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CONSEQUENCES OF NONEQUILIBRIUM RESOURCE AVAILABILITY ACROSS MULTIPLE TIME SCALES: THE TRANSIENT MAXIMA HYPOTHESIS

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Abstract.—Nonequilibrium biotic responses to changes in resource limitation dominate the behavior of tallgrass prairie ecosystems. Rates of leaf photosynthesis on a time scale of minutes, amounts of annual plant productivity, patterns in the productivity of certain consumer groups, and amounts of soil organic matter accumulation over millennia all reflect biotic responses to frequent and recurring shifts in limiting resources. Productivity is higher during a transition period when the relative importance of an essential resource is changing than during an equilibrium interval generated by single resource limitation. These "transient maxima" are both characteristic and easily measurable in the tallgrass prairie because of the unpredictable climate and ecological constraints such as grazing and recurrent fires that modify water, nitrogen, and light availability. Such diverse phenomena as overcompensation for herbivory, the intermediate disturbance hypothesis, maximum levels of productivity observed in successional ecosystems, and widespread nitrogen limitation in terrestrial and aquatic ecosystems can be explained by biotic response to shifts in limiting resources.

Paradigms in ecology have traditionally been divided into equilibrium and non-equilibrium models. For example, the ecosystem maturation hypothesis of Odum (1969), optimization theory in animal ecology (Schoener 1971), the resource ratio hypothesis (Tilman 1982), and plant growth responses to various stresses (Chapin 1991) assume that outcomes are resolved when equilibrium conditions are reached. However, recognition that transitory or nonequilibrium systems predominate in natural systems was a cornerstone of the earliest ecological studies in North America (see McIntosh 1985). Succession and periodic disturbances dictate that most systems are undergoing change in their biotic characteristics (see Strong et al. 1984). Recently, interest has been renewed in nonequilibrium ecological systems on scales ranging from single leaf responses over a few seconds (Percy 1988) to transitional responses involving month- to decade-level observations (Wiens 1984; Tilman 1989) to changes in ecosystem structure over thousands of years (Clark 1988). Such studies are particularly relevant given widespread recognition of the nonequilibrium conditions associated with climate change scenarios.

Here, we show that transitory phenomena are extremely important in determining the structure and characteristics of certain ecological systems. A unifying

characteristic of these responses involves a transient maxima or nonsustainable pulse of key system processes during time periods when availability or demand for limiting resources varies. These transitory responses affect ecological processes when measured on time scales ranging from short-term dynamics of carbon dioxide, water, and energy flux, through annual estimates of net primary productivity (NPP), through decade- to century-scaled patterns in plant succession, organic matter, and nitrogen dynamics in soils.

Our research focus has been the tallgrass prairie ecosystem of North America, a semihumid to humid region where rainfall approaches, equals, or exceeds potential evapotranspiration. As in other humid grasslands, a mechanism for the prevention of forest invasion is essential for the persistence of the system. The seasonally dry conditions of central North America permitted frequent fire, and the relatively flat topography assisted in the widespread nature of these fires (Sauer 1950). Other authors have added periodic drought as a requirement for the persistence of grasslands (e.g., R. Anderson 1982; Wright and Bailey 1982), but all agree that the vegetation of this region would be dominated by woody species in the absence of fire. The grass flora can persist as dominants in the absence of fire, provided a woody seed source is unavailable (Weaver and Rowland 1952). This fact may explain why the tallgrass flora was viewed as an edaphic as well as a fire climax community by F. E. Clements and many of his colleagues.

While rainfall is not commonly limiting to plant growth on the eastern regions of the tallgrass prairie, the very sharp east-to-west gradient in rainfall amounts and the variability in annual amounts creates substantial year-to-year variation in productivity (Risser et al. 1981). On the western edge of the biome, water is likely to become limiting sometime during the growing season even in years of normal rainfall (Knapp 1985). This generates one potential scenario for water to switch positions with either light or nutrients as the resource most immediately limiting to plant growth.

Fire and the vagaries of climate interact with another variable, grazing, which also affects the relative importance of light, water, and nutrients on plant photosynthesis and productivity. Grazing affects fire frequency by modification of fuel load, while fire, in turn, may control the intensity and pattern of grazing by large ungulates (Hobbs et al. 1991). Both fire and grazing influence the availability of photosynthetically active radiation to surface vegetation (Knapp and Seastedt 1986). During certain times of the year, fire can operate like grazing by removing living foliage, which thereby alters leaf area and the physiological state of the remaining leaf area. Inorganic nitrogen availability is negatively affected by frequent fire (Risser and Parton 1982; Ojima 1987; Seastedt 1988), while grazing likely enhances nitrogen availability (Holland and Detling 1990). Both variables also directly and indirectly affect soil moisture. These control mechanisms collectively result in a near-continual shift in factors limiting processes in tallgrass prairie.

INTERACTIONS AMONG ESSENTIAL RESOURCES

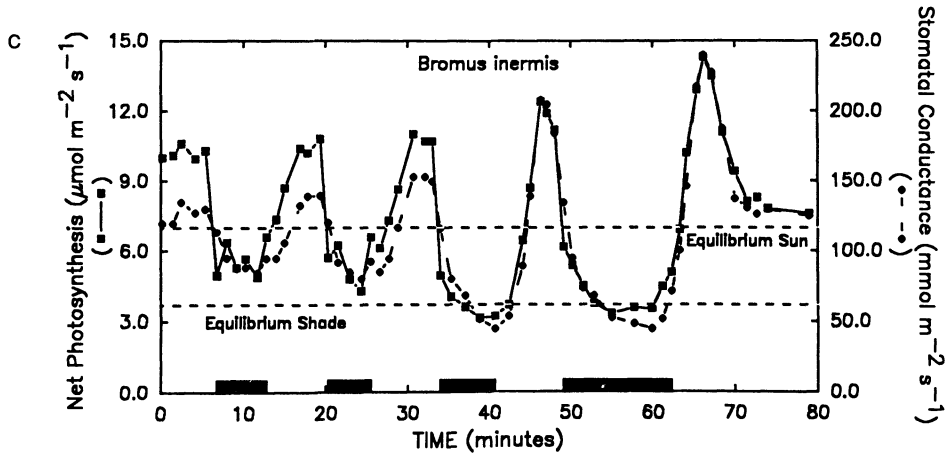
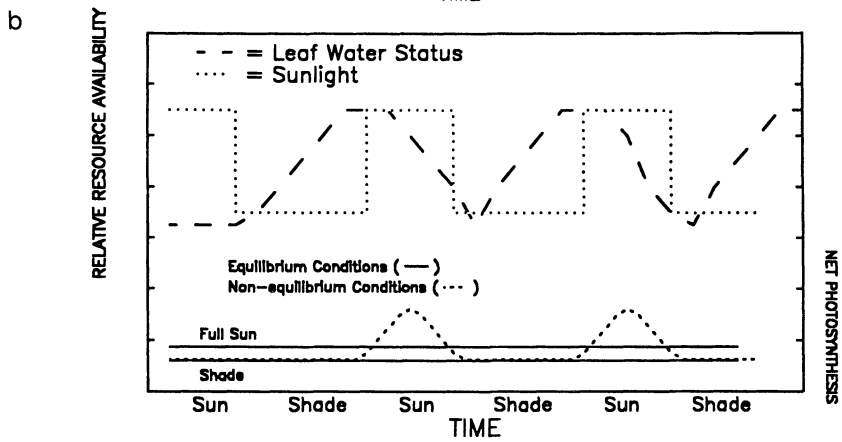
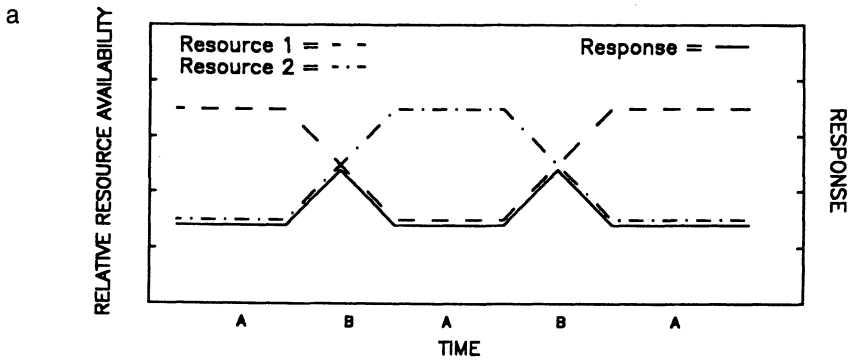
Over 150 yr ago Liebig (1840) proposed that, of the several resources that may potentially limit a process (e.g., growth) under equilibrium conditions, only one,

the resource in lowest supply and/or greatest demand, will limit the process at any point in time. Although multiple environmental factors may interact to set overall, integrated responses (Chapin 1980; Chapin et al. 1986), often a single limiting resource will predominate as a rate-limiting factor from the single-leaf to the ecosystem level. Examples include low air or soil temperature at high elevation, subalpine communities (Smith and Knapp 1990), water stress in deserts, and low sunlight availability in understory environments (Chazdon 1988). Additions of nonlimiting but essential resources may result in either a small response or no response because the limiting resource will be further reduced (Carson and Pickett 1990). For example, in western coniferous understory habitats, low water availability primarily limits leaf photosynthesis in understory herbs at midseason, with sunlight availability (important early in the growing season) often relegated to a secondary role. Experimentally increasing sunlight to these understory plants resulted in greater water stress and occasionally leaf necrosis, but not increased carbon dioxide uptake (Young and Smith 1979). Thus, increasing one resource, sunlight, only increased the demand and reduced the availability of the already-limiting resource, water. An important corollary of this negative relationship between availability of one resource and demand for another is that if a previously nonlimiting but essential resource becomes limiting, demand for other resources decreases and their availability increases. A familiar example of this storage/demand characteristic of resources involves seasonal cycles in soil moisture limitation and availability in plant communities, especially in grasslands. During the growing season, plant canopies, driven by thermal energy, actively transpire enough of the precipitation input to keep soil moisture levels low and potentially limiting to NPP. However, during the nongrowing season, low temperatures limit plant growth and transpiration, allowing soil moisture levels to increase, and, because the moisture is stored, it is available at high levels when temperatures are no longer limiting the next season (K. Anderson 1965).

A similar response in tallgrass prairie occurs between plant growth activity and soil water nitrogen availability (Hayes and Seastedt 1989). The absence of growth due to drought in 1 yr (or during part of the growing season) is correlated with increased growth and a reduction in sensitivity to nitrogen additions in subsequent time periods (Owensby et al. 1970; Seastedt et al. 1991). In addition, tallgrass prairie plants appear to exhibit "luxury uptake" of a nonlimiting resource that guarantees a more-than-adequate supply of this resource once the factor(s) currently constraining growth is removed. The extent to which these resources may be stored influences the magnitude and duration of the growth response once a shift in resource limitation occurs. A key genetic trait of "responsive species" would therefore be this capacity for uptake and storage (Chapin et al. 1986) that characterizes the dominant species of the grasslands.

SHIFTS IN RESOURCE AVAILABILITY UNDER NONEQUILIBRIUM CONDITIONS:
THE TRANSIENT MAXIMA HYPOTHESIS

In ecological systems ranging from single organisms to ecosystems that are in a state of transition because of disturbance or environmental variability, resource demand and availability will increase or decrease at resource-specific rates.



Knowledge of the kinetics of resource change and understanding the implications of differences among rates of change in resources are crucial to predicting system responses at all scales. For example, in an idealized system in which two resources, A and B, are capable of limiting the system response (fig. 1*a*), if the decline and recovery kinetics of these resources are identical, transitions from one state to another (due to biotic or abiotic events) will include two nonsustainable periods of elevated response or transient maxima when A and B are more available than at equilibrium states (fig. 1*a*).

Decline and recovery kinetics of resources are only rarely identical. The effect that differences in the kinetics of resource availability may have on physiological processes has been documented at the leaf level, where carbon dioxide uptake and fixation may be limited by many factors, including nitrogen in the long term (Schimel et al. 1991). Short-term variation in carbon dioxide uptake usually results from the availability of two primary resources, sunlight and water. Photosynthesis in plants exposed to extended periods of constant sunlight often becomes limited by water stress in all but the most mesic habitats (Schulze and Hall 1982). In contrast, periods of shade reduce evaporative demand, stomata close, and leaf water status increases, but carbon dioxide uptake is now limited by energy (Knapp and Smith 1990). These two states are depicted in figure 1*b*. Under nonequilibrium conditions such as those found on intermittently cloudy days or when canopy leaves periodically shade other leaves, sun and shade periods occur alternatively, and resource availability and demand may be constantly changing. In figure 1*b*, as shade and sun periods of several minutes alternate, one resource, energy, varies virtually instantaneously, but leaf water status changes more gradually. The model predicts that nonsustainable periods of high carbon dioxide uptake relative to equilibrium levels should occur during each sun period that follows a shade period of sufficient length to allow leaf water status to increase. This transient maxima has been found in subalpine understory plants exposed to variable sunlight (Knapp et al. 1989; Knapp and Smith 1990) and in native and introduced tallgrass prairie grasses (fig. 1*c*).

On a much broader scale, NPP in tallgrass prairie in nondrought years is limited by energy in unburned sites and by nitrogen availability in annually burned sites (Knapp and Seastedt 1986; Seastedt et al. 1991). Under nonequilibrium conditions of alternating years of fire and no fire, NPP may be higher after an infrequent fire

FIG. 1.—How nonequilibrium conditions produce a transient maximum. *a*, Response of a hypothetical system requiring two resources with identical kinetics, use, and storage by the system. Periods labeled A denote times of equilibrium when either resource 1 or resource 2 limits response. Periods labeled B are nonequilibrium periods that occur when limiting resources change in terms of relative availability. *b*, Conceptual view of changes in sunlight availability and leaf water status in plants exposed to alternating periods of sun and shade. The differing kinetics in water and light limitation result in a photosynthesis maximum when neither resource is limiting, but rates decline to a reduced, constant state at equilibrium when either resource remains limiting. *c*, Net photosynthesis and stomatal conductance in the grassland species *Bromus inermis*, under an experimentally manipulated sunlight regime. Note transient maxima occur during periods of sun that follow shade. *Dark bars* along X-axis denote periods of shade, and *dashed lines* without points indicate equilibrium responses.

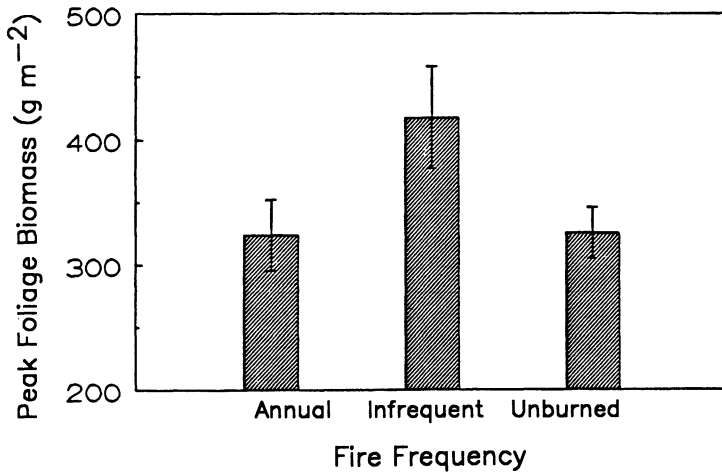


FIG. 2.—Foliage production on annually burned sites, less frequently burned sites (fire intervals of 4 yr or longer) but burned the year of measurement, and sites not burned the year of measurement. Data are from Konza Prairie, Kansas, during the 1987–1989 interval and are means and SEs of 14, 7, and 23 burned, infrequently burned, and unburned plots, respectively.

than at either equilibrium state because both energy and nitrogen availability are increased during that year. Recent comparisons of NPP data from annually burned sites, long-term unburned sites, and intermittently burned sites have confirmed this transient response (fig. 2) (Ojima et al. 1990; Seastedt et al. 1991).

RELEVANCE OF MODEL TO ECOSYSTEM PROPERTIES OF TALLGRASS PRAIRIE

Soils beneath tallgrass prairie contain an immense amount of soil organic matter and nitrogen (Jenny 1930, 1980; Brady 1974; Post et al. 1982). Paired plots (fig. 3) and global averages (fig. 4) indicate that temperate grasslands, in spite of reduced plant productivity, are superior soil carbon sinks when compared to forests with similar climatic characteristics. These large amounts of stored carbon in grassland soils reflect fundamental differences in shoot/root allocation strategies and root depth distributions between grasses and trees, and differences in decomposition rates of plant detritus in these two systems. A moderately frequent fire interval in grasslands is the key to this productivity, with the postfire vegetation increasing carbon inputs via new root growth (generated, in part, by the high nitrogen and water demand created by fire) and via the removal of sufficient amounts of soil moisture such that microbial decomposition processes are slowed (Buyanovsky et al. 1987). As these roots are low in nitrogen content, microbes colonizing senescent roots will remove additional nitrogen from the soil. This activity also contributes to intermittent nitrogen limitations, depending on fire frequency, that further alter plant shoot/root growth strategies. Hence, the combined activities of fire, plants, and microbes ultimately produce a very large

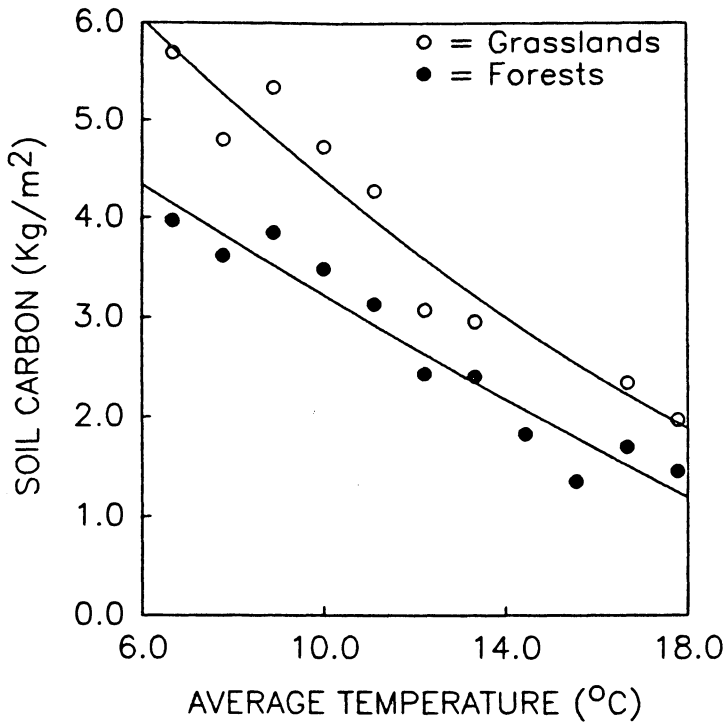


FIG. 3.—Paired plot comparisons of soil carbon in the top 15 cm of grassland and forest soils across a temperature gradient. The graph was constructed from nitrogen and carbon-to-nitrogen ratio data reported in Jenny (1930).

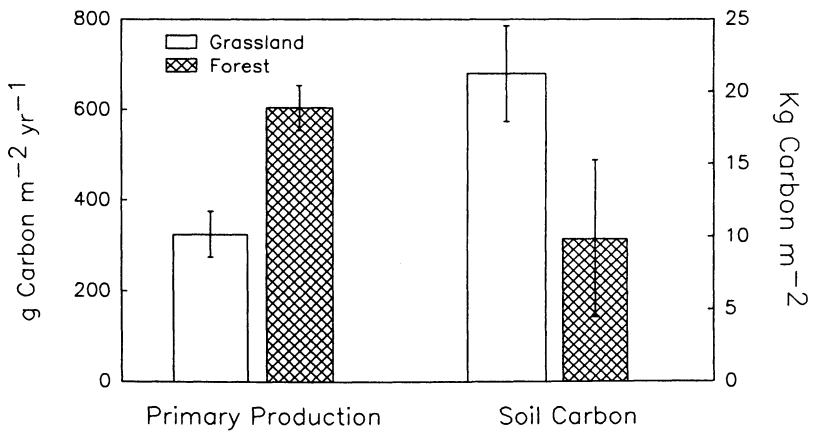


FIG. 4.—Estimates of plant net primary productivity (NPP) and soil carbon amounts in temperate grasslands and forests. These data were compiled from table 10.4 of Melillo et al. (1990).

amount of soil carbon, more than is produced by either a forest under the same environmental conditions or, presumably, in a hypothetical grassland that has been unburned or annually burned exclusively.

This large reservoir of soil carbon in the tallgrass region suggests that, historically, grazing by large ungulates (especially bison) was also an infrequent or a pulsed activity. Chronic, heavy grazing reduces overall plant productivity (Aldous 1930) and, in particular, substantially reduces root production (Weaver 1958). Soils are warmed after grazing (similar to the response observed for spring fires), but fewer deep roots result in reduced evapotranspiration losses. Hence, such soils have potentially lower carbon inputs and a warmer, moister, potentially superior environment for microbial decomposition processes. Chronic grazing on a time scale of decades to centuries may reduce long-term productivity via losses of soil organic matter and associated nitrogen- and water-holding capacity (Bauer et al. 1987; Parton et al. 1987). Chronic grazing can also reduce nitrogen immobilization in soil and increase inorganic nitrogen availability (Holland and Detling 1990), which thereby reduces the role of nitrogen as a limiting factor and contributes to changes in plant species composition that reduce long-term productivity (see, e.g., Owensby et al. 1970).

If, however, grazing occurs at infrequent intervals, grazing creates transient maxima in NPP very similar to the fire response (Turner et al., in press). Even chronically, light-to-moderately grazed prairie may contain infrequently grazed patches; that is, not all areas are grazed each year (Hobbs et al. 1991). Grazing opens the canopy, maintains the foliage in a young physiological state, improves water relations for photosynthesis, and increases nitrogen availability to plant roots (Holland and Detling 1990). Plants reallocate carbon to new foliage rather than to roots, and this reallocation can increase foliage production in the year of grazing by a significant percentage (Turner et al., in press). However, the long-term cost of this excess carbon and nitrogen allocation to foliage is a subsequent decline in production if the system is not allowed to recover and restore belowground root and rhizome reserves; that is, subsequent grazing will have at most a neutral or negative effect on foliage production (Turner et al., in press). Hence, infrequent grazing, like infrequent fire, creates a transient maxima in system productivity. The grazing-generated pulse is probably limited to the aboveground plant response and has a neutral or negative effect on soil organic matter accumulation.

Grazing of foliage also induces a pulse of consumer biomass observed in soil-dwelling fauna (Roberts and Morton 1985; Seastedt et al. 1988). As in responses described above, this transient maximum in consumer production appears to be generated by changes in energy (fixed carbon) and nitrogen content of roots and root detritus (Seastedt et al. 1988). The sustainability of this response has not been studied, but, similar to aboveground grazing, the increase in consumer production is likely ephemeral because of the nonsustainability of root energy inputs under chronic grazing. In contrast to examples discussed previously, root herbivory represents a situation in which resource switching (from an energy-limited to a water- and nutrient-limited state by the destruction of live roots) fails to produce a transient maximum response in plant processes. In this case the herbivores interfere with the plants' ability to exploit additional quantities of essential but

nonlimiting resources (i.e., root damage does not allow the accumulation of water or nitrogen to be exploited). However, nongrazed species or species invading gaps produced by root grazers may exhibit the transient production response by exploiting water and nutrients unavailable to root-damaged species (Reichman et al., in press).

OTHER APPLICATIONS AND ADDED COMPLEXITY

Application of the transient maxima model to variations in resource availability and demand under nonequilibrium conditions is not limited to traditionally defined units of mass and energy. Plant species differ markedly in their ability to respond to specific combinations of water, energy, and nutrient availability (Tilman 1982), and this diversity provides an additional dimension to the simple responses of single species or single groups of species. In an idealized comparison of species diversity as a function of niche availability (an ecological resource) in successional systems, species richness will be limited by a lack of early successional species in mature communities and by a lack of late successional species in pioneer communities. Following a disturbance, the decrease in late successional and increase in early successional niches may be equally rapid, but later increases and decreases in these respective niches are more gradual, which results in a transient period when species diversity is highest because members of both groups are present. This is the mechanism (greatly simplified) proposed for the intermediate disturbance hypothesis (Huston 1979). Long-term climatic shifts have, in similar fashion, left relic species (present, but not necessarily reproducing sexually) in certain biome types that contribute to the species diversity of a given area.

Many ecological systems in transition require more than just two limiting resources, or complex interactions among resources, or the inclusion of additional "biological resources." Predictions of transient maxima responses from this model can be made even with increased complexity given that these complexing factors can be quantified. For example, in forested systems that are placed in nonequilibrium by clear-cutting, sunlight, nutrients, and water availability may be increased rapidly, while leaf area responds more slowly. However, the increase in leaf area is more rapid than reductions in these other resources so that a nonsustainable period of very high NPP occurs prior to reaching an equilibrium state (see Marks 1974; Covington and Aber 1980; Waring and Schlesinger 1985).

Recognition that transient maxima caused by favorable combinations of resources can occur in most biological systems allows for a more mechanistic approach to nonequilibrium phenomena. For example, the overcompensation growth response by plants that are partially consumed by herbivores remains controversial (Belsky 1986, 1987; McNaughton 1986). Plant responses following herbivory are decidedly nonequilibrium, and a rigorous analysis of changes in pre- and postherbivory resource availability provides a framework for more definitive studies (Maschinski and Whitham 1989). Note that the species best known for overcompensation, the scarlet gilia (Paige and Whitham 1987), is a perennial plant that exhibits the overcompensation response in the second year of existence. Similar to the grassland example, chronic grazing would not produce this re-

sponse. Here, however, the alteration in resource limitation induces a maximization response that appears to be under genetic as well as simple physiological responses. The benefits of withholding plant resources until the "switch" has occurred may have had sufficient, directional selection pressure to have been genetically encoded in this and other species.

The concept that many communities exhibit nonequilibrium characteristics is certainly not new (see Wiens 1984; Westoby et al. 1989). However, an analysis of the mechanisms responsible for generating a near-constant state of instability and the patterns resulting from this activity have not been previously identified. Fluctuations in limiting resources across multiple time scales are the underlying cause of ecophysiological and ecosystem behaviors seen in semihumid and humid grasslands. Although grasslands have been the focus of our research, other systems such as the northern taiga also exhibit similar characteristics as a result of interactions of fire, climate, and topography (Van Cleve et al. 1983). Nonequilibrium pulses in plant growth would provide a partial explanation for the widespread occurrence of nitrogen limitation in terrestrial and aquatic ecosystems (see, e.g., Vitousek and Howarth 1991). If increasing levels of atmospheric carbon dioxide are creating a transient pulse in global productivity, then nitrogen limitation should also be widespread.

Recognition that transient maxima responses may occur on multiple time scales in all ecological systems in transition is crucial for ecologists and other scientists evaluating and predicting climate change responses. At the leaf and whole-plant level, physiologists have already recognized the nonsustainable nature of photosynthetic and production increases in plants exposed to elevated carbon dioxide (Oechel and Strain 1985). Acclimation of plant physiological characteristics to alterations in resource availability and demand is a likely mechanism for this nonsustainable response. On broader scales, predicted local and regional responses to directional changes in carbon dioxide, temperature, and rainfall must be tempered by the recognition that system responses may be short-lived and nonsustainable as long as limiting resources are in a nonequilibrium state.

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