

Environmental responses of plants and ecosystems as predictors of the impact of global change

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Abstract. An understanding of plant responses to fluctuations in environment is critical to predictions of plant and ecosystem responses to climate change. In the northern hemisphere, the northern limits of distribution of major biomes are probably determined by the tolerance of their dominant physiognomic types (e.g., deciduous hardwood trees) to minimum winter temperatures and can thus be predicted from long-term patterns of temperature fluctuations. At a more detailed level, the responses of functional groups of plants to altered climate can be predicted from their known responses to fluctuations in soil resources (nutrients and water) and the expected effect of climatic change on these soil resources. Laboratory and field experiments demonstrate the feasibility of this approach.

Keywords. Climate change; growth rate; plasticity.

Introduction

One of the most basic observations in ecology is that the environment is variable in both time and space, making it difficult to predict the future environment or vegetation response. However, physiological plasticity enables organisms to adjust to environmental variation (Bradshaw 1963). Therefore, even if the environment changes substantially, it still may be within the tolerance limits of resident organisms. In this article we address the question of how environmental tolerance of plants can be used to predict their responses and those of ecosystems to climatic change. There are two basic sources of information on which to base these predictions: (i) the relationship of plant distribution to present environment and (ii) observations on the responses of plants to natural or manipulated changes in environment.

Vegetation correlations with climate

Climatic extremes appear more important than climatic averages in predicting patterns of vegetation distribution. The poleward limits of many tree species are determined by frost sensitivity and freezing tolerance (Sakai and Weiser 1973). For example, -40°C is the lower limit of supercooling for most ring-porous hardwood trees. Below this temperature intracellular freezing occurs, killing the cells and therefore the organism. The northern limit of these tree species correlates closely with the record low temperature of -40°C (Sakai and Weiser 1973). Conifers, which have a different mechanism of freezing tolerance, can withstand the temperature of

liquid nitrogen and have a correspondingly more extreme latitudinal limit to their distribution (Woodward 1987). Similarly, chilling-sensitive broad-leaved tropical evergreen trees are killed at 15°C, and their poleward limit coincides with record low temperatures of 15°C (Woodward 1987). Woodward (1987) recognized several major physiognomic types of vegetation: conifer forest, deciduous forests, broad-leaved evergreen forests, shrubland, and herb-dominated vegetation, based on the assumptions that climate governs the low-temperature or low-moisture limit of distribution, and that the mesic limits of distribution are determined by the environmental tolerance of a competitively superior but less tolerant physiognomic type, Woodward (1987) successfully predicted the global distribution of most major physiognomic types of vegetation. These observations suggest that the low-temperature or low-moisture limit of a physiognomic type is governed by the fundamental niche (i.e., physiological tolerance) of the plants, whereas additional limits of plant distribution may be determined by other, more complex factors, probably mediated by competition. These patterns also indicate that extreme events, which are a function of environmental fluctuation, are more useful than average conditions in predicting northern limits of physiognomic types. As climate changes, the location and frequency of these extreme events will certainly change, leading to changes in distribution of biomes. Thus, understanding of patterns of environmental variability are critical to predictions of future vegetation distribution.

Although extreme events predict distributions of general physiognomic types, they are inadequate to predict finer distribution patterns of species or functional groups of species, i.e., groups of species which show similar responses to change in environment. The greater diversity of response by species than by physiognomic types occurs because each species has a unique range of environmental conditions under which it occurs (Gleason 1927; Whittaker 1975), which seldom coincides precisely with their limits of physiological tolerance (Sakai and Weiser 1973).

Correlation of the current distribution of plants with their current average climatic conditions has been the main basis of explaining past patterns of vegetation change (Davis 1981; COHMAP 1988) and predictions of future vegetation distribution (Solomon 1986; Pastor and Post 1988; Cohen and Pastor 1991; Overpeck *et al* 1990). These studies have led to several important generalizations: (i) Each species shows a unique pattern of distribution with climate and responds most strongly to different patterns of climatic factors, so that complex climatic changes cause species to migrate with different patterns and to form new associations. Thus, current plant communities are temporary associations among species that last only hundreds or a few thousand years. These communities did not exist as entities in the past, and there is no reason to expect their continued coexistence in the future. Because of the highly individualistic response of species to climate and because this response depends on interactions with other species in the community, it is difficult to determine which aspects of climate are particularly critical to the distribution of a species, making predictions of future distribution difficult. (ii) Changes in the distribution of a species may lag significantly behind climatic changes where dispersal limits the rate of species migration (Davis 1981). Thus, predictions of the future response to climate requires some understanding of factors governing the regeneration phase. (iii) Projections of the future response of vegetation to climate are quite sensitive to availability of soil resources (Pastor and Post 1988; Cohen and Pastor 1991), so that knowledge of climate alone is inadequate to predict future species distribution. (iv) Finally, in complex and more diverse communities such as

dry or wet tropical forest there are so many important species that we can never hope to understand their climatic controls well enough to predict future vegetation changes. What is needed is a simplified classification of species into functional groups whose environmental controls can be predicted from general ecological principles (Grime *et al* 1988; IGBP 1990a; Chapin 1993). The question is whether there are any predictable responses of groups of species that make a functional-group classification practical.

3. Vegetation correlation with resources

Given the difficulties of predicting direct species responses to climate and the importance of soil resources in mediating plant responses to climate, the correlation of vegetation with soil resources may provide an effective means of predicting the response of functional groups of plants to climate change (figure 1; Hobbie *et al* 1993). Soil resource availability will respond in predictable ways to altered climate. In cold climates, increased temperature will stimulate microbial activity and nutrient cycling, thus increasing the availability of commonly limiting nutrients such as nitrogen and phosphorus (Chapin *et al* 1992). In temperate mesic-to-dry climates, increased temperature and potential evapotranspiration combined with moderate changes in precipitation will decrease soil moisture in mid-continental regions (IGBP 1990b). In tropical coastal dry climates, moderate increases in temperature with high variations in precipitation are expected (Bullock 1986; de Ita-Martinez and Barradas 1986; Garcia-Oliva *et al* 1991; Liverman and O'Brian 1991), as observed in the past (figure 2). Rates of nutrient cycling correlate closely with availability of most soil resources. Forest clearing for agriculture creates early successional habitat with associated increases in light availability. Local and regional variations in climatic projections and soil fertility provide logical bases for refining these predictions. The major point is that patterns of change in soil resources can be predicted from defined scenarios of climatic change (figure 1). Soil moisture responds readily and predictably to changes in climate (e.g., IGBP 1990b). However, considerable research is necessary to determine to the magnitude and timing of the response of soil fertility to changes in climate. At present it is also difficult to predict how changes in the seasonality of climate affect soil resources

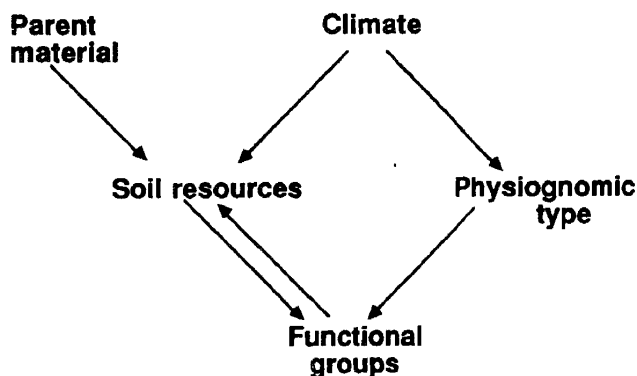


Figure 1. Interrelationship between climate, soil resources, and functional groups of organisms.

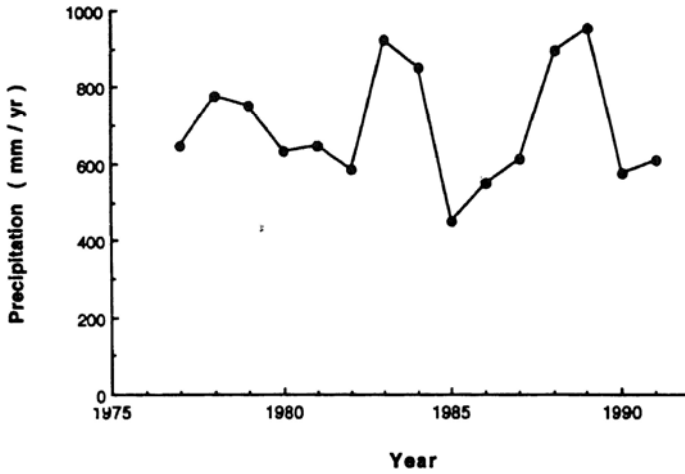


Figure 2. Total annual precipitation of the last fifteen years at the tropical deciduous forest in the Biological Reserve of Chamela, Jalisco, Mexico ($19^{\circ}30'N$, $105^{\circ}03'W$).

and the plant phenological patterns necessary to exploit these soil resources effectively.

Changes in availability of soil resources lead to predictable changes in the types of plants that can be expected (Grime 1977; Chapin 1980; Tilman 1988). In brief, high-resource environments support a high relative growth rate (RGR) through high capacities for photosynthesis and nutrient uptake, which in turn require high tissue-nitrogen concentrations (figure 3; Chapin 1980; Field and Mooney 1986). Continued high rates of resource capture require high rates of root and leaf turnover, a process that can be supported at relatively low cost in a high-resource environment (Bloom *et al* 1985; Chapin *et al* 1987). Conversely, in low-resource environments there are inadequate resources to support rapid growth, so plants are constrained to grow slowly and are likely to achieve a small size. Because of low tissue-nutrient concentrations, plants in low-resource environments have low potentials to photosynthesize, transpire, and absorb nutrients. Plants in these

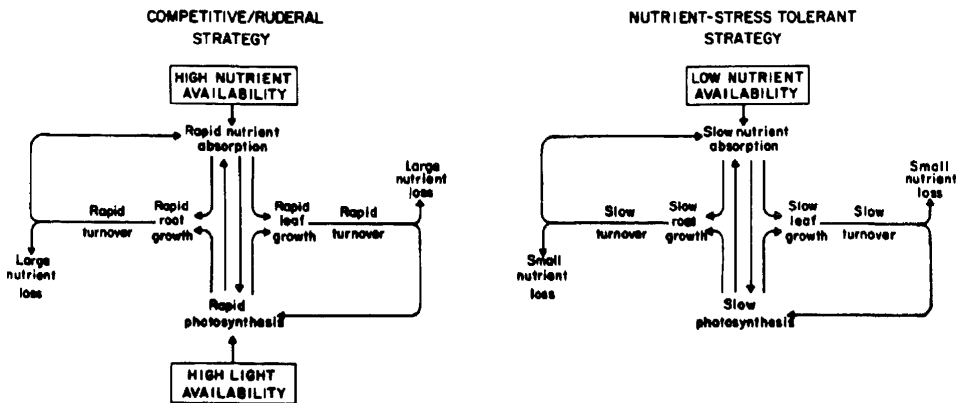


Figure 3. The relationships among physiological traits in plants from high- and low-resource environments (modified from Chapin 1980).

environments have high root-to-shoot ratios to maximize capture of scarce soil resources. Tissue-turnover rates are low, causing tissue nutrients to be retained for a long time but also requiring effective chemical defense against herbivores and pathogens. These chemical defenses reduce litter quality and reinforce the low nutrient availability in these sites (Chapin 1991).

Experimental evidence supporting these predictions has emerged mainly from studies in temperate ecosystems (Chapin 1980; Grime *et al* 1988; Grime 1991; Robinson 1991; Rorison 1991), although recent studies in tropical rain forests (Augsburger 1984; Walters and Field 1987; Sanchez-Coronado *et al* 1989) suggest similar patterns with respect to relative growth rate, root-shoot ratios and mineral nutrient requirements. Less is known about the highly diverse tropical deciduous forest in which the availability of soil resources is restricted by seasonal drought. In these forests tree-seedlings occupying resource-rich disturbed areas (e.g., *Heliocarpus pallidus*) show high relative growth rates, high demands for mineral nutrients and a low root/shoot ratio (Huante *et al* 1992). These species also tend to be more sensitive to water and mineral nutrient stress (E Rincon, unpublished data).

In conclusion, if our objective is to predict future distribution of general functional groups of plants, this is done most readily by predicting how climate will alter resources and how these resources affect different types of plants (figure 4) rather than by trying to predict direct climatic effects on distribution of functional groups (Hobbie *et al* 1993). We suggest that functional groups can be defined which are similar in their response to several resources, whereas it may be more difficult to define functional groups with respect to climate (Chapin 1993). This concept of generalized functional groups can be tested using standardized comparative studies (Grime *et al* 1988) in which the plasticity of key physiological traits (e.g., resource capture and growth) is documented as a function of various soil resources.

4. Environmental responses of individual plants

Differences in resource requirements determine plant response to environmental fluctuations. Plants adapted to high availability of soil resources are sensitive to changes in nutrient supply (Grime 1977; Chapin 1980; Shipley and Keddy 1988; Campbell and Grime 1989) and other resources such as light and water (Rincon and Grime 1989). In these habitats plants respond plastically to localized depletion zones around root systems through morphological changes in roots (Drew and Saker 1975; Crick and Grime 1987), resulting in reallocation of absorptive surfaces from depleted zones into the resource-rich areas. This system of patch exploitation requires shoots and roots with a short life span and high rate of tissue turnover. A high degree of morphological plasticity associated with active foraging will be of selective advantage only where it promotes access to large reserves of light, water, and mineral nutrients (Grime *et al* 1986). Conversely, in habitats where productivity is chronically resource-limited, there is less morphological plasticity. On infertile soils we expect that resource capture and survival will depend on successful exploitation of resource pulses. In unproductive habitats, in which growth is frequently uncoupled from resource capture, plasticity would involve reversible physiological changes (acclimation; Crick and Grime 1987; Rincon and Grime 1989; Campbell and Grime 1989; Jackson *et al* 1990) rather than reallocation of biomass

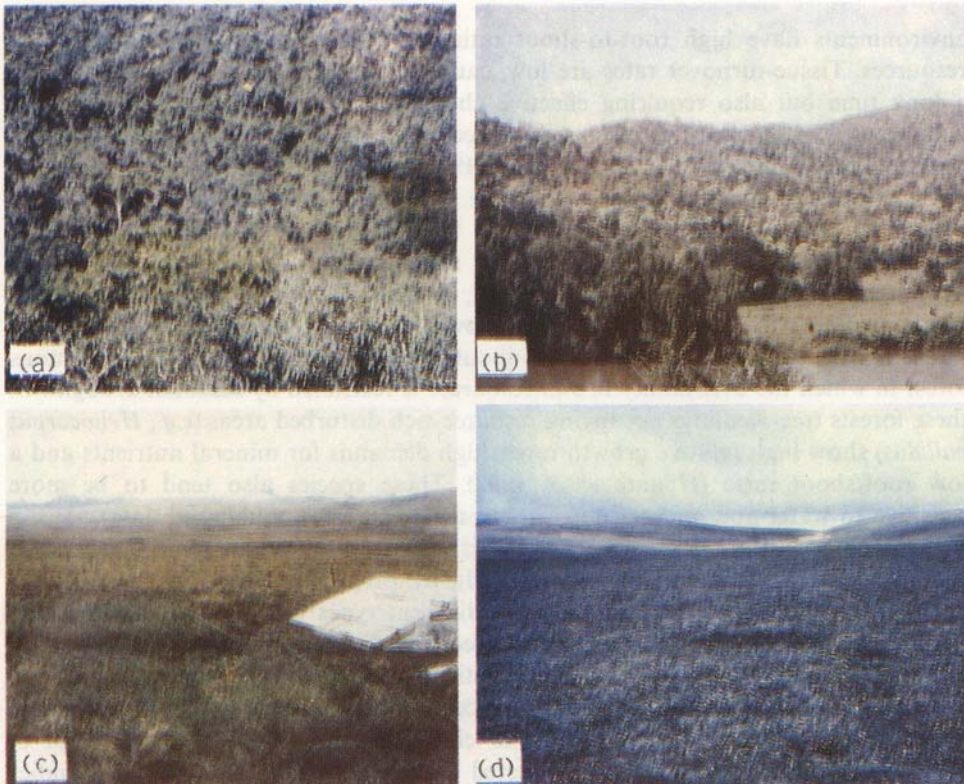


Figure 4. (a) Vegetation of dry tropical forest at Chamela in western Mexico, showing a variety of dominant growth forms depending on local variation in soil resources. (b) Land use change in dry tropical forest at Chamela. (c) Result of experimental manipulation of temperature in tussock tundra at Toolik Lake, Alaska. The plots to the left of the plastic greenhouses have been exposed to elevated summer temperature (foreground) or elevated temperature with added nutrients (background) for three years. (d) Polar desert at Wrangel Island, Russia. Productivity is expected to increase with climatic warming.

to facilitate exploitation of resource pulses. These generalizations come from screening programs which document the responses of plants to fluctuations in resource supply.

5. Environmental responses of communities

The general predictions of the laboratory experiments described above are consistent with responses of communities to field manipulations. In arctic tundra, when light, temperature, and nutrients were manipulated to simulate patterns expected with climatic change, each species initially showed a species-specific, unique response to our manipulations, which was difficult to predict from general principles (Chapin and Shaver 1985). However, after nine years of treatment, there continued to be species-specific, unpredictable responses to temperature, but relatively predictable responses to nutrients (F S Chapin III and G R Shaver, unpublished): For example *Betula nana* and other rapidly growing deciduous shrubs increased growth in response to nutrient addition, whereas *Ledum palustre* and other slowly growing evergreen species responded negatively to nutrient addition (F S Chapin III and G

R Shaver, unpublished). Similarly, all species except the most shade-tolerant understory species responded negatively to reduction in light intensity. These results suggest several important conclusions. First, the resource responses observed in the field were consistent with predictions of laboratory experiments in that rapidly growing species responded positively to nutrient addition but slowly growing species responded negatively to this improvement in resource supply, presumably through changes in competitive balance. Secondly, it was easier to predict responses to altered resource supply than to altered climate. The relatively minor increase in nutrient availability that occurred nine years after initiation of our temperature treatment (F S Chapin III and G R Shaver, unpublished) suggests that our experiment was too short for climate to strongly alter soil resource supply.

A third result of these experiments was that manipulations which benefited some species reduced the biomass of other species. Therefore, the overall production of the ecosystem was affected much less than the productivity of individual species or functional groups. Thus, the contrasting responses of individual species and functional groups buffer ecosystem processes such as production and nutrient cycling, rendering them relatively resistant to environmental change (Chapin and Shaver 1985).

The buffered response of ecosystem processes is also seen in an unmanipulated tundra ecosystem sampled over a period of years. Over a series of years in which the productivity of individual species varied 2-8-fold, there was no significant variation in productivity of the total community (table 1; Chapin and Shaver 1985).

Addition of water and nutrients to grassland also gives predictable responses by functional groups of species (Lauenroth *et al* 1978). Rapidly growing forbs and grasses responded positively to nutrient and water addition, whereas the more slowly growing cactus responded negatively. Moreover, when grassland production

Table 1. Annual variation in production (% of 5-year mean) of major species (tundra) or functional groups (grassland) and total community aboveground production (calculated from Lauenroth *et al* 1978 and Chapin and Shaver 1985).

	Production (% of average)				
	1968	1969	1970	1978	1981
Tundra					
<i>Eriophorum</i>	77	58	148	101	116
<i>Betula</i>	30	52	55	248	121
<i>Ledum</i>	106	138	62	103	91
<i>Vaccinium</i>	135	172	96	28	71
Total production	93	110	106	84	107
	1970	1971	1972	1973	1974
Grassland					
Warm-season-grasses	113	123	90	92	82
Cool-season-grasses	118	88	132	103	59
Shrubs	74	71	101	137	117
Succulents	82	80	70	149	119
Total production	90	88	96	124	102

was examined over a series of years, the productivity of individual species varied much less than did the productivity of the community as a whole (table 1; Lauenroth *et al* 1978), again indicating the extent to which ecosystem processes are buffered by the compensatory responses of individual species.

6. Summary

In conclusion, we suggest that an understanding of plant response to fluctuations in environment is critical to predicting plant and ecosystem responses to climatic change. The poleward limits of distribution of major biomes are probably determined by the tolerance of their dominant physiognomic types (such as deciduous hardwood trees) to minimum winter temperature and can thus be predicted from long-term patterns of temperature fluctuations (Woodward 1987). By contrast, it is more difficult to predict the responses of individual species to climate, because each species in a community shows a unique response to climate and responds most strongly to different aspects of climate (Davis 1981). Moreover, regeneration properties which determine migration rate may strongly influence the rate at which a species changes its distribution with respect to changing climate.

Climatic change will lead to predictable changes in availability of soil resources. For example, tundra will probably experience increased nutrient availability, mid-continental grasslands will see lower soil moisture, and coastal dry tropical forest will experience increased soil moisture. Because we can define functional groups of plants on the basis of response to fluctuations in resource supply we can predict the responses of these functional groups to altered climate as mediated by climatically driven changes in resource availability. We suggest that this provides a general basis for predicting ecosystem response to climate change.

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