000 snow measurements, it was determined that the modeling approach reasonably simulates daily stream discharge from the watersheds (White et al., 1998; Fagre and Peterson, 2002) as well as annual variation in stream temperature (Fagre et al., 1997). Nutrient dynamics for the Glacier NP watersheds have been directly tied to discharge rates and the annual hydrographic period (Hauer et al., in press). This analytical approach will be used for the key watersheds of each national park to determine the

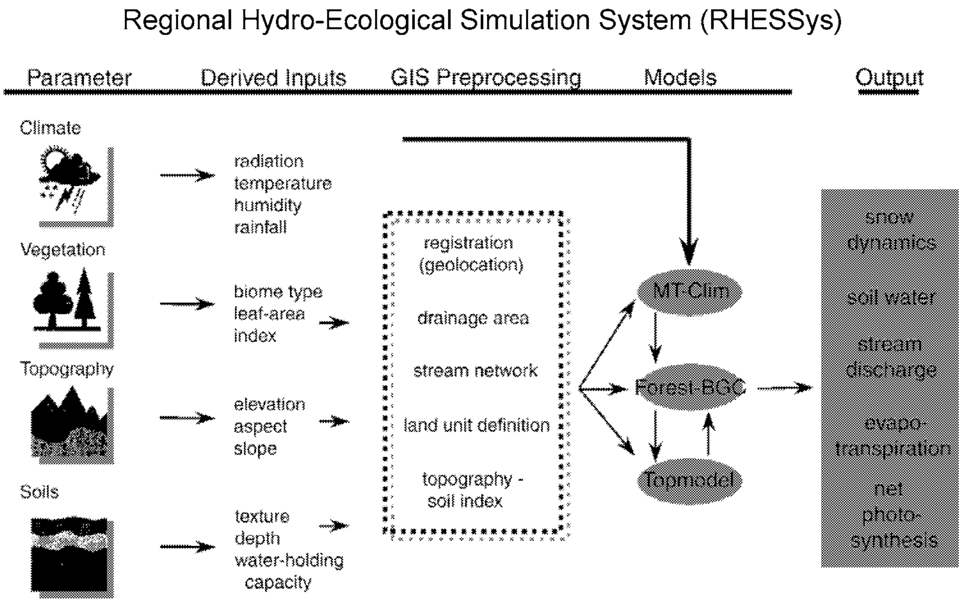

Figure 7. Inputs, outputs, and modeling steps used by RHESSys to simulate ecosystem processes for CLIMET. See text for more detail.

effects of climatic scenarios involving different combinations of precipitation and temperature.

Analysis of productivity within CLIMET takes place at the scale of each national park and each key watershed. Empirical data on forest composition and structure, described by Keane et al. (1996), have been collected in each park specifically for this analysis. For the Lake McDonald and St. Mary watersheds of Glacier NP, 110 circular 0.4-ha forest plots were assessed for numerous ecological characteristics such as stand age and understory biomass for all slope, aspect and elevation combinations. An additional 98 ground-truth plots distributed across both watersheds were used for validation of satellite imagery cover classifications. These data and other existing biophysical data are used to derive parameter estimates for FOREST-BGC (a BioGeoChemical Cycling model) for watersheds or BIOME-BGC (a differently-scaled version of FOREST-BGC) for regions. These models then calculate and map net primary productivity and carbon storage. For Glacier NP, this analysis has been completed at the watershed scale. White et al. (1998) found good agreement between modeled and measured net primary productivity and other ecosystem processes. White et al. (1998) then estimated the potential future changes in productivity after 120 years of increased climatic variability. Although individual plant communities responded differently, on balance, the eastern side of the park (east of the continental divide) became much less productive, and the western side became more productive. A BIOME-BGC productivity simulation across CLIMET closely mirrors field data collected to validate such estimates and clearly shows a spatial pattern of declining productivity from Olympic NP to Glacier NP. With this capability validated, the relative rates of change of each mountain area to potential climate change can soon be examined.

Additional effects of different climatic scenarios on temporal and spatial variation in productivity will be determined for each park and across the span of CLIMET. By knowing the effects of climatic change on productivity across the CLIMET geographic area, we will be able to more confidently predict growth patterns across a broad altitudinal and longitudinal range for many common tree species.

Productivity at the watershed scale is being addressed by linking forest growth with climatic variability at interannual to decadal time scales. Vegetation plots within the key watersheds were located to represent a broad distribution of species, aspect and elevation combinations. A large subsample of trees within these plots was measured for structural dimensions, and trees of various sizes for each common species were cored to obtain time series of radial growth. Empirical data on productivity will be compared with climatic data to determine the relationship between productivity and broad-scale climatic influences (ENSO, PDO). Tree-ring chronologies will be compared to observed climatic indices to quantify the effect of climatic variability on tree growth across multiple species and environmental gradients. Preliminary results for the Stehekin watershed in North Cascades NP indicate that species such as Douglas-fir are both highly productive and highly sensitive to climatic variability (Figure 8), which suggests that this species may be a good bioindicator of the effects of climatic change across the entire CLIMET transect.

4.3. ECOLOGICAL DISTURBANCE

CLIMET uses FIRE-BGC (Keane et al., 1996), a process-based model of fire succession on forest landscapes, for spatially explicit simulations of long-term changes in vegetation composition and structure under different climatic scenarios. FIRE-BGC requires parameterization of (1) site-specific environmental variables, (2) site-specific biogeochemical constants, species composition, fuel loading and mean fire return intervals, and (3) tree species variables (scale independent). Most of these data were collected as part of the empirical database described above. FIRE-BGC is being implemented for each key watershed in each national park. A stochastic weather generator provides multiple annual weather patterns that reflect the mean and natural range of variability in climatic scenarios. Simulations are run for >200 years, and model output is used to create coverages of tree species dominance, stem density and forest floor biomass for each watershed. FIRE-BGC simulates long-term changes in fuels, fire hazard, fire behavior and consequent effects on ecological characteristics such as total biomass, leaf area index and nitrogen cycling.

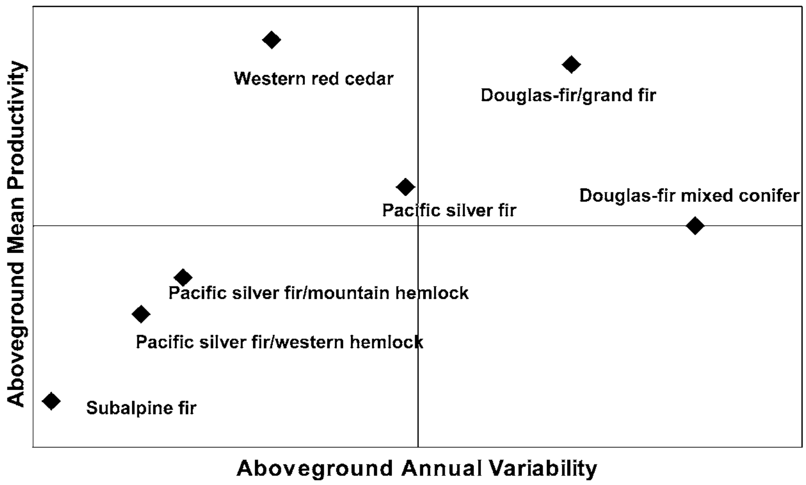

Figure 8. Mean annual aboveground productivity derived from annual increment and species-specific allometric equations plotted against annual variability in mean annual aboveground productivity. Mean productivity values increase upward and variability values increase from left to right. Forest types that are characterized by high variability and sensitivity such as subalpine fir may not generate large effects on landscape level carbon cycling due to low productivity. Instead, forest types with high productivity, high variability in productivity and high sensitivity to climate, like Douglas-fir, may generate large effects on carbon cycling in response to climatic change.

For a warmer, wetter climatic scenario (temperature +2–5 °C, precipitation +25–30%), FIRE-BGC indicates that forest landscapes in the Lake McDonald and St. Mary watersheds of Glacier NP will be more productive and have more frequent and severe fires than these landscapes have experienced historically (Keane et al., 1997). The resulting early successional vegetation will release less carbon to the atmosphere and be more diverse than landscapes with low-frequency fire. This clearly has implications for how forest landscapes could be managed in the face of climatic change.

5. How CLIMET Relates to Other Mountain Ecosystems

The CLIMET study area covers a broad range of physical landscapes, encompasses a diversity of climatic regimes, and includes a wide range of forest and fuel conditions. As a result, output from this research program can potentially be used to develop inferences about the effects of climatic variability and change in mountain ecosystems throughout western North America.

In this paper we document a number of mountain ecosystem responses to climatic change at different temporal, spatial and ecological scales in three mountain ranges. We describe our efforts to obtain a comprehensive regional understanding of mountain systems by compiling and analyzing existing databases at broad spatial scales. We refer to the procedures and protocols for collecting common biophysical databases necessary for modifying and validating models across the range of mountain environments in CLIMET. Finally, we describe two complementary modeling approaches, empirical/statistical and process-based, that have been extensively tested and applied to selected areas within CLIMET to produce different insights regarding the effect of climatic change on mountain ecosystems. With these capabilities, we now can apply scenarios of climatic change (e.g., warming) or variability (e.g., PDO) at watershed, park and mountain system scales for the entire CLIMET region to contrast responsiveness and potential future conditions. The approach of using large empirical databases in combination with an established modeling framework could be readily applied to other mountain ecoregions. Alternatively, the results of our research could be used to develop inferences for mountain ecosystems with similar species and biophysical landscapes.

The integrated approach developed in CLIMET (Figure 1) could be expanded to the Western Mountain Initiative (WMI, http://www.cfr.washington.edu/research.fme/wmi), a network of mountain protected areas in the western United States that have major programs in global change research. This network includes the CLIMET study area plus the south-central Sierra Nevada and central Rocky Mountains. The objective of WMI is to develop an integrated approach for investigating the effects of climatic variability and change on the natural resources of mountain ecosystems. By sharing information, analytical techniques and results, we intend to identify common interpretations of climatic-change effects as well as potential management strategies for addressing those effects.

It is critical that we understand the effects of climatic variability on mountains, because mountains support a high diversity of ecosystems and provide a wide range of ecological services to human populations (Beniston and Fox, 1996). Mountains serve as the world's 'water towers' by providing 50% of the freshwater consumed by humans (Messerli and Ives, 1997). Mountains and downstream areas of the western United States have some of the highest human population growth rates in the nation (Riebsame et al., 1996), so climatic influences on mountain ecosystems will have direct effects on natural resources and human economies. In addition, the carbon dynamics related to emissions and storage in mountain forests and soils has become an increasingly important issue at national to regional scales. By using the CLIMET approach in the northwestern United States and beyond, we are increasing our understanding of how climate interacts with mountain ecosystems at broad spatial and temporal scales, supporting management strategies and policy at the same scales.

Acknowledgements

We thank members of the CLIMET team for their ideas and work on different aspects of the research program, especially Ze'ev Gedalof, Bob Keane, Don McKenzie, Steve Running, and Peter Thornton.

References

Aber, J. D.: 1997, 'Why Don't We Believe the Models?', *Bull. Ecol. Soc. Amer.* **78**, 232–233.

Agee, J. K.: 1993, *Fire Ecology of Pacific Northwest Forests*, Island Press, Washington, D.C.

Bachelet, D., Neilson, R. P., Lenihan, J. M., and Drapek, R. J.: 2001, 'Climate Change Effects on Vegetation Distribution and Carbon Budget in the United States', *Ecosystems* **4**, 164–185.

Band, L. E., Patterson, P., Nemani, R. R., and Running, S. W.: 1993, 'Forest Ecosystem Processes at the Watershed Scale: Incorporating Hillslope Hydrology', *Agric. For. Meteorol.* **63**, 93–126.

Bekker, M. F., Alftine, K. J., and Malanson, G. P.: 2000, 'Effects of Biotic Feedback on the Rate and Pattern of Edge Migration', *Ecological Soc. America, Abstr.* **85**, 247.

Beniston, M. and Fox, D. G.: 1996, 'Impacts of Climate Change on Mountain Regions', in Watson, R. T., Zinyowera, M. C., Moss, R. H., and Dokken, D. J. (eds.), *Climate Change 1995 – Impacts, Adaptations and Mitigation of Climate Change: Scientific-Technical Analyses*, Cambridge Univ. Press, Cambridge, U.K., pp. 101–213.

Bitz, C. M. and Battisti, D. S.: 1999, 'Interannual to Decadal Variability in Climate and the Glacier Mass Balance in Washington, Western Canada, and Alaska', *J. Climate* **12**, 3181–3196.

Butler, D. R. and DeChano, L. M.: 2001, 'Environmental Change in Glacier National Park, Montana: An Assessment through Repeat Photography from Fire Lookouts', *Phys. Geog.* **22**, 291–304.

Butler, D. R., Malanson, G. P., and Cairns, D. M.: 1994, 'Stability of Alpine Treeline in Glacier National Park, Montana, U.S.A.', *Phytocoenologia* **22**, 485–500.

Carrara, P. E.: 1989, *Late Quaternary Glacial and Vegetative History of the Glacier National Park Region, Montana*, U.S.G.S. Bulletin 1902, Denver CO, 64 pp.

Cramer, W., Bondeau, A., Woodward, F. I., Prentice, I. C., Betts, R., Brovkin, V., Cox, P. M., Fischer, V., Foley, J. S., Friend, A. D., and others: 2001, 'Global Responses of Terrestrial Ecosystem Structure and Function to CO_2 and Climate Change: Results from Six Dynamic Global Vegetation Models', *Glob. Change Biol.* **7**, 357–373.

Environmental Systems Research Institute, Inc. (ESRI): 2000, *ARC-INFO Version 8. 0.2*, Redlands, CA.

Fagre, D. B., Comanor, P. L., White, J. D., Hauer, F. R., and Running, S. W.: 1997, 'Watershed Responses to Climate Change at Glacier National Park', *J. Amer. Water Resour. Assoc.* **33**, 755–765.

Fagre, D. B. and Peterson, D. L.: 2000, 'Ecosystem Dynamics and Disturbance in Mountain Wildernesses: Assessing Vulnerability of Natural Resources to Change', in McCool, S. F., Cole, D. N., Borrie, W. T., and O'Loughlin, J. (eds.), *Wilderness Science in a Time of Change, Vol. 3: Wilderness as a Place for Scientific Inquiry*, USDA Forest Service Proceedings 15, Rocky Mtn. Res. Stn., Ogden, UT, pp. 74–81.

Fagre, D. B. and Peterson, D. L.: 2002, 'Modelling and Monitoring Ecosystem Responses to Climate Change in Three North American Mountain Ranges', in Körner, C. and Spehn, E. (eds.), *Mountain Biodiversity: A Global Assessment*, Parthenon Publishing, London, pp. 249–259.

Finklin, A. I.: 1986, *A Climatic Handbook for Glacier National Park – with Data for Waterton Lakes National Park*, Intermountain Res. Station Gen. Tech. Rept. INT-204, USDA Forest Service, Ogden UT, 124 pp.

Foley, J. A., Levis, S., Costa Marcos, H., Cramer, W., Pollard, D.: 2000, 'Incorporating Dynamic Vegetation Cover Within Global Climate Models', *Ecol. Appl.* **10**, 1620–1632.

Gaines, W. L., Naney, R. H., Morrison, P. H., Ebey, J. R., Wooten, G. F., and Almack, J. A.: 1990, 'Use of Landsat Multispectral Scanner Imagery and Geographic Information Systems to Map Vegetation in the North Cascades Grizzly Bear Ecosystem', *International Conf. on Bear Research and Management* **9**, 533–547.

Gavin, D. G. and Brubaker, L. B.: 1999, 'A 6000-Year Soil Pollen Record of Sub-Alpine Meadow Vegetation in the Olympic Mountains, Washington, U.S.A.', *J. Ecol.* **87**, 106–122.

Gavin, D. G., McLachlan, J. S., Brubaker, L. B., and Young, K. A.: 2001, 'Postglacial History of Subalpine Forests, Olympic Peninsula, Washington, U.S.A.', *The Holocene* **11**, 177–188.

Gedalof, Z., Mantua, N. J., and Peterson, D. L.: 2002, 'A Multi-Century Perspective of Variability in the Pacific Decadal Oscillation: New Insights from Tree Rings and Coral', *Geophys. Res. Lett.* **29**, 2204–2207.

Gedalof, Z. and Smith, D. J.: 2001, 'Dendroclimatic Response of Mountain Hemlock (Tsuga mertensiana) in Pacific North America', *Can. J. Forest Res.* **31**, 322–332.

Grabherr, G., Gottfried, M., and Pauli, H.: 2000, 'GLORIA: A Global Observation Research Initiative in Alpine Environments', *Mount. Res. Dev.* **20**, 190–191.

Granshaw, F. D.: 2001, *Glacier Change in the North Cascades National Park Complex, Washington State U.S.A., 1958–1998*, Master's Thesis, Portland State Univ., Portland OR.

Graumlich, L., Brubaker, L. B., and Grier, C. C.: 1989, 'Long-Term Growth Trends in Forest Net Primary Productivity: Cascade Mountains, Washington', *Ecology* **70**, 405–410.

Hall, M. H. P. and Fagre, D. B.: 2003, 'Modeled Climate-Induced Glacier Change in Glacier National Park, 1850–2100', *BioScience* **53**, 131–140.

Hamlet, A. F. and Lettenmaier, D. P.: 1999, 'Effects of Climate Change on Hydrology and Water Resources Objectives in the Columbia River Basin', *J. Amer. Water. Resour. Assoc.* **35**, 1597–1623.

Hauer, F. R., Fagre, D. B., and Stanford, J. A.: 2003, Climatic Patterns, Hydrologic Processes and Nutrient Dynamics in a Pristine Montane Catchment in Northwest Montana, U.S.A. Verh. Internat. Verein. Limnol., in press.

Hessl, A. E. and Baker, W. L.: 1997, 'Spruce and Fir Regeneration and Climate in the Forest-Tundra Ecotone of Rocky Mountain National Park, Colorado, U.S.A.', *Arc. Alp. Res.* **29**, 173–183.

Hungerford, R. D., Nemani, R. R., Running, S. W., and Coughlan, J. C.: 1989, *MT-CLIM: A Mountain Microclimate Simulation Model*, USDA For. Serv. Res. Pap. INT-414, Intermtn. Res. Stn., Fort Collins, CO, 52 pp.

Iverson, L. R. and Prasad, A. M.: 2001, 'Potential Changes in Tree Species Richness and Forest Community Types Following Climate Change', *Ecosystems* **4**, 186–199.

Keane, R. E., Hardy, C. C., Ryan, K. C., and Finney, M. A.: 1997, 'Simulating Effects of Fire on Gaseous Emissions and Atmospheric Carbon Fluxes from Coniferous Forest Landscapes', *World Resource Review* **9**, 177–205.

Keane, R. E., Ryan, K., and Running, S. W.: 1996, *FIRE-BGC – A Mechanistic Ecological Process Model for Simulating Fire Succession on Coniferous Forest Landscapes of the Northern Rocky Mountains*, USDA For. Serv. Res. Pap. INT-484, Intermtn. Res. Stn., Fort Collins, CO, 122 pp.

Key, C. H., Fagre, D. B., and Menicke, R. K.: 2002, 'Glacier Retreat in Glacier National Park, Montana', in Williams, R. S. and Ferrigno, J. G. (eds.), *Satellite Image Atlas of Glaciers of the World*, U.S. Geol. Surv. Professional Paper 1386-J-2, Washington, D.C., pp. J365–J375.

Klasner, F. L. and Fagre, D. B.: 2002, 'Spatial Changes in Alpine Treeline Vegetation Patterns along Hiking Trails in Glacier National Park, Montana', *Arc. Ant. Alp. Res.* **34**, 53–61.

Krimmel, R. M.: 2000, *Water, Ice, Meteorological, and Speed Measurements at South Cascade Glacier, Washington, 1986–1991 Balance Years*, U.S.G.S. Water-Resources Investigations Report 97-4143, Tacoma, WA, 34 pp.

Liang, X., Lettenmaier, D. P., Wood, E. F., and Burges, S. J.: 1994, 'A Simple Hydrologically Based Model of Land Surface Water and Energy Fluxes for GSMs', *J. Geophys. Res.* **99**, 14415–14428.

Marr, J. W.: 1977, 'The Development and Movement of Tree Islands near the Upper Limit of Tree Growth in the Southern Rocky Mountains', *Ecology* **58**, 1159–1164.

McCullagh, P. and Nelder, J. A.: 1989, *Generalized Linear Models*, Chapman and Hall, London.

McKenzie, D., Hessl, A. E., and Peterson, D. L.: 2001, 'Recent Growth of Conifer Species of Western North America: Assessing Spatial Patterns of Radial Growth Trends', *Can. J. Forest Res.* **31**, 526–538.

McKenzie, D., Peterson, D. W., and Peterson, D. L.: 2003, 'Modelling Conifer Species Distributions in Mountain Forests of the Pacific Northwest', *For. Chron.*, in press.

Messerli, B. and Ives, J. D. (eds.): 1997, *Mountains of the World: A Global Priority*, Parthenon Publ., New York.

Mote, P. W., Canning, D., Fluharty, D., Francis, R., Franklin, J. F., Hamlet, A., Hershman, M., Holmberg, N., Ideker, K. G., Keeton, W., and others: 1999b, *Impacts of Climate Variability and Change: Pacific Northwest*, Report of the Pacific Northwest Regional Assessment Group for the U.S. Global Change Research Program, JISAO/SMA Climate Impacts Group, Univ. Washington, Seattle.

Mote, P. W., Keeton, W. S., and Franklin, J. F.: 1999a, 'Decadal Variations in Forest Fire Activity in the Pacific Northwest', Summary Paper presented at the 11th Conf. on Applied Climatology, Boston, MA.

Mote, P. W., Parson, E. A., Hamlet, A. F., Keeton, W. S., Lettenmaier, D., Mantua, N., Peterson, D. W., Peterson, D. L., Slaughter, R., and Snover, A. K.: 2003, 'Preparing for Climatic Change: The Water, Salmon, and Forests of the Pacific Northwest', *Clim. Change*, in press.

National Assessment Synthesis Team: 2000, 'Climate Change Impacts on the United States: The Potential Consequences of Climate Variability and Change', U.S. Global Change Res. Prog., Washington, D.C.

Neilson, R. P.: 1995, 'A Model for Predicting Continental-Scale Vegetation Distribution and Water Balance', *Ecol. Appl.* **5**, 362–385.

Peterson, D. L.: 1998a, 'Climate, Limiting Factors, and Environmental Change in High-Altitude Forests of Western North America', in Beniston, M. and Innes, J. L. (eds.), *The Impacts of Climate Variability on Forests*, Springer, Heidelberg, pp. 191–208.

Peterson, D. L. (ed.): 1998b, *Large-Scale Fire Disturbance in Pacific Northwest Ecosystems*, Northwest Sci. **72**, special issue, pp. 103.

Peterson, D. L. and Parker, V. T. (ed.): 1998, *Ecological Scale: Theory and Applications*, Columbia Univ. Press, New York.

Peterson, D. L., Schreiner, E. G., and Buckingham, N. M.: 1997, 'Gradients, Vegetation and Climate: Spatial and Temporal Dynamics in the Olympic Mountains, U.S.A.', *Global Ecol. Biogeog. Lett.* **6**, 7–17.

Peterson, D. W. and Peterson, D. L.: 2001, 'Mountain Hemlock Growth Responds to Climatic Variability at Annual and Decadal Scales', *Ecology* **82**, 3330–3345.

Rasmussen, L. A. and Conway, H.: 2001, Estimating South Cascade Glacier Mass Balance From a Distant Radiosonde and Comparison with Blue Glacier, *J. Glaciol.* **47**, 579–588.

Riebsame, W. E., Gosnell, H., and Theobald, D. M.: 1996, 'Land Use and Landscape Change in the Colorado Mountains I: Theory, Scale, and Pattern, *Mount. Res. Dev.* **16**, 395–405.

Rochefort, R. M., Little, R. L., Woodward, A., and Peterson, D. L.: 1994, 'Changes in Sub-Alpine Tree Distribution in Western North America: A Review of Climatic and other Causal Factors', *The Holocene* **4**, 89–100.

Rochefort, R. M. and Peterson, D. L.: 1996, 'Temporal and Spatial Distribution of Trees in Subalpine Meadows of Mount Rainier National Park, Washington, U.S.A.', *Arc. Alp. Res.* **28**, 52–59.

Running, S. W. and Gower, S. T.: 1991, 'FOREST-BGC, a General Model of Forest Ecosystem Processes for Regional Applications. II. Dynamic Carbon Allocation and Nitrogen Budgets', *Tree Physiol.* **9**, 147–160.

Schmoldt, D. L., Peterson, D. L., Keane, R. E., Lenihan, J. M., McKenzie, D., Weise, D. R., and Sandberg, D. V.: 1998, *Assessing the Effects of Fire Disturbance on Ecosystems: A Scientific Agenda for Research and Management*, USDA For. Serv. Gen. Tech. Rep. GTR-PNW-455, Pac. Northwest Res. Stn., Portland, OR.

Selkowitz, D. J., Fagre, D. B., and Reardon, B. A.: 2002, 'Interannual Variations in Snowpack in the Crown of the Continent Ecosystem', *Hydrol. Proc.* **16**, 3651–3665.

Swetnam, T. W. and Betancourt, J. L.: 1990, 'Fire-Southern Oscillation Relations in the Southwestern United States', *Science* **249**, 961–976.

Thornton, P. E., Running, S. W., and White, M. A.: 1997, 'Generating Surfaces of Daily Meteorological Variables over Large Regions of Complex Terrain', *J. Hydrol.* **190**, 214–251.

Urban, D. L., Harmon, M. E., and Halpern, C. B.: 1993, 'Potential Response of Pacific Northwestern Forests to Climatic Change: Effects of Stand Age and Initial Composition', *Clim. Change* **23**, 247–266.

Vegetation/Ecosystem Modeling and Analysis Project (VEMAP) Members: 1995, 'Vegetation/Ecosystem Modeling and Analysis Project: Comparing Biogeography and Biogeochemistry Models in a Continental-Scale Study of Terrestrial Ecosystem Responses to Climate Change and $C0_2$ Doubling', *Global. Biogeochem. Cycles* **9**, 407–437.

White, J. D. and Running, S. W.: 1994, 'Testing Scale Dependent Assumptions in Regional Ecosystem Simulations', *J. Veg. Sci.* **5**, 687–702.

White, J. D., Running, S. W., Thornton, P. E., Keane, R. E., Ryan, K. C., Fagre, D. B., and Key, C. H.: 1998, 'Assessing Simulated Ecosystem Processes for Climate Variability Research at Glacier National Park, U.S.A.', *Ecol. Appl.* **8** 805–823.

Woodward, A., Schreiner, E. G., and Silsbee, D. G.: 1995, 'Climate, Geography, and Tree Establishment in Subalpine Meadows of the Olympic Mountains, Washington', *Arc. Alp. Res.* **27**, 217–225.

Zolbrod, A. N. and Peterson, D. L.: 1999, 'Response of High-Elevation Forests in the Olympic Mountains to Climatic Change', *Can. J. Forest Res.* **29**, 1966–1978.

(Received 6 March 2002; in revised form 26 February 2003)