

Watersheds and Vegetation of the Greater Yellowstone Ecosystem

RICHARD A. MARSTON

Department of Geography
University of Wyoming
Laramie, WY 82071, U.S.A.

JAY E. ANDERSON

Department of Biological Sciences
Idaho State University
Pocatello, ID 83209, U.S.A.

Abstract: *This paper describes major watershed systems and broad patterns of vegetation within the Greater Yellowstone Ecosystem, explains the geographic links between these systems, and proposes factors that could be used to measure the integrity (condition and naturalness) of watersheds and vegetation. The Greater Yellowstone Ecosystem can be geographically defined as the Yellowstone Plateau and elevations in the 14 surrounding mountain ranges above the 2130-meter (7000-foot) contour; certain lower elevations need to be included to account for some ecological processes. The Greater Yellowstone Ecosystem is the headwaters for three major continental-scale river systems: the Missouri-Mississippi, Snake-Columbia, and Green-Colorado. Features, processes, and materials of watersheds provide structure and key functions to ecosystems of Greater Yellowstone. Changes in elevation—and the accordant changes in precipitation, temperature, land forms, and the stream network—exert the strongest control on the distribution of plant species in the Greater Yellowstone Ecosystem. The condition and naturalness of watersheds and vegetation remain to be quantified, but both decline with distance away from the core of the Greater Yellowstone Ecosystem due to timber harvest, oil and gas exploration and development, mineral exploration and development, reservoir operations, flood control, agricultural development, and livestock grazing.*

Resumen: *Este documento describe los sistemas de cuencas mayores y los patrones generales de vegetación dentro del ecosistema de Greater Yellowstone, explica las uniones geográficas entre estos sistemas y propone factores que podrían ser utilizados para medir la integridad (condición y naturaleza) de las cuencas y la vegetación. El ecosistema de Greater Yellowstone puede ser definido geográficamente como la planicie de Yellowstone y las elevaciones, en los 14 complejos montañosos, arriba de los 2130 m; ciertas elevaciones bajas necesitan ser incluidas para explicar algunos de los procesos ecológicos. El ecosistema de Greater Yellowstone es la fuente de abasto de agua para tres de los grandes sistemas de ríos continentales: Missouri-Mississippi, Snake-Columbia and Green-Colorado. Las características, los procesos y los materiales de las cuencas ofrecen estructura y funciones clave para los ecosistemas de Greater Yellowstone. Los cambios en las elevaciones—y los cambios concordantes en precipitación, temperatura, orografía y la red de arroyos—ejercen el mayor control sobre la distribución de las especies de plantas en el ecosistema de Yellowstone. Las condiciones y la naturalidad de las cuencas y su vegetación falta de ser cuantificada, pero ambas disminuyen con la distancia del centro del ecosistema de Greater Yellowstone debido a la tala de árboles, a las exploraciones y al desarrollo del gas y del petróleo, a la exploración y desarrollo de la minería, a las operaciones de las presas de almacenamiento, al control de las inundaciones, al desarrollo de la agricultura y al pastoreo por ganado.*

Paper submitted December 27, 1990; revised manuscript accepted January 20, 1991.

Introduction

Implementation of ecosystem management in the Greater Yellowstone Ecosystem (GYE) will demand refined scientific understanding of the components that form the ecosystem, of the processes that maintain and change it, and of indicators of its health (Clark & Harvey 1988). The structure and function of the GYE is largely controlled by watersheds and vegetation. The purpose of this paper is to describe major watersheds and broad patterns of vegetation within the GYE, explain the geographic links between these systems, and propose factors that could be used to measure watershed integrity in the GYE.

No single criterion can be used to precisely define the geographic limits of the Greater Yellowstone Ecosystem (see Anderson 1991), but topography, geologic materials, vegetation, and geomorphic and hydrologic processes all exhibit notable changes at the 2130-meter (7000-foot) contour, the approximate boundary between the forested terrain of the mountains and the rangelands of the surrounding basin country. Defining the GYE on the basis of all watersheds above the 2130-meter contour recognizes that the headwaters of key watersheds form the core of the GYE. To satisfy the criteria for ecologically sound boundaries for natural areas set by Theberge (1989), adjacent foothill areas at lower elevations would also need to be included in the GYE (e.g., see Berger 1991).

A physiographically diverse landscape has been created by episodes of mountain building, vulcanism, and glaciation, acting over the time scale of tens of thousands of years or longer, coupled in more recent times with massive slope failures and the action of running water. It is beyond the scope of this paper to review the geologic evolution of the Greater Yellowstone Ecosystem landscape. However, we develop the thesis that the present-day range in elevation—which resulted from past geologic processes—exerts the strongest control on the distribution of plant species and on the structure and function of aquatic ecosystems in the GYE.

Watershed Systems of the GYE

The headwaters of three major continental-scale watersheds are found in Greater Yellowstone (Fig. 1): the Missouri-Mississippi, Snake-Columbia, and Green-Colorado. In fact, a "triple divide" exists along the crest of the Wind River Range that serves as a common point for the Missouri, Snake, and Green drainages. The headwaters of the Missouri-Mississippi watershed are composed of the Wind, the North Fork and South Fork of the Shoshone, Clarks Fork of the Yellowstone, the Lamar, the Yellowstone, the Gallatin, the Madison, and the Red

Rock rivers. Several major lakes and reservoirs are found in this watershed, including Buffalo Bill Reservoir, Yellowstone Lake, Hebgen-Earthquake Lakes, and Red Rock Lakes. Red Rock Lakes have been ascribed special importance in the GYE because they are fed by warm springs that may be linked to the hydrothermal systems of Yellowstone National Park and because the lakes are heavily used by the animal communities that help define the ecosystem (Corn & Gorte 1986).

The headwaters of the Snake-Columbia watershed are composed of Henry's Fork of the Snake, the Snake, Grey's, the Salt, the Gros Ventre, and the Hoback rivers. Major lakes and reservoirs in this watershed include Island Park Reservoir, Shoshone Lake, Lewis Lake, Heart Lake, Jackson Lake, and Palisades Reservoir. The Green River drains the southern slopes of the Wind River Range and eventually combines with the Colorado River in Utah. Green Lakes and Fremont Lake are situated in the Greater Yellowstone Ecosystem near the headwaters of the Green River watershed.

Very few data exist on rates of groundwater storage, recharge, or withdrawals from bedrock aquifers in the GYE. One exception to this is the Gros Ventre Range, where extensive karst development in soluble Paleozoic rocks has created high permeability and extensive groundwater circulation (Mills 1989). Valley alluvium along major rivers is recognized as a significant source of groundwater for domestic and agricultural uses (Wyoming State Engineer's Office 1973; Hogan 1988; Ostresh et al. 1990).

The extract boundaries of the Yellowstone geothermal reservoir are not known with any certainty and are still under investigation. The famous geysers and other geothermal features of Yellowstone National Park are most likely hydrologically connected to recharge areas beyond the Park boundaries. Some geochemical similarity has been reported by the U.S. Geological Survey between water in the Yellowstone geothermal system and surface water collected in the Gallatin Mountains, suggesting that recharge for the hydrothermal basin comes from north and northwest of the Park (Corn & Gorte 1986). The link between the geothermal reservoir and surface waters has also been demonstrated by the introduction of arsenic to surface waters from the geothermal reservoir. Other Known Geothermal Resources Areas (KGRA) in the GYE are the Yellowstone KGRA located outside of the western boundary of Yellowstone National Park on lands managed by the Bureau of Land Management, the Island Park KGRA located southwest of Yellowstone National Park in the Targhee National Forest, and the Corwin Springs KGRA which adjoins Yellowstone National Park along its north boundary.

Several key features, processes, and materials of these watersheds provide structure and function to ecosystems of Greater Yellowstone:

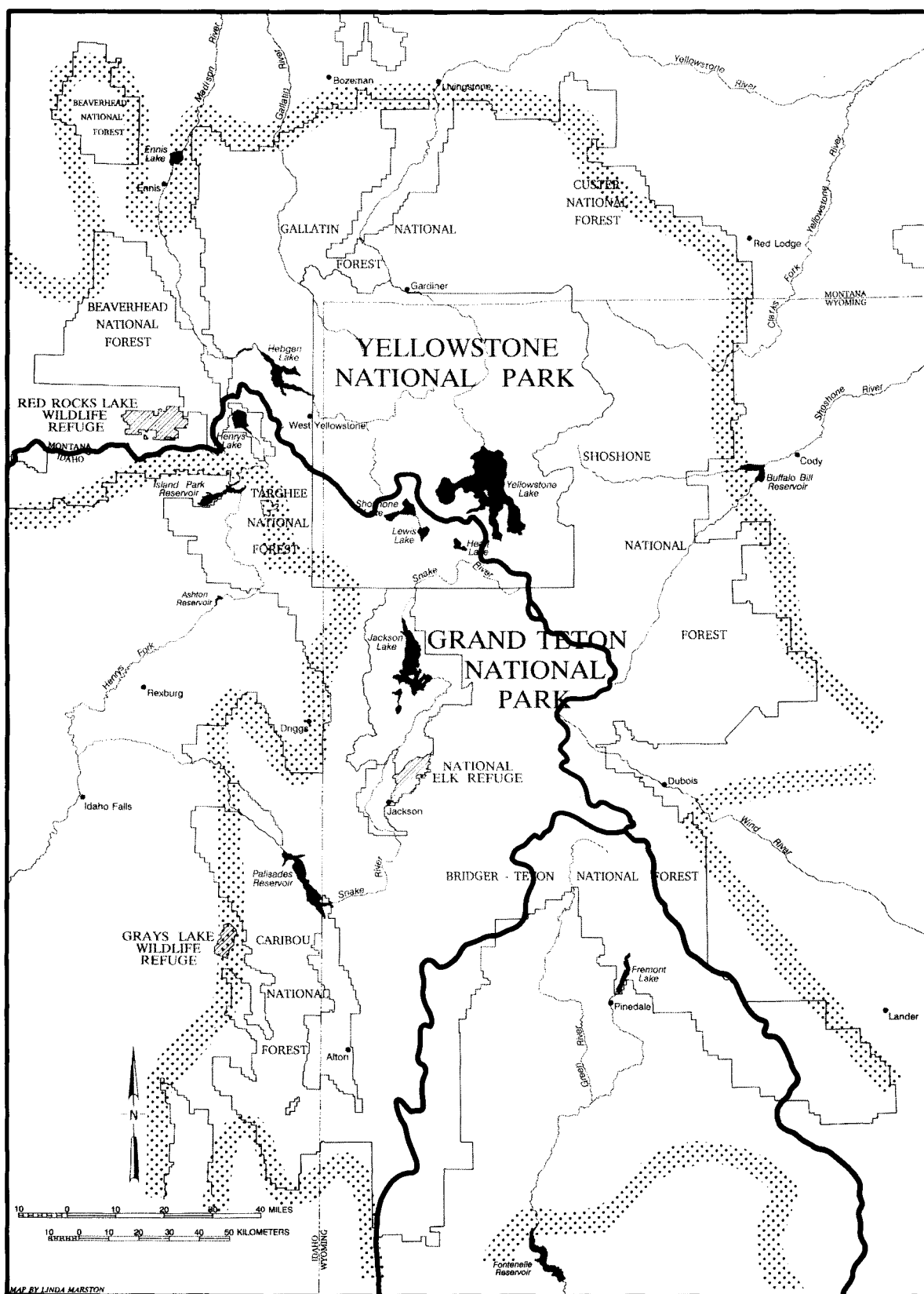


Figure 1. Hydrography and land ownership in the Greater Yellowstone Area. Highlighted map features include the generalized location of the 2130-meter (7000-foot) contour and continental-scale drainage divides between the Snake-Columbia, Yellowstone-Missouri, and Green-Colorado rivers.

1. The path of fires depends, in part, on the interaction between wind and topographic features, especially watershed divides (GYCC 1988).
2. Major watershed divides influence the seasonal range and migration routes of large ungulates (GYCC 1987).
3. The composition, density, and diversity of hill-slope vegetation depends, in part, on the topographic diversity as expressed by the range in elevation, local relief, pattern and density of drainage, degree of channel incision, slope gradient, and association with other land forms (see Romme and Knight 1982 for a discussion of landscape diversity within Yellowstone National Park).
4. The channel network defines the extent of potential aquatic habitat and riparian zones (GYCC 1987, pp. 3–12); the GYE is an “island of water surplus” where precipitation exceeds loss to the atmosphere, surrounded by lower-elevation regions of water deficits (Ostresh et al. 1990). The high percentage of perennial streams creates aquatic habitat and provides water for riparian systems and ground-water recharge.
5. The upstream-to-downstream change in stream habitat structure, sources of carbon (terrestrial input vs. algal production), and functional groups of macroinvertebrates are controlled by stream-adjacent topography, flood-plain width, channel substrate (see Vannote et al. 1980 for a more detailed description of the stream continuum concept; see GYCC 1987 and Ostresh et al. 1990 for discussion on the extent of valuable fisheries in the GYE).
6. Streams transfer nutrients in soluble form and as adsorbed on sediment (see Marston 1989 for a review of these processes).
7. Watersheds of the GYE are sources of high-quality water for lowland areas outside the GYE, with the seasonal exception of sediment during the peak of snow-melt season, during summer thunderstorms, and for the first two years following the 1988 fires (GYCC 1988; Ostresh et al. 1990).

Vegetation Patterns

Elevation and Climate

Elevation is probably the most important single factor affecting the distribution of plant species in the GYE, but its effects are manifested through influences on temperature and moisture availability (Whittaker 1978; Peet 1988). Average air and soil temperatures decrease about 0.6° C per 100 m gain in elevation (Bamberg & Major 1968; Anderson & McNaughton 1973; Despaign 1987). The resulting frost-free period ranges from 60 to 90 days at the lowest elevations to essentially zero in alpine regions where frost may come at any time and the growing season may only last a few weeks.

Precipitation generally increases with elevation (e.g., Ehleringer 1988) and typically is highest on the windward sides of mountain ranges. Most precipitation arrives in the Greater Yellowstone region on prevailing westerlies. Precipitation is rather evenly distributed throughout the year in this region (Baker 1986), but at low to middle elevations there is a precipitation peak in late spring while the summer and early fall months tend to be dry (Fig. 2; see also Weaver 1980). The highest elevations have a distinct winter peak in precipitation (Despain 1987). For Yellowstone National Park, there is a decreasing gradient in precipitation from the southwest to the northeast (Baker 1986, cf. Old Faithful and Yellowstone Lake, Fig. 2). This results from the westerly and southwesterly winds blowing across the relatively low Snake River Plain and then suddenly cooling adiabatically as they gain elevation upon reaching the Yellowstone Plateau (see Despaign 1987 for a more detailed analysis).

Elevation and Vegetation Communities

The patterns of precipitation and temperature produce predictable vegetation patterns. At the lowest elevations, foothill grasslands or shrub steppes occur. Common dominants of these grasslands include wheatgrasses (*Agropyron*), needlegrasses (*Stipa*) and Idaho fescue (*Festuca idahoensis*). Various bluegrasses (*Poa*), prairie Junegrass (*Koeleria cristata*), and, on the northern and eastern limits of the Ecosystem, blue gramma (*Bouteloua gracilis*), are also abundant. The shrub steppes typically are dominated by big sagebrush (*Artemisia tridentata*); other common shrubs include the rabbitbrushes (*Chrysothamnus*), threetip sagebrush (*Artemisia tripartita*), bitterbrush (*Purshia tridentata*), serviceberry (*Amelanchier alnifolia*), and fringed sagebrush (*Artemisia frigida*). With increasing moisture, open stands of Rocky Mountain juniper (*Juniperus scopulorum*), limber pine (*Pinus flexilis*), ponderosa pine (*Pinus ponderosa*), or Douglas-fir (*Pseudotsuga menziesii*) occur. Ponderosa pine occurs only along the northeastern edge of the Ecosystem. Douglas-fir forests are found on north-facing slopes, and stands of aspen (*Populus tremuloides*) may form the interface between sagebrush steppes and higher-elevation coniferous forests. These grassland, steppe, and low-elevation forest communities often occur on glacial till or alluvial soils that are relatively fertile. Consequently, these communities are rich in plant species, especially grasses and forbs, except where they have been severely degraded by livestock grazing. For more detailed descriptions see Reed (1952), Mueggler and Stewart (1980), Youngblood and Mueggler (1981), and Mueggler (1988).

Cottonwoods (*Populus angustifolia*, *P. balsamifera*, and *P. trichocarpa*) typically dominate riparian commu-

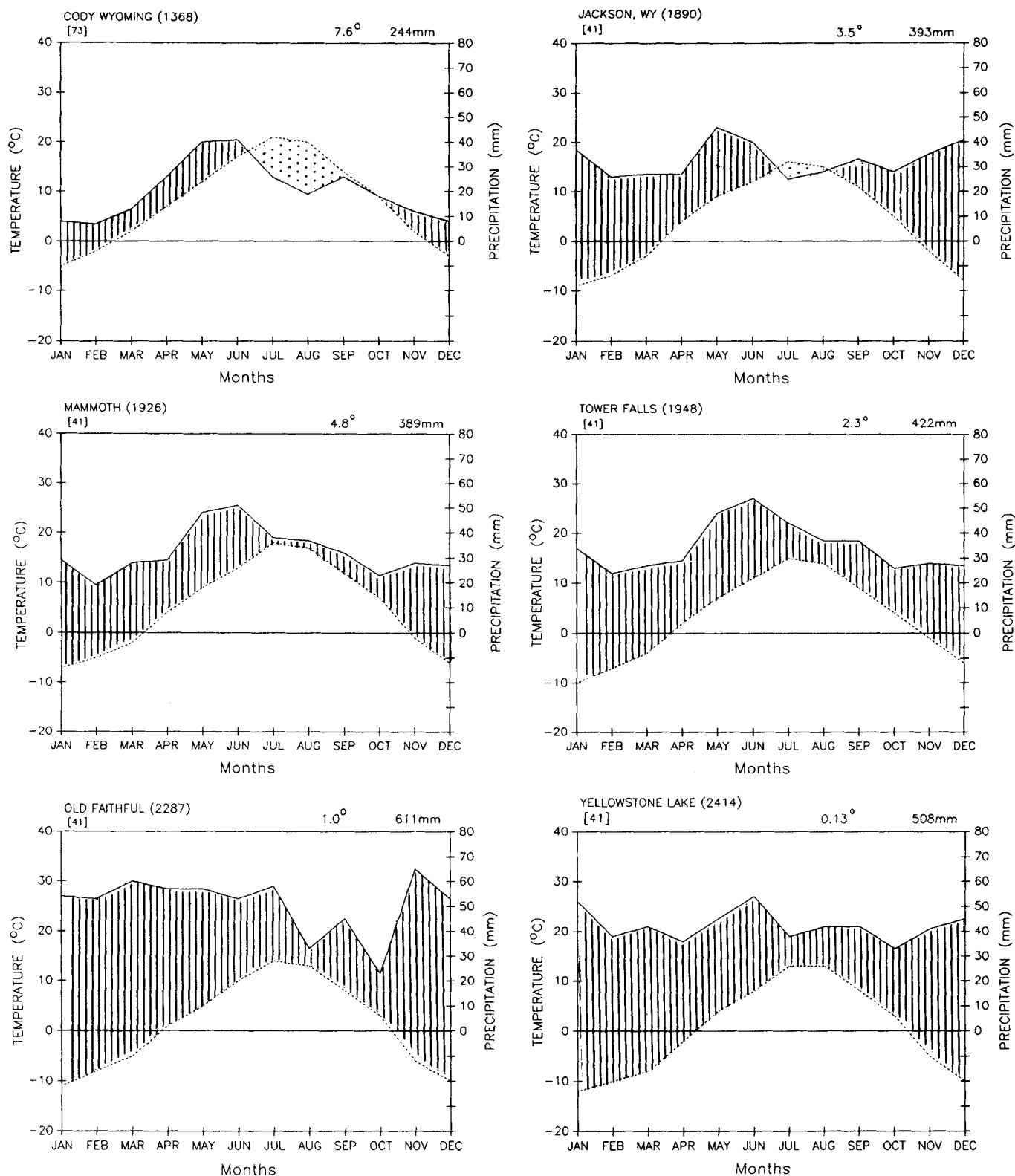


Figure 2. Climographs for selected stations in the Greater Yellowstone Ecosystem. On the same line the station names are elevation (m), mean annual temperature °C, and mean annual precipitation (mm). The number of years of record is shown below the station name. The solid line shows mean monthly precipitation; the dashed line shows mean monthly temperatures. Vertical hatching indicates periods when precipitation generally exceeds evapotranspiration; stippling indicates periods when evapotranspiration generally exceeds precipitation. The diagrams are arranged in order of increasing elevation. Note that Old Faithful, which lies to the west of Yellowstone Lake but at lower elevation, has considerably higher mean annual precipitation.

nities along the lowest stream reaches in the GYE; at higher elevations, willows (*Salix* spp.) are dominant. These riparian communities are highly productive and support a rich flora and an abundance of wildlife. Because of the availability of water and succulent forage, large ungulates, especially domestic cattle, congregate in these streamside communities. The presence of rhizomatous grasses and sedges makes riparian areas reasonably tolerant of heavy use and quite resilient; however, they can be damaged by heavy ungulate use.

In the foothills of southeastern Idaho and western Wyoming mountain shrub communities consisting of variously mixed stands of shrubs including snowberry (*Symphoricarpos*), chokecherry (*Prunus virginiana*), serviceberry (*Amelanchier alnifolia*), Oregon grape (*Berberis repens*), bitterbrush, rabbitbrushes, and sagebrushes are found below the lower timberline. In some areas, especially on soils derived from limestone, curl-leaf mountain mahogany (*Cercocarpus ledifolius*) stands are common.

Throughout much of the region, Douglas-fir forms the lowest-elevation forest communities (Fig. 3). Shrubs and herbaceous species found in the adjacent sagebrush steppes or mountain shrub communities are common in the understory of the lowest-elevation Douglas-fir forests; common understory dominants in higher-elevation Douglas-fir forests include elk sedge (*Carex geyeri*),

pine grass (*Calamagrostis rubescens*), birch-leaved spiraea (*Spiraea betulifolia*), heartleaf arnica (*Arnica cordifolia*), and blue huckleberry (*Vaccinium globulare*).

At middle elevations, especially on the extensive Yellowstone Plateau, forests of lodgepole pine (*Pinus contorta*) are ubiquitous (Fig. 3). Soil parent material appears to be a major factor affecting the distribution of lodgepole pine in the Yellowstone area (Despain, in press). Lodgepole pine is a persistent dominant on areas underlain by Quaternary rhyolite flows, whereas at similar elevations, subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) are usually dominant in old-growth forests on soils derived from Tertiary andesites. Soils developed on rhyolite are nutritionally poor and coarse-textured, creating relatively xeric conditions. Lodgepole pine trees grow slowly on such soils and may reach ages of over 500 years (D. Despain, pers. comm.). Lodgepole pine forests typically consist of dense, nearly pure stands with only sparse coverage of shrubs and herbs in the understory. Common understory species include elk sedge, pine grass, Ross's sedge (*Carex rossii*), heartleaf arnica, birch-leaved spiraea, and grouse whortleberry (*Vaccinium scoparium*).

With increasing elevation or precipitation, or a change in substrate to andesite or sedimentary rock, the impoverished lodgepole communities give way to spruce-fir or subalpine forests where Engelmann spruce, subalpine fir, and whitebark pine (*Pinus albicaulis*) are dominants (Fig. 3). Except near the upper timberline, lodgepole pine often is a codominant, even in old-growth forests. Many of the understory species mentioned above are common in these forests, but the understory typically has higher species richness and productivity than in the pure lodgepole pine forests. Subalpine forests are often open-grown and support a rich diversity of herbaceous plants. Stands of stunted subalpine fir, Engelmann spruce, and whitebark pine form the upper timberline. Detailed descriptions of these forest communities can be found in Reed (1976), Steele et al. (1983), Habeck (1988), Peet (1988) and Despain (in press).

Alpine tundra is found on the highest reaches of all the major ranges, but it is most extensive on the Beartooth Plateau, one of the largest expanses of alpine tundra in the conterminous United States (see Johnson & Billings 1962). Alpine communities typically consist of a mixture of perennial grasses, sedges, forbs, and dwarf willows; dry fellfields are typically occupied by mat-forming and other low-growing forbs interspersed with rocks and gravel. Wet meadows support dense stands of grasses, sedges, and willows.

Both aspect and substrate geology play critical roles in defining biotic patterns in the Greater Yellowstone area. Mesic forest vegetation extends to lower eleva-

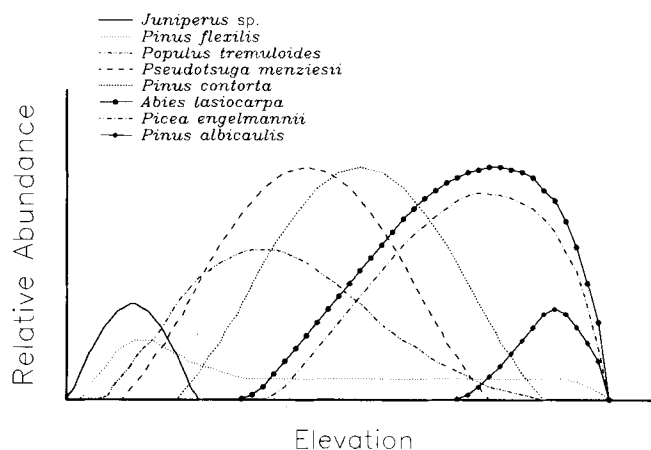


Figure 3. Generalized distributions of the most common tree species in the GYE along an elevational gradient. Rocky Mountain juniper (*Juniperus scopulorum*) occurs at lower elevations in northern portions of the Ecosystem; to the south, Utah juniper (*J. osteosperma*) becomes dominant on exposed slopes and Rocky Mountain juniper tends to be restricted to ravines or other sites having slightly higher moisture. Limber pine (*Pinus flexilis*) occurs over a broad range of elevations, often on rather extreme sites such as exposed ridges. Its relative abundance is typically low. See text for comments on distributions of other species.

tions on cooler north- and wetter east-facing slopes, and the xeric steppes extend farther upward on south- and west-facing ones. Abrupt changes in topography such as ridgelines produce sudden changes in environment and equally abrupt changes in vegetation. Similarly, abrupt changes in substrate that affect soil chemistry or water-holding capacity may result in abrupt floristic changes.

Disturbance

Most, if not all, vegetation in the GYE is subject to periodic disturbances. At any point in time the composition and structure of a patch of vegetation reflects its disturbance history. Fire is the most widespread natural disturbance, but smaller-scale disturbances by hoofed animals, pocket gophers, wind, slope failures, and geothermal activity are ubiquitous. Prior to settlement of the region, the shrub steppe, grassland, and forest edge communities of Yellowstone's northern range were subject to an average frequency of about four fires per century (Houston 1982). The fire-return interval in coniferous forests at higher elevations ranged from 200 to 400 years (Romme & Despain 1989). Although large-scale fires such as those of 1988 are relatively infrequent, they shape the landscape pattern for centuries (Romme 1982; Romme & Despain 1989).

Integrity of Watersheds and Vegetation

Integrity, or intactness (see Anderson 1991) implies that critical ecosystem structures and functions are present and operating within natural limits. Watershed integrity depends upon condition (defined below) and naturalness (see Anderson 1991). A watershed could be in satisfactory condition with a low degree of naturalness or in unsatisfactory condition with a high degree of naturalness, hence the two separate measures of integrity. Similar arguments apply to vegetation. We might judge a meadow of exotic species to be in satisfactory condition in terms of function (e.g., productivity, soil stabilization), but the criteria for integrity would only be partially attained. The hydrologic functions of vegetation (e.g., controlling erosion, shading, disposing of precipitation, supplying organic matter to stream biota) play important roles in watershed integrity. Conversely, watershed condition can control the rate and nature of vegetation development or deterioration.

Watershed Condition

Condition describes the degree to which equilibrium has been achieved between morphological and cascading variables within the watershed. Morphological variables describe the configuration and composition of biophysical features and materials that comprise the watershed, such as land forms, soils, climate, and vege-

tation. Examples of morphological variables include drainage density, soil moisture content, albedo, and leaf-area index. Cascading variables describe the rate of flux of materials (e.g., water, sediment, nutrients) and energy (e.g., radiation, chemical, potential/kinetic energy of streams) through the watershed. Examples of cascading variables are rates of movement of water, sediment, nutrients, radiation, chemical energy, and potential/kinetic energy transformations in streams (see Strahler 1980 for a more complete list and discussion of these variables).

The condition of watershed systems can be quantified, but results depend on the time span being considered. Periods of rapid change in morphology or in the energy and material cascades of watersheds may be part of an adjustment to a new equilibrium condition (stability), or they may represent progressive deterioration away from equilibrium (instability). Stability occurs when the mean recurrence interval of events capable of producing change is longer than the time required for the watershed to recover from those events. A good correlation is likely to exist between morphological and cascading variables, even while both are changing. Instability occurs when the watershed cannot adjust to new conditions before the next major disturbance occurs. Channel and hill-slope forms are transient, and a poor correlation exists between form and process (Brunsdon & Thornes 1979). Additional diagnostic criteria of watershed condition include temporal variations in runoff and water quality parameters, ability of channels to conduct water and sediment, accelerated vertical and horizontal channel shifts, accelerated hill-slope erosion (mass wasting, erosion by rain splash and overland flow), and aberrations in the stream continuum.

A satisfactory watershed condition is characterized not by absolute stability, but rather by short-term hydrologic and geomorphic fluctuations about a longer-term mean value. In turn, these longer-term values may be changing either progressively (dynamic equilibrium) or in episodes after a threshold of force and resistance is exceeded (dynamic metastable equilibrium). The morphological components and energy and material cascades of watersheds are less susceptible to external change than are flora and fauna. Periods of accelerated geomorphic change can truncate ecosystem succession and control the rate of subsequent plant community development. These important contrasts explain why geomorphic instability can sometimes add to landscape diversity by creating microhabitats (e.g., aspen stands on mass wasting scars, additional in-stream cover for fish through bank undercutting). Based on a review of Reese (1984), Corn and Gorte (1986), and GYCC (1987) plus our own field experience and ongoing research, it can be said with some confidence that watershed condition is satisfactory within the national parks of the GYE but declines with distance away from its core. Even within

the parks, slope failures are frequent and large, the potential for future mass wasting is high, and sediment supply to streams is considerable (GYCC 1988; Marston 1990).

Vegetation Condition

Vegetation in satisfactory condition implies that the productive capacity of the site and plant species diversity are being maintained. Recognizing the role of natural disturbances in structuring vegetation in the GYE, we include the criterion of self-repair or recovery. This does not mean that vegetation in satisfactory condition is necessarily static or returning to some equilibrium. Rather, it is stable in the sense that species are not being lost and the vegetation can recover from extreme events such as fire that may drive species to low densities (Chesson & Case 1986).

Naturalness of Watersheds and Vegetation

Anderson (1991) proposes three measures of naturalness: (1) the degree to which the system would change if humans were removed; (2) the amount of cultural energy required to maintain the current functioning of the system; and (3) the complement of native species presently in the area compared with the suite of species in the area prior to settlement. These measures can be applied to the condition criteria above to judge the degree of watershed and vegetation naturalness in the GYE. Reliable measurement of watershed naturalness depends on the ability to separate change triggered by human activities from change that would have occurred without human intervention. In concert with watershed condition, the degree of naturalness declines with distance from the core of the GYE. Degradation of naturalness has been caused principally by timber harvest (especially accelerated slope failures, erosion, and sedimentation from roads), oil and gas exploration and development (erosion and sedimentation), mineral exploration and development (release of trace metals), reservoir operations (alteration of the hydrograph, disruption of the stream continuum), flood control (lower diversity of floodplain communities), agricultural development, and livestock grazing (loss of habitat).

The ratio of exotic to native plant species provides a direct index of naturalness. Alpine, subalpine, and montane forest communities in the national parks and wilderness areas typically have a high proportion of native species. Outside of these core areas, exotic species are more common because of disturbances and propagule dispersal associated with the human activities mentioned above. In addition, exotic species have been used routinely for rehabilitation of burned or overgrazed areas on lands administered by the U.S. Forest Service and Bureau of Land Management. Again we find that the trend for vegetation parallels that of watersheds: natu-

ralness declines with distance from the core of the ecosystem.

Conclusions

The headwaters of the Snake-Columbia, Yellowstone-Missouri, and Green-Colorado rivers form the core of the GYE. The 2130-meter (7000-foot) elevation contour provides an approximate lower limit to the GYE based on key components and processes of watersheds and vegetation. Changes in elevation are largely responsible for predictable patterns in terrestrial vegetation communities. Watersheds control much of the structure and function of ecosystems in the GYE, while vegetation affects a number of key components and processes of hydrologic and geomorphic systems. The condition and naturalness of watersheds and vegetation decline with distance away from the core of the GYE due to the impacts of timber harvest, oil and gas exploration and development, mineral exploration and development, reservoir operations, flood control, agricultural development, and livestock grazing. These trends remain to be quantified, a key step before implementing ecosystem management to the GYE.

Acknowledgments

This paper benefited from the comments of David Chalinor, Barrie Gilbert, William Romme, and anonymous reviewers.

Literature Cited

- Anderson, J. E. 1991. A conceptual framework for evaluating and quantifying naturalness. *Conservation Biology* 5:347–352.
- Anderson, J. E., and S. J. McNaughton. 1973. Effects of low soil temperature on transpiration, photosynthesis, leaf relative water content, and growth among elevationally diverse plant populations. *Ecology* 54:1220–1233.
- Baker, R. G. 1986. Sangamonian (?) and Wisconsin paleoenvironments in Yellowstone National Park. *Geological Society of America Bulletin* 97:717–736.
- Bamberg, S. A., and J. Major. 1968. Ecology of the vegetation and soils associated with calcareous parent materials in three alpine regions of Montana. *Ecological Monographs* 38:127–167.
- Berger, J. 1991. Greater Yellowstone's native ungulates: myths and realities. *Conservation Biology* 5:353–363.
- Brunsdon, D., and J. B. Thornes. 1979. Landscape sensitivity and change. *Transactions of the Institute of British Geographers, New Series* 4:463–484.
- Chesson, P. L., and T. J. Case. 1986. Overview: nonequilibrium community theories—chance, variability, history, and coexistence. Pages 229–239 in J. Diamond and T. J. Case, editors. *Community ecology*. Harper and Row, New York.

- Clark, T. W., and A. N. Harvey. 1988. Management of the Greater Yellowstone Ecosystem: an annotated bibliography. Northern Rockies Conservation Cooperative, Jackson, Wyoming.
- Corn, M. L., and R. W. Gorte. 1986. Yellowstone: ecosystem, resources, and management. Congressional Research Service Report 86-1037 ENR prepared for the Committee on Interior and Insular Affairs. Library of Congress, Washington, D.C.
- Despain, D. G. 1987. The two climates of Yellowstone National Park. *Proceedings of the Montana Academy of Science* 47:11–20.
- Despain, D. G. Yellowstone vegetation: consequences of environment and history. Roberts Rinehart Publishing Company. In press.
- Ehleringer, J. A. 1988. Changes in leaf characteristics of species along elevational gradients in the Wasatch Front, Utah. *American Journal of Botany* 75:680–689.
- Greater Yellowstone Coordinating Committee (GYCC). 1987. The Greater Yellowstone Area: an aggregation of national park and national forest management plans. National Park Service and U.S. Forest Service, Washington, D.C.
- Greater Yellowstone Coordinating Committee (GYCC). 1988. Ecological consequences of the 1988 fires in the Greater Yellowstone Area. National Park Service and U.S. Forest Service, Washington, D.C.
- Habeck, J. R. 1988. Present-day vegetation in the northern Rocky Mountains. *Annals of the Missouri Botanical Garden* 74:804–840.
- Hogan, D. W. 1988. Wyoming 1988 water quality assessment. Wyoming Department of Environmental Quality, Cheyenne.
- Houston, D. B. 1982. The northern Yellowstone elk. Macmillan and Company, New York.
- Johnson, P. L., and W. D. Billings. 1962. The alpine vegetation of the Beartooth Plateau in relation to cryopedogenic processes and patterns. *Ecological Monographs* 32:105–135.
- Marston, R. A. 1989. Particulate and dissolved losses of nitrogen and phosphorus from forest and agricultural soils. *Progress in Physical Geography* 13:234–259.
- Marston, R. A. 1990. Changes in geomorphic processes in the Snake River following the impoundment of Jackson Lake and potential changes due to 1988 fires in the watershed. Semi-annual project report prepared for the University of Wyoming–National Park Service Research Center, Laramie.
- Mills, J. P. 1989. Foreland structure and karstic ground water circulation in the eastern Gros Ventre Range, Wyoming. M.S. thesis. University of Wyoming, Laramie, Wyoming.
- Mueggler, W. F. 1988. Aspen community types of the Intermountain Region. USDA Forest Service General Technical Report INT-250. Intermountain Research Station, Ogden, Utah.
- Mueggler, W. F., and W. L. Stewart. 1980. Grassland and shrubland habitat types of Western Montana. USDA Forest Service General Technical Report INT-66. Intermountain Forest and Range Experiment Station, Ogden, Utah.
- Ostresh, L. M., Jr., R. A. Marston, and W. M. Hudson. 1990. Wyoming water atlas. Wyoming Water Development Commission and University of Wyoming, Cheyenne and Laramie, Wyoming.
- Peet, R. K. 1988. Forests of the Rocky Mountains. Pages 63–101. M. G. Barbour and W. D. Billings, editors. *North American terrestrial vegetation*. Cambridge University Press, New York.
- Reed, J. F. 1952. The vegetation of the Jackson Hole Wildlife Park, Wyoming. *American Midland Naturalist* 48:700–729.
- Reed, J. F. 1976. Coniferous forest habitat types of the Wind River Mountains, Wyoming. *American Midland Naturalist* 95:159–173.
- Reese, R. 1984. Greater Yellowstone: the National Park and adjacent lands. *Montana Magazine*, Helena.
- Romme, W. H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. *Ecological Monographs* 52:199–221.
- Romme, W. H., and D. G. Despain. 1989. The long history of fire in the Greater Yellowstone Ecosystem. *Western Wildlands* 15:10–17.
- Romme, W. H., and D. H. Knight. 1982. Landscape diversity: the concept applied to Yellowstone National Park. *BioScience* 32:664–670.
- Steele, R., S. V. Cooper, D. M. Ondov, D. W. Roberts, and R. D. Pfister. 1983. Forest habitat types of eastern Idaho–western Wyoming. USDA Forest Service General Technical Report INT-144. Intermountain Forest and Range Experiment Station, Ogden, Utah.
- Strahler, A. N. 1980. Systems theory in physical geography. *Physical Geography* 1:1–27.
- Theberge, J. B. 1989. Guidelines to drawing ecologically sound boundaries for national parks and nature reserves. *Environmental Management* 13:695–702.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Science* 37:130–137.
- Weaver, T. 1980. Climates of vegetation types of the northern Rocky Mountains and adjacent plains. *American Midland Naturalist* 103:392–398.
- Whittaker, R. H., editor. 1978. Ordination of plant communities. *Handbook of vegetation science* 5. 2nd edition, Junk, The Hague, Netherlands.
- Wyoming State Engineer's Office. 1973. The Wyoming framework water plan. Wyoming State Engineer's Office, Cheyenne, Wyoming.
- Youngblood, A. P., and W. F. Mueggler. 1981. Aspen community types of the Bridger-Teton National Forest in western Wyoming. USDA Forest Service Research Paper INT-272. Intermountain Forest and Range Experiment Station, Ogden, Utah.