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Implications of Global Climate Change for Biogeographic Patterns in the Greater Yellowstone Ecosystem

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Abstract: *Projected changes in global climate have substantial ramifications for biological diversity and the management of natural areas. We explored the potential implications of global climate change for biogeographic patterns in the Greater Yellowstone Ecosystem by using a conceptual model to compare three likely climate scenarios: (1) warmer and drier than the present; (2) warmer and drier, but with a compensating increase in plant water use efficiency; and (3) warmer and wetter than the present. The logical consequences of each scenario are projected for several species and community types chosen to represent a range of local climate conditions and biotic responses in the Greater Yellowstone Ecosystem. The upper and lower timberline appear to be particularly sensitive to climate change. The upper timberline is likely to migrate upward in elevation in response to temperature changes, whereas the lower treeline may retreat under drier conditions or move down slope under wetter conditions. In all scenarios, the extent of alpine vegetation in the ecosystem decreased. Climate-induced changes in the fire regime in the Greater Yellowstone Ecosystem would probably have substantial consequences for the extent and age-class distribution of forest communities. Alterations in the distribution and extent of grassland communities would affect the populations of large ungulates. Our analyses suggest directions for establishing long-term measurements for the early detection of responses to climate change.*

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Resumen: *Los proyectados cambios globales del clima tienen ramificaciones substanciales para la diversidad biológica y el manejo de las áreas naturales. Exploramos las implicaciones potenciales de los cambios globales del clima en los patrones biogeográficos del ecosistema de Greater Yellowstone utilizando un modelo conceptual para comparar tres posibles escenarios climáticos: (1) más caliente y seco que el actual; (2) más caliente y seco pero con un incremento compensatorio en la eficiencia del uso de las plantas de agua; y (3) más caliente y mas húmedo que el actual. Las consecuencias lógicas de cada caso son proyectadas para varias especies y tipos de comunidad escogidos para representar un rango de condiciones climáticas locales y de respuestas bióticas en el ecosistema de Greater Yellowstone. El límite superior e inferior de presencia de árboles parece ser particularmente sensitivo a los cambios climáticos. Es posible que el límite superior migre hacia altas elevaciones en respuesta a los cambios de temperatura mientras que el inferior puede retractarse en condiciones más secas o moverse ladera abajo en condiciones mas húmedas. En todos los escenarios climáticos analizados, se disminuyó la extensión de la vegetación alpina del ecosistema de Greater Yellowstone. Los cambios climáticos inducidos con régimen de incendios en el ecosistema de Greater Yellowstone seguramente tendrán consecuencias substanciales en la extensión y la distribución de edad-clase de las comunidades de bosque. Alteraciones en la distribución y la extensión de comunidades de pastizales afectará a la población de los grandes ungulados. Nuestro análisis sugiere directrices para el establecimiento de medidas a largo plazo para detectar tempranamente las respuestas a los cambios climáticos.*

Introduction

A changing environment presents challenges to the conservation of biological diversity and the management of natural areas. The challenges arise in part from the tremendous uncertainty about the direction and magnitude of future environmental changes. For example, climate is a central controlling factor in all ecosystems and is projected to change dramatically in some regions during the next century. Global climate change would have far-reaching ramifications for natural areas (Peters & Darling 1985; Tangley 1988; Davis 1989*a*; Graham et al. 1990; Davis & Zabinski, in press), but the magnitude, rate, and spatiotemporal characteristics of potential changes in temperature and precipitation regimes are not well understood. In the face of environmental change, effective nature reserve management must be based on (1) an understanding of the major biotic and abiotic controls on the ecological components and processes of the area, (2) an expectation of how these controls may change, either through natural events or human actions, and (3) an evaluation of the probable effects of these changes on the biota in the reserve (Golley 1984). In this paper, we explore potential implications of global climate change for biological diversity in Yellowstone National Park (YNP) and the Greater Yellowstone Ecosystem (GYE), which includes YNP, Grand Teton National Park, and portions of surrounding national forests and other lands (Clark & Harvey 1988).

From paleoecological reconstructions in the GYE, we know that major changes in regional climate and vegetation have occurred in the past. During the most recent glacial period (ca. 20,000 to 16,000 yrs ago), the upper timberline in this part of the Rocky Mountains apparently was 600 to 1200 m lower than today, and most of the Yellowstone Plateau was glaciated (Barnosky et al. 1987:312). As global temperatures increased and glaciers retreated at the end of the Pleistocene (ca. 14,000 to 13,000 yrs ago in Yellowstone; Barnosky et al. 1987:299), the upper timberline shifted upward, and coniferous forests became established on the Yellowstone Plateau (Baker 1970, 1976, 1986; Waddington & Wright 1974). The early Holocene (ca. 10,000 to 4,000 yrs ago) was a period of maximum warmth in the Yellowstone region, and some species such as Douglas-fir (*Pseudotsuga menziesii*) apparently grew at higher elevations than today (Barnosky et al. 1987:302). The climate became somewhat cooler and possibly wetter in the mid-Holocene, and the lower timberline in the eastern portion of the GYE moved downward about 5400 to 4400 yrs ago (Reider et al. 1988).

As a result of anthropogenic increases in carbon dioxide and other greenhouse gases, another episode of global climate change is expected in the coming century (Bolin et al. 1986). The climate change may be of a magnitude similar to that at the end of the Pleistocene, but the projected rate is likely to be an order of magnitude greater than changes that occurred in the past. Current simulations using the general circulation models (GCMs) (e.g., Hansen et al. 1988; Schlesinger & Zhao 1988; Wetherald & Manabe 1988) project an average rise in global temperature ranging from 1.5 to 4.5° C, with greater warming in winter than summer and increased warming with increased latitude (Dickinson 1986). Increased precipitation at high latitudes and decreased summer precipitation and soil moisture at middle latitudes of the northern hemisphere are also predicted. These projections are at the global scale; the magnitude and even the directions of climate change will probably differ regionally.

Projected Climate Scenarios in the GYE

In the Rocky Mountains, regional projections of climate change based on GCM simulations suggest elevated temperatures, reduced winter precipitation, earlier spring runoff, and elevational shifts in vegetation zones (Neilson et al. 1989). In Figure 1, we summarize the potential effects of these changes on the GYE. All of the general circulation models project increased temperatures in response to elevated concentrations of atmospheric CO_2 and other greenhouse gases, and warmer temperatures will lead to higher potential evapotranspiration (PET). Thus, the Greater Yellowstone Ecosystem would be subjected to higher temperatures and greater evaporative demands than at present. There is considerable uncertainty about other effects of climate change (Lamb 1987; Cushman & Spring, in press). The GCMs cannot reliably predict regional precipitation patterns; thus, rainfall may increase, decrease, or remain the same in the GYE (Cushman et al. 1988; Neilson et al. 1989). In addition, elevated atmospheric CO_2 may have direct effects on vegetation. For example, water use efficiency (WUE) may increase with elevated CO_2, but the magnitude and duration of this increase are unknown (Norby & O'Neill 1989). Thus, the warmer temperatures and the rise in potential evapotranspiration would increase plant water stress unless compensated for by increased precipitation or enhanced water use efficiency. Finally, atmospheric CO_2 enrichment could stimulate increased primary productivity, although this potential increase may not be realized because other constraints (e.g., drought stress or nutrients) may be more limiting (Strain & Bazzaz 1983; Oechel & Reichers 1986).

We explore the possible implications of these changes and their uncertainties by creating three climate scenarios that encompass the range of conditions likely to exist by the end of the next century:

1. A warm, dry scenario, in which temperature and PET increase, precipitation decreases or remains

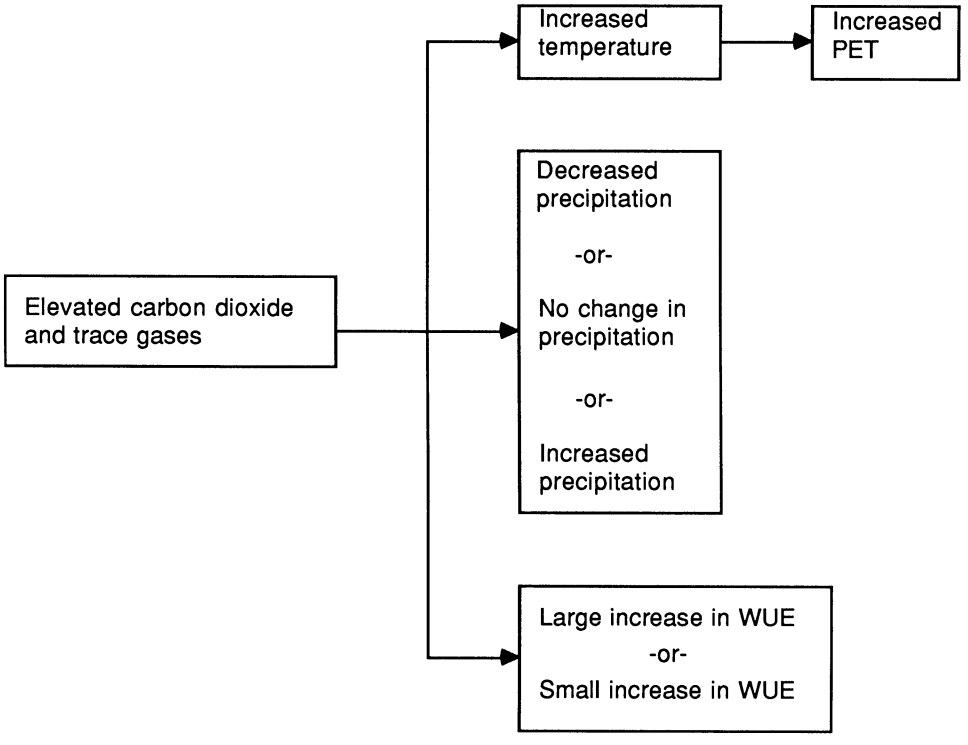

Figure 1. Potential effects of projected climate change in the Greater Yellowstone Ecosystem. PET = potential evapotranspiration; WUE = plant water use efficiency.

unchanged, and WUE increases only slightly; plants are subjected to elevated temperatures, CO_2, and drought stress.

2. An intermediate scenario, in which temperature and PET increase, precipitation decreases or remains unchanged, and WUE increases sufficiently to compensate for elevated PET; plants are subjected to elevated temperatures and CO_2 but there is no change in drought stress.
3. A warm, wet scenario, in which temperatures and CO_2 increase, precipitation increases, and WUE increases significantly; plants are subjected to elevated temperatures and CO_2, but to reduced drought stress.

For each scenario, we projected the probable effects on several species and community types chosen to represent a range of local climate conditions and biotic responses in the GYE. Community types included alpine communities above the upper timberline, nonforest communities below the lower timberline, and the forested zone. Species included whitebark pine (*Pinus albicaulis*), an important tree near upper timberline; Douglas-fir (*Pseudotsuga menziesii*), which grows near lower timberline; and elk (*Cervis elaphus*) and bison (*Bison bison*), which generally live at higher elevations during summer but migrate to lower elevations in winter.

We emphasize that the ecological changes we described in this paper are projections, not predictions. Our present understanding of the impending climate changes and of the biotic and abiotic constraints on the distribution and abundance of species and communities in the Greater Yellowstone Ecosystem are still too rudimentary to permit confident predictions. Nevertheless, we think that this exercise has heuristic value in that it helps delimit the range and magnitude of possible changes in the system. It also may suggest areas where research and monitoring programs may be most urgent if managers are to deal effectively with the potential climate changes that we face in the next century.

(1) The Warm, Dry Scenario

The possible consequences of warmer, drier conditions, with minimal physiological compensation, are summarized in Figure 2. An important direct effect of elevated summer temperatures would be a lengthening of the growing season at high elevations. Because low temperatures and a short growing season apparently are the primary constraints on tree growth at the upper timberline in the Rocky Mountains (Daubenmire 1954; Krebs 1985), it is likely that the upper timberline would shift to a higher elevation. Interpretations of the general-circulation-model predictions suggest an elevational displacement of temperature zones of 462 to 1155 m (Neilson et al. 1989). This would be comparable to the

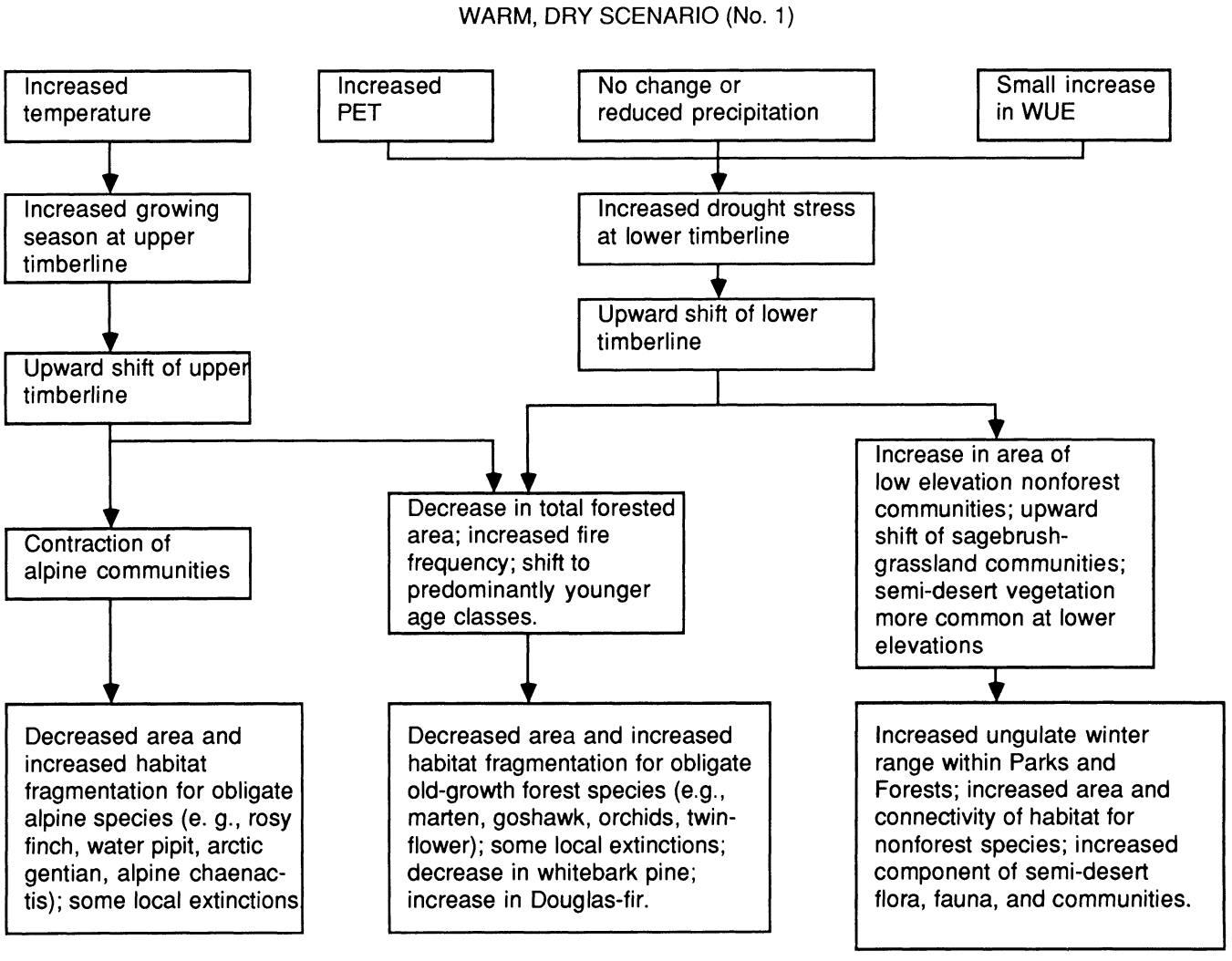

Figure 2. Potential effects on the Greater Yellowstone Ecosystem of a climate that is warmer and drier than the present climate (scenario 1).

upward shift in species distributions of 400 to 1000 m that may have occurred in Yellowstone during the Sangamonian interglacial period some 127,000 yrs ago (Baker 1986:728). For the projections in this paper, we use a conservative estimate of 460 m. The upper timberline in the GYE at present is around 2900 m (Patten 1963; Waddington & Wright 1974; Despain, 1991); thus, global warming could move the upper timberline to around 3360 m or higher.

A higher upper timberline would mean a substantially smaller alpine zone. Indeed, the alpine zone could disappear completely within the borders of Yellowstone National Park, where the highest point (Eagle Peak) reaches only 3440 m. There are higher mountains nearby, in the Absaroka, Teton, and Wind River ranges, where an alpine zone would persist. Nevertheless, the habitat area for obligate alpine species would be reduced and fragmented throughout the Greater Yellowstone Ecosystem (Figs. 5 and 6). This in turn could lead to local extinctions of some alpine species and communities (MacArthur & Wilson 1967; Diamond 1975; Soulé et al. 1979; Wilcox 1980). Examples of species restricted to the alpine zone include the arctic gentian (*Gentiana algida*), alpine chaenactis (*Chaenactis alpinus*), rosy finches (*Leucosticte* spp.), and water pipit (*Anthus spinoletta*).

The lower timberline in the Rocky Mountains appears to be controlled mainly by summer drought stress (Daubenmire 1943; Krebs 1985). Increased potential evapotranspiration without compensating increases in precipitation or water use efficiency would result in accentuated drought stress at lower elevations and an upward shift in the lower timberline of 460 m or more (Neilson et al. 1989).

With a comparable upward shift in both the upper and lower timberlines, the total forested area would become smaller than at present, because there is less land area available at progressively higher elevations (Figs. 5

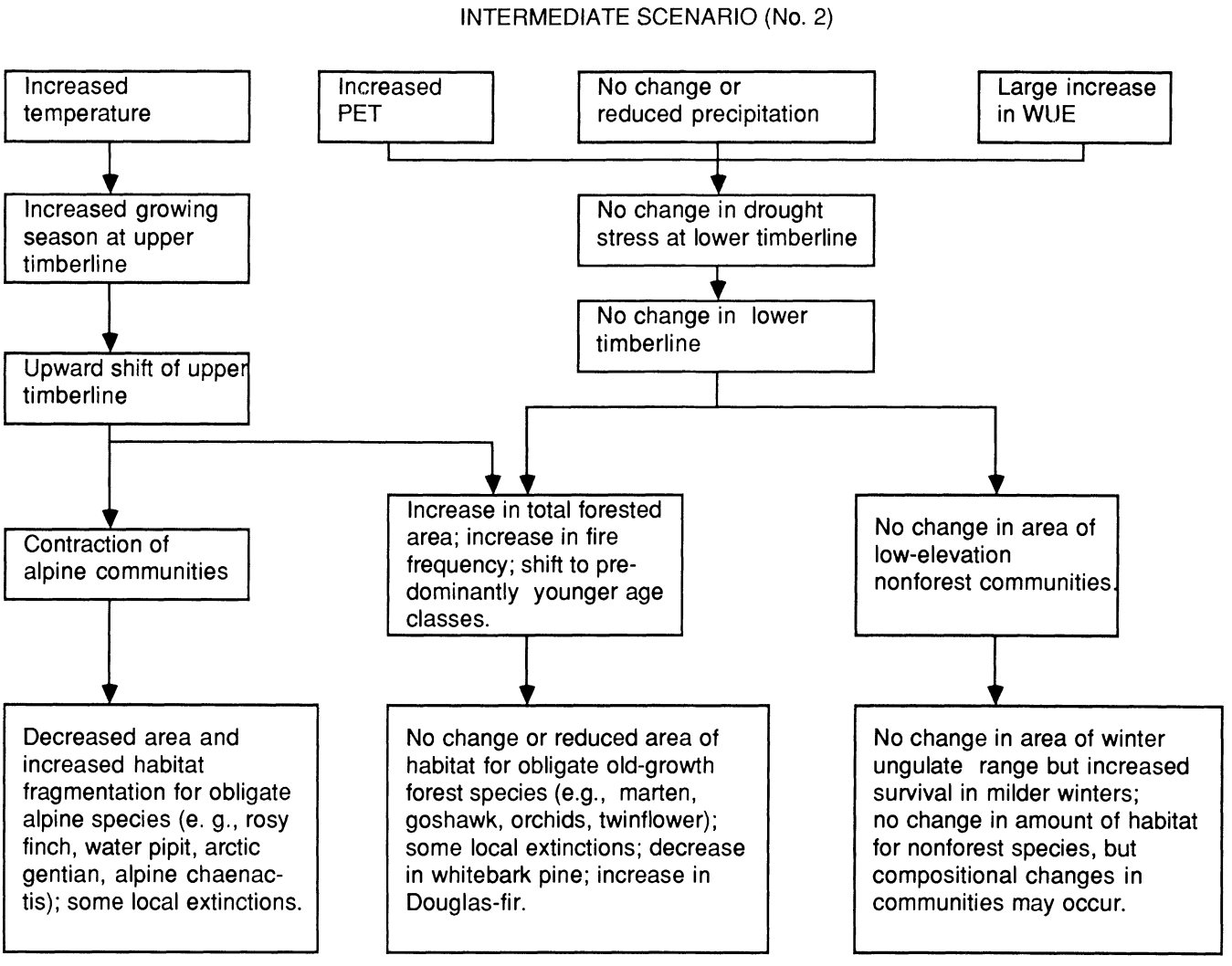

Figure 3. Potential effects on the Greater Yellowstone Ecosystem of a climate that is warmer and drier than the present climate, but with a compensating increase in plant water use efficiency (scenario 2).

and 6). An upward shift in the forested zone also would have a disproportionate effect on the extent of high-elevation forest types. For example, whitebark pine forests presently occur in a zone from 2600 to 2900 m, which occupies an area of about 250,000 ha within YNP and on the adjacent high peaks (Despain, in press; unpublished YNP data). The upper elevational limit of whitebark pine apparently is controlled by low temperatures; the lower limit may be set partly by competition with other conifers, particularly lodgepole pine. If vegetation zones shifted by 460 m, then whitebark pine would be found from about 3060 to 3360 m, with an area of only 27,000 ha (Figs. 5 and 6). This represents a 90% decrease in available habitat for whitebark pine. Such a reduction would have additional ramifications, because this species not only forms a distinctive forest type at the upper timberline but also is an important food source for Clark's nutcrackers (*Nucifraga columbiana*), red squirrels (*Tamiasciurus hudsonicus*), and grizzly bears (*Ursus arctos*).

Quite a different situation is projected for the lower-elevation tree species, Douglas-fir. The lower timberline presently is around 1900 m, and Douglas-fir occurs from about 1900 to 2200 m (Patten 1963; Waddington & Wright 1974). A 460-m upward shift in elevational zones would result in a larger potential range for this species within the borders of Yellowstone Park since most of the park area lies above 2000 m (Figs. 5 and 6). However, Douglas-fir would probably disappear from lower-elevation areas elsewhere in the GYE, so its regional abundance would remain the same or decrease. Furthermore, even within YNP this species might not occupy all of the sites that were climatically suitable, because it requires high calcium levels that are available mainly in soils derived from calcareous substrates (Patten 1963; Despain, 1991). Most of the higher-

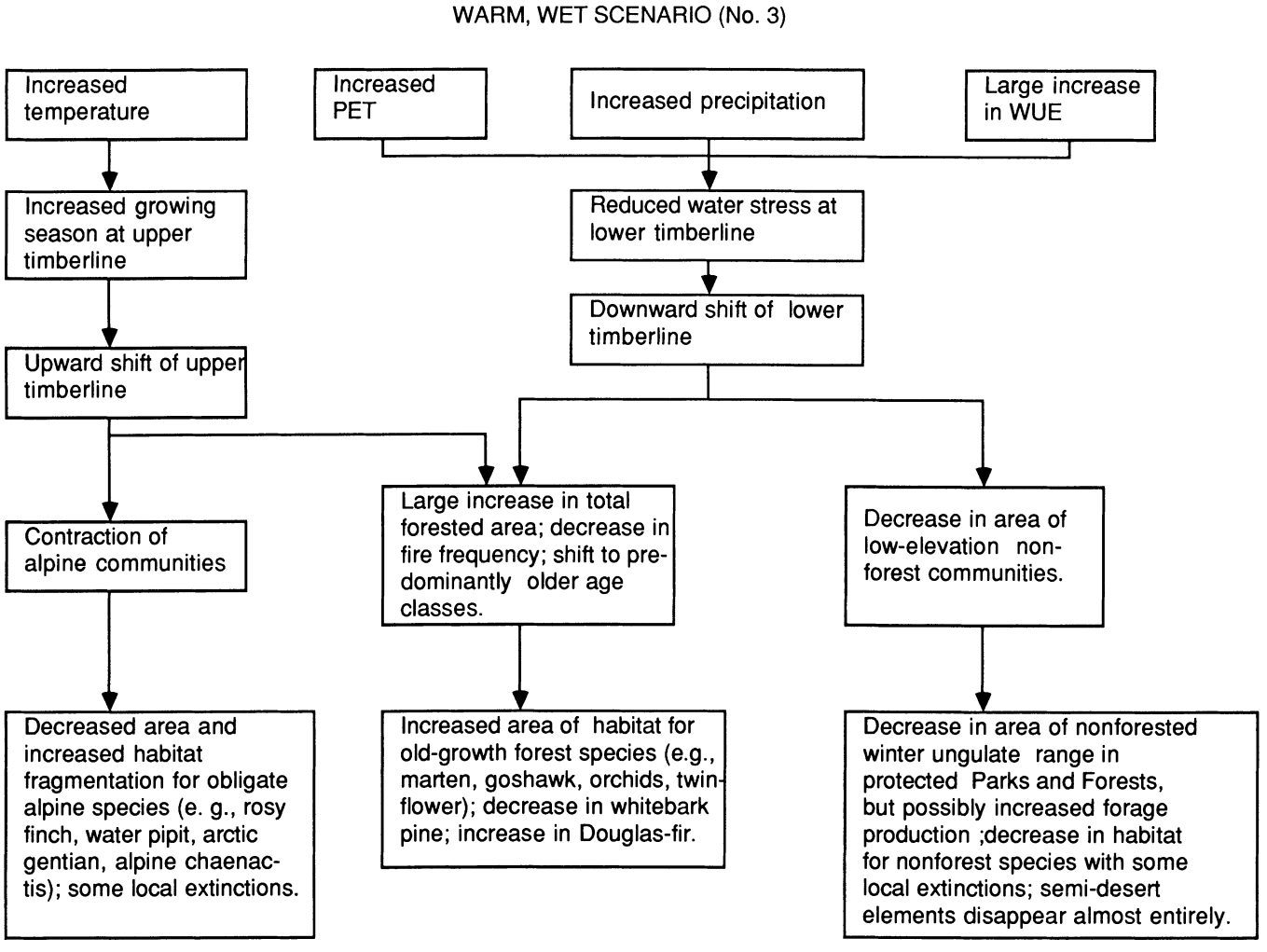

Figure 4. Potential effects on the Greater Yellowstone Ecosystem of a climate that is warmer and wetter than the present climate (scenario 3).

elevation areas in YNP are underlain by rhyolite and other extrusive igneous rocks containing low calcium levels (Despain, 1991).

The age class distribution throughout the forest zone could change substantially if the climatic changes also alter the disturbance regime, particularly the frequency and severity of fires. The occurrence of extensive, stand-replacing fires in the GYE is controlled largely by weather conditions; large fires only occur during summers of below-normal precipitation (Swetnam & Betancourt 1990; Despain, 1991; Turner & Romme, in press; Renkin & Despain, in prep.). The subalpine forest landscape of the GYE presently contains a large component of old-growth stands that exceed 200 years in age (Romme & Despain 1989). However, if a warmer, drier climate leads to an increased frequency of severe stand-replacing fires, the landscape could be converted into one dominated by younger stands, as is the current configuration in parts of the Canadian Rockies and the subarctic (e.g., Johnson & Fryer 1987; Tande 1979; Johnson 1979; see summary in Turner and Romme, in press).

The combination of a slightly smaller forest zone and a shift to predominantly younger forest age classes means that habitat for old-growth species in the Greater Yellowstone Ecosystem could become smaller in area and more fragmented than at present. Old-growth habitat already is being reduced in portions of the GYE that are managed for timber production. If changing climatic conditions and disturbance regimes also reduce old-growth forests in protected parks and wilderness areas, then some species could be threatened with local extinction. Examples of old-growth forest species in the GYE include the northern twinflower (*Linnaea borealis*), fairy slipper (*Calypso bulbosa*), pine marten (*Martes americana*), and goshawk (*Accipiter gentilis*).

With an upward shift in the lower timberline, the area of low-elevation nonforest vegetation would increase. Animals characteristic of treeless landscapes, such as pronghorn (*Antilocapra americana*) and badger (*Taxidea taxus*), might become more numerous. Sagebrush-grasslands, dominated by big sagebrush (*Artemisia tridentata*), bluebunch wheatgrass (*Agropyron spi-*

catum), and Idaho fescue (*Festuca idahoensis*), probably would move to higher elevations than they presently occupy. At the lowest elevations, sagebrush-grasslands could be replaced by semidesert vegetation, characterized by saltbush (*Atriplex gardneri*) and greasewood (*Sarcobatus vermiculatus*). This type of vegetation presently is rare in Yellowstone Park, where it is restricted to soils developing in marine shales and other extremely droughty substrates (Despain, 1991). With a warmer, drier climate, these xerophytic communities could expand to occupy a greater variety of sites at lower elevations, though they may remain limited by edaphic conditions.

Compositional changes within vegetation zones could be just as important as the elevational shifts. Species respond individually to the environmental changes because of differing physiological tolerances, and altered competitive interactions between species are likely to result (Strain & Bazzaz 1983; Davis 1984; Neilson et al. 1989). Thus, community composition and dynamics could shift. In addition, a relatively small shift in the seasonality of precipitation could have dramatic effects on overall vegetation physiognomy in the Greater Yellowstone Ecosystem even if total precipitation does not change. Winter precipitation favors woody vegetation, whereas summer precipitation favors grasses and forbs (Neilson et al. 1989). In YNP today there is a gradient in the seasonality of precipitation; western portions of the Park have more winter precipitation, characteristic of the Great Basin region, while the eastern parts have more spring and early summer precipitation, similar to the Great Plains (Despain 1987).

These kinds of changes could lead to the development of plant communities in the Greater Yellowstone Ecosystem quite unlike any that we know today. Paleoecological reconstructions of eastern North American vegetation during the last 20,000 years have demonstrated the widespread occurrence of species assemblages that have no modern analogues (Solomon & Webb 1985; Davis 1984, 1989*a*). Our understanding of the biotic and abiotic processes that presently control community structure in the GYE, and of the specific ways those processes would be altered by global climate change, are inadequate to permit any specific projections of how communities may change in the next century. At present, all we can say is that change in community structure and composition is likely, and that the changes could be striking (Davis 1989*a*).

Another aspect of the warm, dry scenario to be considered is its implication for the large, free-ranging ungulates that constitute one of the special features of the Greater Yellowstone Ecosystem. The total numbers of elk, bison, and other native ungulates are limited primarily by the availability of winter forage (Meagher 1973; Houston 1982). Nonforested areas at low elevations provide the major winter habitat for these animals.

Milder winters and a larger nonforest area at low elevations could mean higher populations of ungulates in the GYE. Of particular significance would be the increased winter habitat within protected parks, which lie at relatively high elevations. Large numbers of ungulates presently travel out of YNP every winter into surrounding lands where they are subjected to hunting, artificial feeding, and other kinds of management that complicate the overall management of these animals (Berger 1991). With milder winters and more habitat within YNP, a greater number of animals might remain within the park boundaries. However, the associated drier conditions also could depress plant production, and elevated atmospheric CO_2 could alter C/N ratios in plant foliage (Strain & Bazzaz 1983). The result could be reduced forage quantity and quality and a lessening of the improvement in winter ungulate habitat produced by milder winter weather and a larger winter range.

Ungulates intensively utilize the vegetation in parts of the GYE, influencing plant growth form and possibly plant community composition. For example, heavy browsing appears to prevent regeneration of aspen (*Populus tremuloides*) stands except following extensive fires (Jones 1974; DeByle 1985; Mueggler & Bartos 1977). Changes in ungulate habitat selection or foraging behavior in response to vegetation changes would further alter the composition and structure of plant communities at low elevations in the GYE.

(2) The Intermediate Scenario

In the intermediate scenario, a large, compensating increase in water use efficiency is hypothesized to accompany the increased temperature, increased potential evapotranspiration, and reduced or unchanged precipitation described above. This combination of climatic and physiological changes probably would produce the same effects at high elevations as were just presented for the warm, dry scenario: length of the growing season would increase, the upper timberline would move upward, the alpine zone would be reduced, and local extinction of some obligate alpine species could occur (Fig. 3). The range of whitebark pine also would shift to a higher elevational zone with a substantially smaller area (Fig. 6).

The position of the lower timberline might not shift, however, because the effects of higher PET would be compensated for by increased WUE. Thus, the elevational range of Douglas-fir could expand, since its upper limits apparently are determined by low temperatures and snow depth (Leverenz & Lev 1987), which would be ameliorated in this scenario, while its lower limits are set by drought stress, which could remain the same (Fig. 6). As noted earlier, Douglas-fir might not move into all of the sites that were climatically suitable, because of its edaphic requirements.

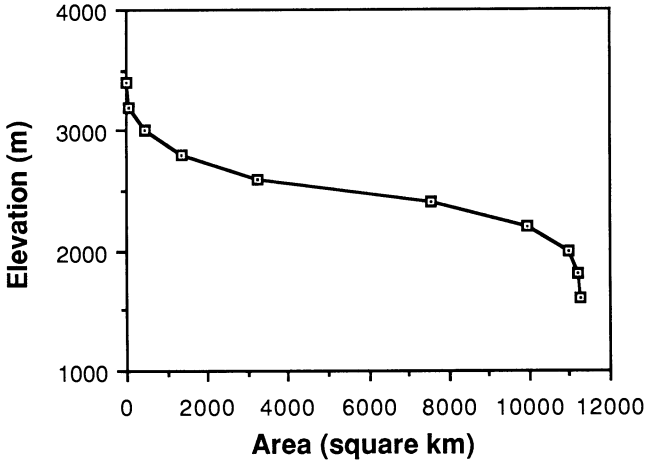

Figure 5. Cumulative area above each elevation zone within Yellowstone National Park and the adjacent mountains along its eastern border. (Data courtesy of the National Park Service.)

With a higher upper timberline and no change in lower timberline, the total forest area would increase (Fig. 6). However, the age class distribution of the forests probably would shift to a predominance of younger age classes just as in the warm, dry scenario. This is because the increase in WUE could compensate for physiological drought stress but would not affect the expected increase in fire frequency and severity under warmer and drier climatic conditions. The result of increased forest area and a shift in age class distribution could be either no change or a decrease in old-growth habitat.

The area of nonforest communities at low elevations would not change in this scenario. However, there could be dramatic changes in species composition, since plant species would respond individually to the effects of CO_2 on WUE and net photosynthesis. These physiological changes would alter species tolerances and competitive abilities. The area of nonforested ungulate winter range also would not change in this scenario, but more of the range could be accessible for longer periods if winters became milder. The fertilization effect of elevated CO_2 could potentially increase net primary productivity and forage production, leading to a further increase in the number of ungulates that could be supported on the winter range, although soil nutrient limitations and altered C/N ratios might reduce the importance of the latter effect (Strain & Bazzaz 1983).

(3) The Warm, Wet Scenario

In this as in the previous scenarios, warmer temperatures probably would lead to an upward shift in the upper timberline, a reduction in area of the alpine zone, and local extinction of some alpine species and communities (Fig. 4). The range of whitebark pine also would shift up the mountains and occupy a smaller area (Fig. 6). With increased precipitation accompanying the elevated temperatures, however, even the remaining subalpine environment in the GYE could become unsuitable for this species because of increased competition.

Whitebark pine is near the southern limit of its distribution in this area (Arno & Hoff 1989). The mechanistic explanation for its southern range limit has not been demonstrated, but examination of its range map shows that it is absent in the central and southern Rocky Mountains where moisture-laden air masses from the Gulf of Mexico augment late-summer precipitation (the "Arizona monsoon"). In fact, the northern limit of the Arizona monsoon marks the biogeographic boundary for several plant species (Mitchell 1976; Neilson & Wullstein 1983). Whitebark pine also is absent in the wet coastal mountain ranges of the Pacific Northwest (Arno & Hoff 1989). If whitebark pine presently is restricted, either physiologically or via competitive interactions, to the drier summer climates that presently characterize the northern Rockies, then a climatic shift to wetter summers in the GYE could result in further reduction or even local extinction of whitebark pine in this area.

With increased precipitation and water use efficiency, drought stress at low elevations would be alleviated, and the lower timberline could shift down slope to a lower elevation. The range of Douglas-fir could expand both upward and downward in this scenario, unless it is limited by edaphic factors, as discussed above (Fig. 4). The total forested area would increase as the upper timberline moved upward and the lower timberline moved downward (Fig. 6). Pollen data indicate that such an expansion of subalpine forest both up and down slope in Central Colorado occurred during a mid-Holocen period (ca. 7000 to 4000 yrs ago) that apparently was warmer and wetter than today (Fall 1985). Wetter conditions, especially in summer, could lead to a decrease in fire frequency and severity and a shift in forest age-class distribution to older age classes. The successional mosaic of subalpine forests in the GYE could become more like that seen today in the subalpine landscapes of the Colorado Rockies, where stands >500 years old are common (e.g., Peet 1981; Veblen 1986; Aplet et al. 1988; see summary in Turner and Romme, in press). With increased forest area and a shift to older age classes, the habitat available for old-growth species would increase (Fig. 4).

The nonforest area at low elevations would be reduced if the lower treeline moved down slope. Semi-desert species and communities, presently restricted to severe substrates at the lowest elevations, could disappear entirely from YNP. Nonforested winter range for ungulates would be reduced, which potentially could lead to smaller numbers of animals on the winter ranges.

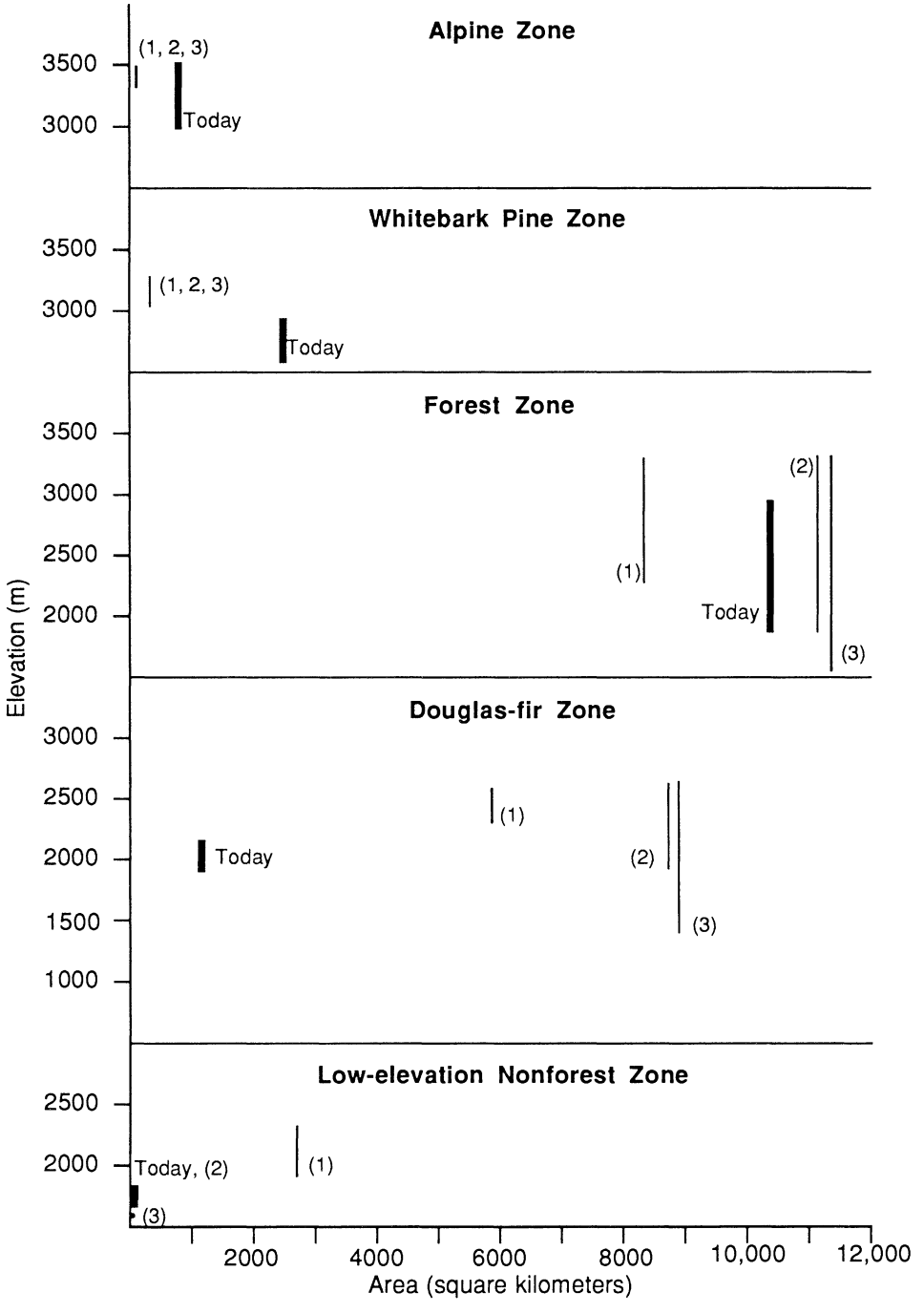

Figure 6. Present and projected areas and elevational ranges of vegetation zones in Yellowstone National Park and the adjacent mountains along its eastern border. Scenario (1) is elevated temperature, CO_2, and drought stress. Scenario (2) is elevated temperature, but no change in drought stress. Scenario (3) is elevated temperature and CO_2, but reduced drought stress. See text for details.

However, ungulates are quite adaptable and probably would increase their use of forests in this situation (Murie 1951; Meagher 1973; Geist 1982; Houston 1982). Milder winter temperatures and possible increases in forage production also would compensate for the reduction in nonforest habitat for elk and bison. Populations of obligate grasslands species such as pronghorn and badger, however, probably would be reduced in the GYE and some could become locally extinct.

The combination of warmer temperatures, longer growing seasons, increased precipitation, and elevated CO_2 could produce substantial increases in primary productivity throughout the vegetation zones of the Greater Yellowstone Ecosystem. The potential augmen-

tation of productivity might not be realized, however, because other limiting factors such as nutrients might become more important under these conditions. Patterns in herbivory also would undoubtedly be altered, with probable but presently unpredictable effects on primary productivity. Again, because of individual plant species responses to all of the changes in limiting factors, some dramatic changes in community composition could occur throughout the vegetation of the GYE.

Discussion

The three climate scenarios share some similarities. The upper treeline in the GYE is likely to move toward higher elevations in response to increased temperatures, regardless of the direction and magnitude of changes in precipitation and water use efficiency, and the distribution of Douglas-fir is likely to expand. Concomitantly, the alpine and whitebark pine zones decrease in extent and become more fragmented under all scenarios considered here (Fig. 6). Thus, it appears that, under these climate scenarios, several or many species and communities that are restricted to the alpine zone are likely to become locally extinct within Yellowstone Park and possibly the Greater Yellowstone Ecosystem during the next few centuries. However, the total number of species within YNP and the GYE actually may change little. Semidesert vegetation, which is currently rare and restricted to specialized habitats, may expand in lower-elevation portions of the GYE, especially under the warm, dry scenario.

The simplistic prospect of a smooth northerly and upward migration of plant species and communities is complicated by individual species responses and by the *rate* at which climate change may occur (Davis 1989*b*; Davis & Zabinski, in press). Neilson et al. (1989:76) state that thermal regimes could move 4 to 6 degrees northward within 100 years; this is a rate of 70 to 100 km per decade. Similarly, elevational zones could shift 65 to 90 m per decade (Neilson et al. 1989:56). By the time a slow-growing tree reaches reproductive age, the environment may no longer be suitable for seedling survival (Davis 1989*b*; Davis & Zabinski, in press). Probably the species that will track the moving thermal zones are those with short, rapid life histories, for example, introduced weeds, or species with a broad distribution such as lodgepole pine (Strain & Bazzaz 1983). The species that will respond least effectively are the long-lived species that reproduce late or irregularly and those with already limited, fragmented distributions, for example, whitebark pine and alpine species. Competitive interactions between species also would be complicated as new species from lower elevational zones would have to become established in the higher zones where adults of the formerly dominant species would still be present even if they were no longer reproducing locally.

Mature individuals of many long-lived species may persist in their present locations for as much as decades, even centuries, after the climate becomes unsuitable for survival of their offspring (Davis 1984; Brubaker 1986). Plant communities in the GYE might appear to be stable for a long time, but after a disturbance (such as fire, insect outbreak, or windstorm) the mature forest community could be replaced by a completely different suite of species. Indeed, many of the vegetational changes caused by climate change would be mediated by disturbance (Brubaker 1986; Neilson et al. 1989; Sandenberg et al. 1987), and the disturbance regimes themselves will be altered by the climatic changes, as noted in the discussion of the warm, dry, and intermediate scenarios. There is paleoecological evidence for rapid changes in community composition following disturbance of mature communities that had persisted for some time despite climatic change (Brubaker 1986; Dunwiddie 1986; Cwynar 1987).

Research and Monitoring Needs

The range of scenarios we presented and their potential implications suggest some directions for research and monitoring in the Greater Yellowstone Ecosystem. Because of the complexity and spatiotemporal scales of potential ecological responses, it is important to design long-term measurements creatively so that they are particularly sensitive to early indications of ecological change. For example, species or individuals that are near the limits of their range of tolerance are likely to respond more rapidly than those that are well within their physiological range. Our analyses suggest that the location of the upper and lower timberline in the GYE will probably respond to any of the likely climate scenarios. Research in subarctic North America and Europe and in mountain ranges of the Pacific Northwest and Great Basin in western North America has shown that timberlines can respond quickly even to climate changes of the magnitude observed in the last 100 to 500 years (Davis 1984; Brubaker 1986). Therefore, upper and lower timberlines should be high-priority sites for research and monitoring.

A first step in the GYE timberline studies would be to relate the present location of the upper and lower timberlines to underlying variables such as geologic substrate, slope, aspect, and disturbance and land-use history. This information is needed before we can select specific sites for monitoring or distinguish between local and global causes of timberline change. Yellowstone National Park's geographic information system is an excellent tool for this analysis within park boundaries, although adjacent public and private lands must also be

evaluated. Research is then needed to clarify the mechanisms that explain the site-specific composition and location of timberlines. Differences in soils, local climate, and species availability contribute to variability among sites (Krebs 1985). After clarifying the present timberline patterns and mechanisms, we recommend the establishment of permanent transects that traverse upper and lower timberline areas. The transects should span a gradient from forest interior to nonforest zones. Tree mortality and seedling establishment would be measured along these transects at regular time intervals. These long-term measurements must be coupled with research designed to understand the underlying mechanisms of any changes detected in timberline location or composition. For example, yearly or decadal variation in tree establishment and mortality could be correlated with comparably scaled fluctuations in temperature and precipitation to clarify climatic constraints on tree growth and survival.

Another early indicator of global climate change may be alterations in the frequency and severity of disturbances, which may be the proximal cause of substantial changes in the structure and function of natural landscapes. Given the importance of fire in the Greater Yellowstone Ecosystem, particular emphasis should continue to be placed on increasing our ability to predict the occurrence and effects of fire. Postfire succession should be monitored following the 1988 fires and after future fires, especially in areas near the upper and lower timberlines. Monitoring of disturbances also must be coupled with research directed at understanding the mechanisms of postdisturbance change and the individualistic responses of species to disturbances of differing magnitudes and severities. For example, the widespread and abundant establishment of aspen seedlings following the 1988 fires was surprising (Despain & Renkin, unpubl. ms.). It was previously thought that aspen seedlings could not become established under current climatic conditions in the northern Rocky Mountains. We do not yet know whether this aspen establishment was a normal response to large-scale fires or whether it heralds a fundamental change in postfire succession in the GYE since the last extensive fires that occurred during the eighteenth and nineteenth centuries. The survival of these aspen seedlings under a variety of site conditions must be studied. Additional research should be initiated to understand the potential limits of aspen distribution, abundance, and reproduction in the Greater Yellowstone Ecosystem in response to local climate, soils, herbivory, disturbance, and competitive interactions with other plants.

Long-term measurements of net primary production and community composition would be most appropriate in the lower-elevation sagebrush-grasslands. The grasses and shrubs are likely to show more rapid changes in productivity and composition in response to climate than the subalpine forests. The grasslands also are influenced by native ungulates, so research into vegetation-climate-herbivore interactions should continue.

The use of remotely sensed data and simulation models to complement long-term field measurements is desirable. The detection of broad-scale ecological changes is complicated by practical limitations such as the difficulty of replicating extensive experiments or sampling regimes and extrapolating local data to an entire region (Turner et al. 1989). Remote sensing holds great promise for gathering synoptic data on vegetation composition, structure, and processes. Landsat imagery has been used to estimate productivity in the low-elevation grasslands (Merrill et al. 1988), and repeated observations would permit the detection of directional changes over large areas. Models are of particular importance because of the time lags in forest responses. In addition, simulation models can be used to explore hypotheses about ecological responses, identify sensitive parameters, and extrapolate from fine scales to the region. For example, Pastor and Post (1988) explored the impact of climate change on mature forests in eastern North America by linking an individual-based stand simulation model with an ecosystem model. The nitrogen cycle and water balance were modeled explicitly, and a variety of soils were simulated. Results illustrated how broad-scale soil heterogeneity influenced forest ecosystem responses to climate over long time periods. Similarly, models would be needed to predict landscape changes in response to altered fire frequency and severity over long time scales in the GYE under varying climate regimes. Fire regimes are sensitive to the average climate over decades to centuries, as well as the interannual variability of water balance (Clark 1990). Thus, a model linking meteorological conditions, fire initiation and spread, and plant reestablishment could be extremely helpful in projecting long-term landscape dynamics in the GYE.

Although the inevitability of global climate change is not assured, the potential implications are of sufficient magnitude that it would be foolish to ignore them. The conservation of biological diversity in extensive natural areas such as the Greater Yellowstone Ecosystem will become increasingly difficult as the broad-scale constraints on the biota undergo changes that are more rapid than those experienced in the past. Explorations of scenarios such as those we have presented can provide useful heuristic tools to increase our understanding of ecological dynamics in response to climate change, and can stimulate discussion regarding the strategies appropriate for maintaining biological diversity in the face of environmental change.

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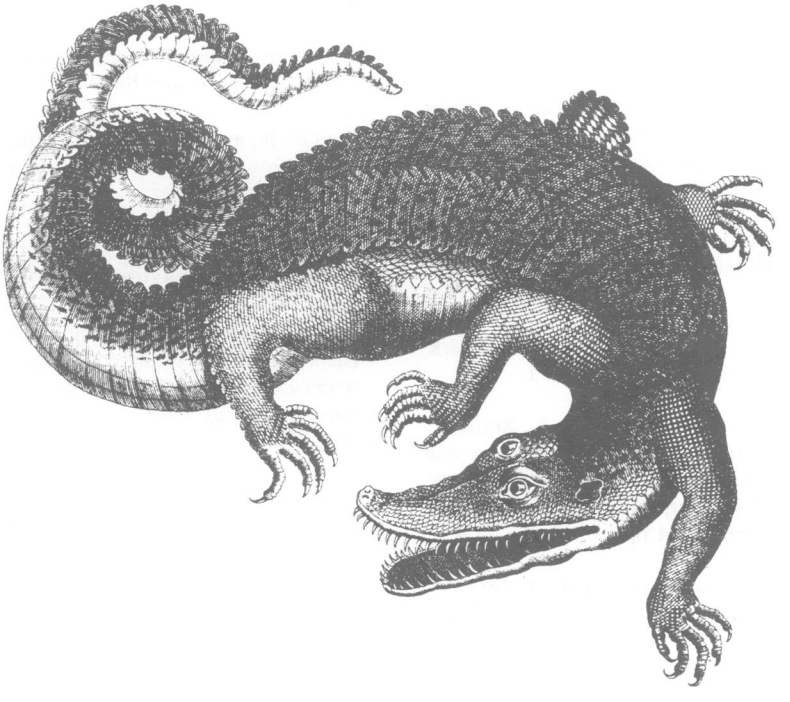
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