Review

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# Extreme events as shaping physiology, ecology, and evolution of plants: toward a unified definition and evaluation of their consequences

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## Summary

Here we consider how extreme events, particularly climatic and biotic, affect the physiology, development, ecology and evolution of organisms, focusing on plants. The marked effects on organisms are of increasing interest for ecological prediction, given the natural and anthropogenic changes in spectra of extreme events being induced by global change. Yet there is currently a paucity of knowledge or even a common world-view of how extreme events shape individuals, communities and ecosystems. We propose that extreme events need be defined in terms of organismal responses of acclimation and of de-acclimation or hysteresis. From this definition we proceed to develop a number of hypotheses, including that fitness effects of extreme events occur primarily during recovery. We review evidence that, on the evolutionary time scale, selection is virtually absent except during extreme events; these drive strong directional selection, even to trait fixation and speciation. We describe a number of new tools, both conceptual and technological, that are now at hand or that merit rapid development.

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# I. Introduction

Extreme events are not unprecedented but are uncommon and formative. Here we suggest that these events play a disproportionate role in shaping the physiology, ecology and evolution of organisms, with a focus on terrestrial plants. To evaluate this role, we require first a definition of what constitutes an extreme event; this has varied widely in the literature. In part, this is a result of comparing divergent types of events – climatic extremes, physical disturbances, insect outbreaks and invasions by exotic species, as examples. Extremity also occurs on multiple time scales, as may be expressed in the 50-yr flood, the 500-yr flood, and so on. Extreme events are also notoriously difficult to capture 'in the act', because they have large stochastic components. Stochasticity challenges researchers as much as it challenges organisms to respond adaptively. The frequency and likelihood of a given type of extreme is not well known: the statistical characterizations of extreme events, while showing some remarkable regularities (e.g. Gaines & Denny, 1993), are incomplete and, in some cases, adherent to flawed models (Katz *et al.*, 2002). Therefore, their detailed actions have been studied often anecdotally rather than systematically. Finally, the lack of a precise and biologically meaningful definition of extreme events may have impeded adequate scientific discourse in some important phenomena, including prolonged recovery phases, or genetic constraints in population responses.

Toward the goal of evaluating the roles of extreme events in the physiology, ecology and evolution of organisms, we offer an organism-based definition of extremity. To date, most discussion of extreme events has aimed at the statistical description (e.g. Pickett & White, 1985), often in terms of driving variables such as climate, while we argue here that a definition based on processes within organisms is needed. Other discussions also clustered on the level of ecosystems; some detailed discussion of issues of scale have been offered (e.g. Allen & Hoekstra, 1992), but again based on statistical description. We propose, simply, that an extreme event is an episode in which the acclimatory capacities of an organism are substantially exceeded. Consequently, after the event passes, the organism (or population) exhibits physiological and developmental responses to the environment that are significantly different from normal acclimation. As a basic example, leaf photosynthetic (carboxylation) capacity varies exponentially with temperature in normal times. Variations are reversible as the temperature returns to any given value. An excursion to temperatures that are abnormally low or high, after accounting for normal seasonal acclimation, often results in lower capacity at all subsequent temperatures, for an extended time (Havaux, 1993). Greater excursions lead to greater persistent effects; extremity can thus have a continuous distribution, appropriate to descriptions on various scales of time (*return times*: Gaines & Denny, 1993) or of space. Extremity is distinguished from simple stress, which can include extremity but most often covers reversible, fast down-regulation with no persistent after-effects.

An important aspect of our definition is that the recovery phase is commonly prolonged. We propose that the greatest part of effects on fitness accrue during the recovery phase. Moreover, we propose that long-term net directional selection on most traits is nearly zero except for a small subset of traits largely selected by extreme events. We provide arguments for this view in Section V. First, we cite mechanistic studies in physiology, development, and ecology. Second, we argue that excess genetic deaths would be insupportable if selection were to be significant on a large number of traits (cf. Kimura, 1983). We argue why highly selected traits include not only traits for tolerance of the extreme but also traits for acquisition and usage efficiency of resources.

A focus on extreme events is timely, in view of global change. The global 'fingerprint' of climate change, viewed in its own right as a century-scale extreme, is already evident in plant phenology (Myneni *et al.*, 1997; and phenology of many taxa globally (Parmesan & Yohe, 2003; Root *et al.*, 2003). Biogeographic distributions may be poised to change markedly from climate change directly (Neilson, 1993; Solomon & Kirilenko, 1997; larger context by Holt, 2003), perhaps primarily from changes in extremes of weather rather than from changes in mean climatic variables that are commonly used in biogeographic predictions (Loehle & LeBlanc, 1996). New distributions of diseases and vectors (Djurle *et al.*, 1996; Sutherst, 1998) or human introductions of exotica (Kokko & Sutherland, 2001) constitute new biotic extremes.

We review the utility of a process-based, organismal-based definition of extreme events. We then elaborate on a number of challenges in characterizing extreme events. We close by describing ways to meet these challenges with new tools (such as environmental monitoring arrays and novel genetic analyses, etc.) and with effective ways to use many existing tools. Our examples are drawn from the plant kingdom, given our backgrounds and the current venue, but many extensions to other kingdoms are noted.

# II. Moving to an organismally based definition of extreme events

## 1. Contingent effects on the organism are more important than driving variables

It is tempting to describe extremity in terms of environmental variables that drive organismal responses. In part, this is because these variables seem to be closely related to organismal responses and because the statistical distributions of these driving variables, hence their extremes, appear to be well known. Both of these ideas are misleading, however, as we will show in the course of this review. Organisms acclimate on numerous time scales, such that a temperature of 40°C – or 0°C – may be extreme in one season and normal in another.

**Fig. 1** Leaf development in creosotebush, *Larrea tridentata*, showing responses to extreme events. Julian date is computed from beginning of the year 1996. LAnorm is leaf area of one individual shrub, normalized to its long-term average, and computed from image analysis; RWC, leaf relative water content; SWC, soil water content, as volumetric fraction, in top 90 cm; T[min], daily minimum air temperature; P, precipitation in mm on any day. The five quantities are not all recorded at the same discrete times. Collapse of leaf area by leaf loss and folding is noted at points labelled '4', where T[min] either drops below −5°C or drops rapidly (Julian date 683) to near 0°C. Points labelled '1' represent positive extremes of high water availability. From Gutschick *et al.*, unpublished.
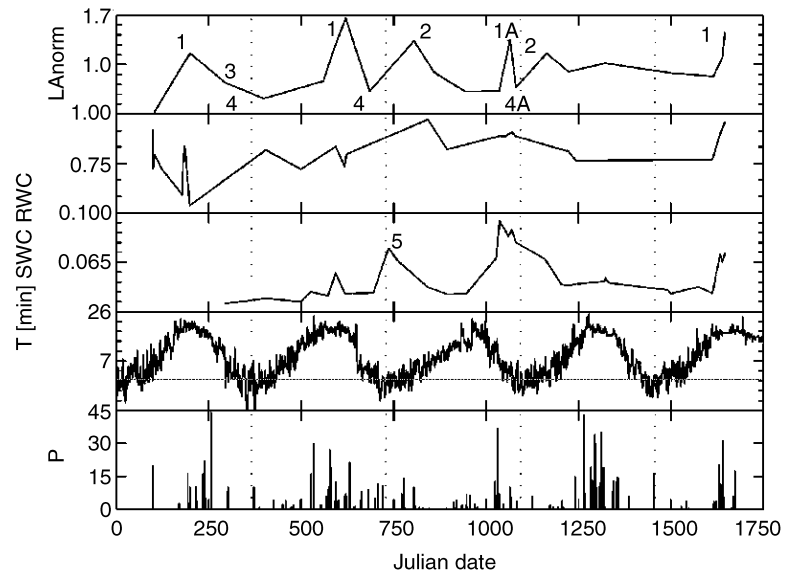
**Fig. 2** Disparate responses of two chaparral shrub species to severe drought at Sky Oaks, CA, USA, measured optically with a tram traversing a 100-m path, as vegetation greenness via reflectances at two wavelengths (in nm) (R750 − R705)/ (R750 + R705). Evergreen manzanita, *Arctostaphylos pungens*, acclimates late and has delayed recovery, behaving as if drought is an extreme event. Semi-deciduous chamise, *Adenostoma vesiculatum*, acclimates continuously and recovers without hysteresis, behaving as if stressed but not experiencing an extreme. Courtesy of D. Sims, California State University, Los Angeles, CA, USA.
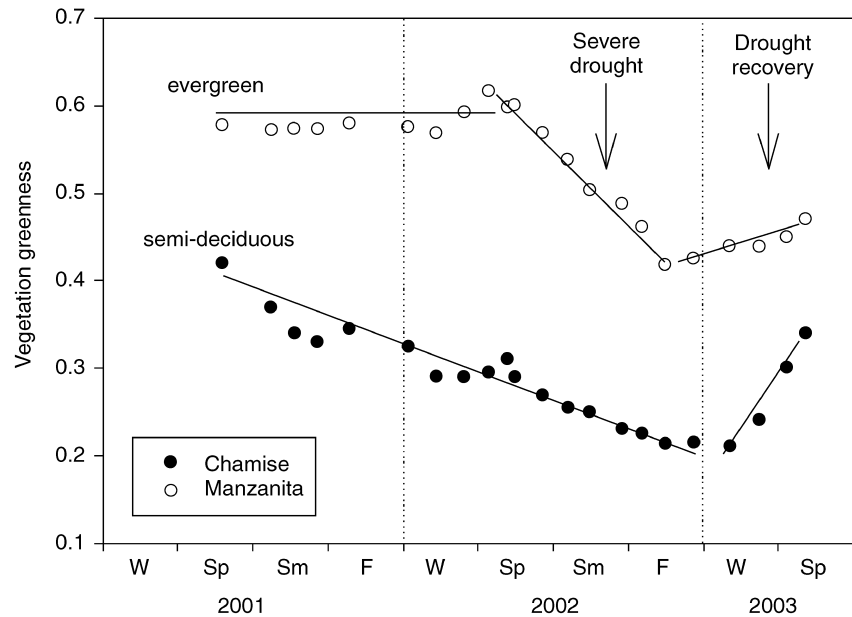
This can be seen on a rather fine scale in Fig. 1, where leaf loss and folding occurs at −5°C in one winter, but at 0°C in another winter when temperatures drop too rapidly for effective acclimation. Clearly, quantitative descriptions or models of plant responses must remove smooth trends in temperature to which plants acclimate, but not faster components. However, what is the proper degree of removing such trends in environmental variables? Again we must turn to the organism and not the environment alone. Different species in the same location and even different individuals are exposed to different conditions; marked temperature profiles occur within vegetation canopies (Jones, 1992). The individuals and species also differ in their acclimation capacities. Figure 2 illustrates strong differences in drought

acclimation in two co-occurring plants of the chaparral, with only one showing rapid recovery. One species is stressed, 'normally', while the other may be said to experience an extreme event.

Even more so than for temperature, it is inherently problematic to define extremes of drought without reference to the organisms themselves. Drought in arid zones may appear extreme to a maladapted human observer or for an introduced organism such as an irrigated crop plant, while native plants acclimate well and respond as if drought were normal. Plants native to arid zones suffer no notable changes in fitness from drought, provided it is within the range to which they acclimate well. We might say, no *contingent* effects: even though the degree of water stress may vary over an extended time
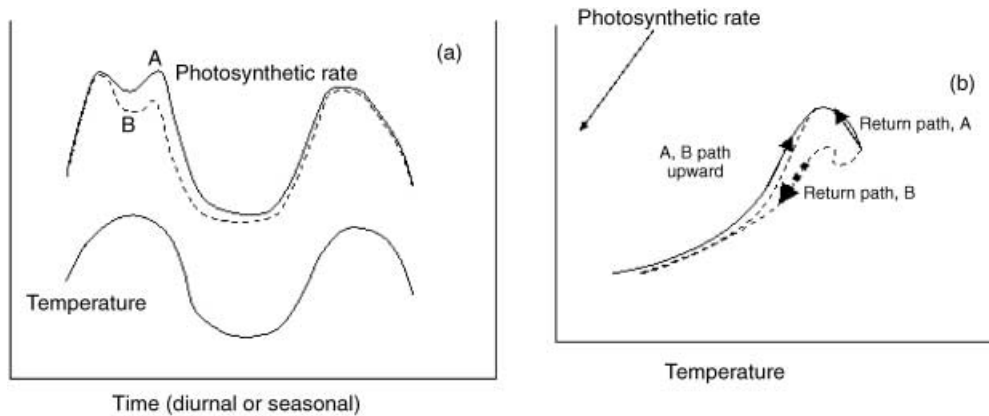
**Fig. 3** Schematic of differences between stress and an extreme event, with notional data on leaf photosynthetic rates (no units). Both plants A and B experience identical temperatures; A acclimates continuously and shows no hysteresis as temperatures cycle; B experiences peak temperature on first cycle as an extreme event and shows hysteresis, or a change in response to temperature after the event. Fig. 3b replots the responses as trajectories of photosynthetic rate in temperature as driving variable. Plant A returns on the same path as on the original upswing in temperature; plant B deviates on the return path and slowly returns to original path on the second temperature cycle.

course, most of this course may be defined as normal, if we can predict growth, seed set, etc. without reference to the order of events. An extreme leaves a legacy in which the physiology and development have an altered relation to the immediate environment. This alteration arises from acclimation capacity being exceeded, in rate or in magnitude. To be extreme, drought must be unusually prolonged or unusually 'deep.' Prolongation is to be measured as beyond the mean for a chosen time interval, such as 10 yrs.

To illustrate how incomplete acclimation leads to contingent effects, we return to the simpler case of temperature in Fig. 3, using notional data. Over the course of a day (or a season; our time scale can be either), plant *A* varies widely in photosynthetic rate and even suffers high-temperature stress in the middle of the time interval. Plant *B* suffers an extreme: the peak temperatures induce a lingering depression of photosynthetic rate, such that a return to any given normal temperature does not result in the same photosynthetic rate as did that temperature on the upswing. Such patterns can be discerned in published data (Havaux, 1993; Hamerlynck *et al.*, 2000).

Extreme events can also be positive, presenting an unusual availability of resources. An example is the El Niño event of 1983 that enabled Darwin's finches (two *Geospiza* species) in the Galapagos Islands to have as many as 10 clutches rather than their normal five (Grant *et al.*, 2000). Episodic changes in oceanic currents have similar effects on selected marine animals (Tanasichuk, 1998). Disturbances such as fire or road-cutting can mobilize large quantities of nutrients for ruderal plants, which consequently show very high growth rates and seed sets. In this case, the measure of extremity of an event is the extent to which its magnitude or its rapidity precludes full use of the opportunity. For many (most?) wild plants, high nutrient availability appears to be such an extreme, in that they respond minimally (Chapin, 1980; Aerts & Chapin, 2000), unlike ruderals and the well-studied crop plants

chosen from among them. The extremity can be amplified by competition for resources during the pulse of resources (Goldberg & Novaplansky, 1997). A larger pulse, used better by competitors, can add to the extremity, or show a second, biotic dimension to the extremity. Competition can also occur during drought, with resources such as water being used for survival rather than growth. Competition need not be direct: for example, water availability to a chosen organism may be affected primarily by abiotic processes of evaporation and drainage (*ibid.*).

Extremity, as a set of effects on physiology, ecology and evolution, will therefore be seen as a quantitative variable, increasing in effect with degree of deviation from the norm, but not as a qualitative variable with a sudden an obvious threshold in its effects. The onset of steep penalties in fitness with increasing duration or depth is only apparent with attention to quantitative detail. Consider the performance of the shrub *Larrea tridentata* in the Chihuahuan Desert. During drought it loses photosynthetic capacity, and also leaf area (Fig. 1). Over several years, the duration and depth of drought varies, as does the degree of leaf loss. How does the degree of leaf loss relate to the increasing loss of fitness? This is not yet known. It is also notable that acclimation capacities and adaptations in populations of native organisms are to be evaluated in complexes of traits, not in individual traits. The co-occurring native species have divergent combinations of traits that define effective strategies of coping with the environment (Gutschick, 1987; Meinzer, 2003; Suding, Goldberg & Hartman, 2003).

## 2. Quantifying contingent effects of extremes, or hysteresis in organismal responses

The lags in acclimation or incompleteness in acclimation that lead to persistent effects on performance need to be described
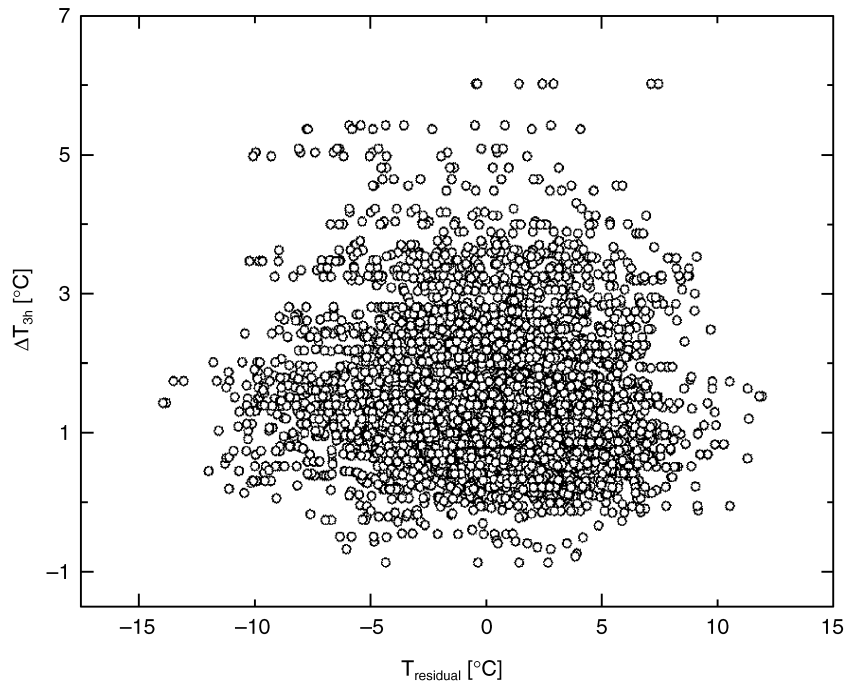
**Fig. 4** Evidence that at least one type of extreme event does not occur more rapidly than do normal events. Data are derived from air temperature T at screen height on the Jornada Experimental Range near Las Cruces, NM, USA. $T_{residual}$ is the deviation of T from average seasonal and diurnal trends each fitted to sine waves; $\Delta T_{3h}$ is the rate of change of T in the preceding 3 h. Note that $\Delta T_{3h}$ does not increase in magnitude at extreme high or low values of $T_{residual}$.

in quantitative fashion. One particularly useful concept is that of hysteresis, which we adapt from the physical sciences. It simply expresses that a system does not retrace its path as a driving variable varies cyclically. A common example is ferromagnetism, in which reversal of an imposed magnetic field does not reverse the magnetism of a specimen except with a considerable lag in magnitude. We may display hysteresis the response of photosynthesis by plant B in Fig. 3, by replotting it as a function of temperature rather than time as the driving variable, obtaining Fig. 3b. Plant A has a unique photosynthetic rate for each temperature, while plant B's rate depends on whether or not the temperature has gone to a high value previously. That is, the response is contingent.

Hysteresis may result from a driving variable changing at a rate that exceeds acclimation rates of the organism (of course, there is always a small lag; one must choose a magnitude of lag or hysteresis as being functionally significant). Hysteresis may also result from an environmental variable exceeding an absolute upper or lower limit of acclimation. The degree of up- or down-regulation of the organismal response is then commonly dependent upon the time spent outside this limit. With regard to rate, it should be noted that extreme events are not necessarily more rapid in development than normal events. Some extreme events do involve more rapid rates of change than normal events, such as changes in atmospheric and oceanic circulation. Dickson (1995) cites examples from air temperatures at Franz Josef Land, salinity in the Labrador Sea and phytoplankton abundances. Yet some mundane extremes as air temperature may show no such rapidity (Fig. 4).

Many other examples of hysteresis exist in plant responses. For example, plants, once droughted, often maintain lower stomatal conductance (e.g. Yeo *et al.*, 1997; Riseman, Jensen & Williams, 2001), deficits in leaf area development (Tardieu *et al.* 1999) and greater sensitivity to later water stress (Maury *et al.*, 1996; Ruiz-Sanchez *et al.*, 2000). Xylem cavitation from drought or freeze-thaw events (Pockman & Sperry, 1997; Martinez-Vilalta & Pockman, 2002) is another clear example. A plant once stressed and partially cavitated does not follow the same pattern of transpiration and assimilation at normal water potentials and temperatures as does a plant that was not stressed. Similarly, flooding and attendant anoxia leaves plants with different uptake capacities for water and nutrients after the flood abates, compared with plants never flooded (Rubio *et al.*, 1997).

Hysteresis should be distinguished from forking of trajectories from chaotic dynamics. Divergent trajectories have been described in ecology, such as multiple steady states in succession (Law & Morton, 1993; Tausch *et al.*, 1993). There is evidence that forking originates in chaotic dynamics, with divergence resulting from very small differences in initial conditions rather than from a resetting of internal state.

To quantify deviations from full acclimation during extremes, we must be able to quantify acclimation to normal conditions. Consider, for example, changes in leaf electron-transport capacity or antioxidant contents that might be measured as responses to average seasonal trends in air temperature. We subtract these normal trends from the net changes observed in any real season in which extremes occur, big or small. The residuals (detrended behaviors) represent

responses to extremes. This is not trivial to do, given that extreme-free seasons are abnormal; controlled conditions may be required. Normal trends need to be recognized in the driving variables. As an example, we may examine variations in air temperature ($T_{air}$) or sea-surface temperature over an entire season. This appears to have both deterministic and stochastic parts. The deterministic part on the seasonal scale is a 'smooth' part, such as the lowest-frequency component in $T_{air}$ in Fig. 1. We cannot, however, take all the stochastic part as representing extremity: first smooth behavior itself can extend to abnormally high levels, and second smooth behavior can be very rapid at times; the rapid drop in minimum temperature in October to November 1998 in Fig. 1 is such a case.

What is deterministic or, better, capable of being acclimated to, must be defined in physiological and developmental terms. This definition brings in the consideration of costs and benefits. Daily temperature fluctuations are commonly over a range as large as changes in mean temperature that occur over several months (Fig. 1). Plants show minimal or negligible acclimation to such daily excursions. While leaf carboxylation capacity might acclimate to a 10°C seasonal rise in leaf temperature with, say, a 15% decrease in rubisco content (a 15% decrease in carboxylation rate, measured at a common reference temperature), it will change minimally over a daily excursion of the same magnitude. Clearly, reallocation of leaf N and other biochemical traits has both finite rates and significant metabolic cost (Hikosaka, 1997). The cost of rapid reallocation on a daily scale would outweigh the benefit of superior gross benefit; the net benefit would be negative (Gutschick, 1987). Thus, we should evaluate the degree of acclimation (its incompleteness) relative to the optimal degree, not the maximal degree possible physiologically if conditions were to remain static.

### 3. The importance of a prolonged recovery phase

Long recovery is obvious after some extremes such as fire. Fires not only remove adults and many propagules; the clearance of vegetation can lead to soil erosion with decadal or longer effects on regeneration of entire communities (Allen & Breshears, 1998). Defoliation by insects can remove dominant plant species and periodically restructure whole ecosystems (Carson & Root, 2000). Also dramatic for recovery dynamics is massive defoliation of clonal goldenrods by chrysomelid beetles (Morrow & Olfelt, 2003). Shoots disappear for years, recovering then from underground stems. Less obvious as constituting prolonged recovery phases are the water and nutrient uptake after a drought ends. Arid-zone species show marked differences in resource acquisition at this time (BassiriRad & Caldwell, 1992a,b; BassiriRad et al., 1999; Gebauer & Ehleringer, 2000).

The greatest extremes may be lethal, in which case the fitness effects occur during the extreme. More commonly, extremes are nonlethal but lead to new balances of costs and benefits to organisms. These altered costs and benefits accrue predominantly in the recovery phase. Many of the changes are in resource acquisition and use, but resource use is commonly small during an event (Goldberg & Novaplansky, 1997). Consider the effect of high-temperature stress that causes reduced photosynthetic capacity and stomatal conductance ($g_s$), in turn decreasing water use (E) and photosynthetic $CO_2$ assimilation (A), and increasing the water-use efficiency (WUE). Let the stress endure for 1 d, with time-averaged changes of −50% in A and +70% in E. For the ensuing week, the time-averaged changes may amount to −20% in A and −30% in E. The time-integrated effects amount to the loss of 1.4 d of photosynthesis and 2.1 d of transpiration, much exceeding the magnitudes of 0.5 d of A and −0.7 d of E during the temperature extreme itself. Droughts may last even longer but also bear their effects during the recovery phase. In shrubs of the Chihuahuan Desert, water stress may become significant at 8% volumetric water content (W) in the top 1 m of soil (Gutschick et al., unpubl.), which may drop to 5% over several months. Both A and E are sharply curtailed. Water-use efficiency may change minimally in some species such as Larrea tridentata. Rainfall terminates the drought, raising W to 13%. The recovery phase, considered to last until W again drops to 5%, may span less than a month. However, this phase entails the use of an 8% swing in W, almost threefold the water consumption during the drought itself, entailing a 3% swing in W.

## III. Features to discern in extreme events

### 1. Cascades of phenomena over time

An extreme event may bear very apparent effects but a host of less-apparent effects. For example, fire in chaparral clearly removes above-ground parts, but it required some time to appreciate its persistent effects on soil temperatures (Frazer & Davis, 1988; Thomas & Davis, 1989) and water relations that strongly interact with regeneration strategies of different species (Williams et al., 1997).

Temporal cascades may also be subtle at the level of the organism. Consider the reduction in leaf area expansion rates caused by water stress, low temperature, or low light levels. These stresses affect cell division and cell elongation during formative periods. Their effects are manifest only 7–10 d later, and are uncorrelated with the environment in the intervening time of maximal expansion (Tardieu et al., 1999). Even the time scale is rescaled by the environment, with phenomena occurring in thermal time (degree-days), for reasons that go to the core of cell-cycle control (Granier, Inze & Tardieu, 2000).

### 2. The importance of concurrent changes in several environmental variables

Extremes of temperature may be obvious to us with our own physiology, but the organisms may respond physiologically to

more subtle combinations of variables. For example, damage to leaves of *Eucalyptus pauciflora* in winter arises not primarily from freezing events but from the co-occurrence of low temperatures and high light intensities that leads to photo-inhibition (Ball *et al.*, 1991; Ball *et al.*, 1997, 2002). This is not a case of multiple stresses (Mooney *et al.* 1991), as neither the high light nor the subfreezing temperatures are themselves very adverse for the plant (*ibid.*). The interaction is critical, and it explains phenomena that otherwise had been taken to represent resource competition with neighboring grasses (*ibid.*). Similarly, levels of $CO_2$ interact with temperature extremes (Lutze *et al.*, 1998; Hamerlynck *et al.*, 2000). Common weather variables such as temperature and cloudiness do show important cross-correlations and temporal correlations (Weber, 1994); these correlations have consequences for productivity and ecological interactions (Strandman *et al.*, 1993).

### 3. Evolutionary constraints to responses in populations

The detailed genetic structures within populations are important. Etterson & Shaw (2001) showed that genetic traits of leaf function and allocation in a native North American forb (*Chamaecrista fasciculata*) are linked. The correlations are antagonistic to the direction of selection in each trait that is most adaptive for climate change, which we may view as an extreme event in progress. Such genetic constraints are likely to be common. In addition to affecting responses to new means – and to new extremes – the constraints affect our ability to predict directions of microevolution from comparing phenotypes in populations along current environmental gradients. These populations evolved with multiple, concurrent gradients of which we are unaware. Further arguments are presented later in this review.

Such microevolution is rarely studied in climate-change experiments, and the genetic limitations and constraints are even less studied. Attempts to quantify the genetic variability and constraints by reciprocal transplantation, common gardens and breeding in controlled environments are problematic. The very structure of such experiments radically changes the spectra of events whose actions we think are important. There is a critical need for ability to trace gene flow and frequency in undisturbed field conditions. Fortunately, some new techniques of population genetics may help materially (Milligan, 2003). We discuss these in more detail in Section VII.4.

### IV. Additional challenges in the study of extreme events

### 1. Shortcomings in statistical descriptions

Our current accounting of the statistics of extreme events has some flaws, which fortunately are being discovered.

Hydrologists have recently demonstrated that the distributions of large floods in various watersheds have 'fat tails', falling off more slowly with flood size than the standard models to which data were fit (Katz, Parlange & Naveau, 2002). Consequently, the return times of large floods are markedly shorter than expected; the 500-yr flood becomes the 50-yr flood. Similar surprises may await us in other meteorological data, and perhaps more so in descriptors of biotic variables. Clearly, the deficiencies are remediable.

The extremes in weather are clearly major drivers of organismal extreme events. We must describe the weather variables' statistical properties accurately, including extremes in combinations of several variables such as temperature and light intensity. Weather-variable extremes are demonstrably sensitive to climate change (Katz & Brown, 1994; Wagner, 1996). Will an increase in mean temperature (Trenberth, 1992) simply shift the entire probability distribution of point-in-time temperatures by the same amount, or will the shape of the distribution change? How will temporal correlations, as in time series of temperatures, change? Given the importance of some long time series for organismal responses, it is important to predict such sequences in a statistical sense, for many time slices. Statistical techniques (*ibid.*; Prichard & Theiler, 1994; Kalvova & Nemesova, 1998; Park *et al.*, 2001) might be termed as insufficiently developed.

We must await some improvements in statistical characterizations of climate, but even basic statistical descriptions show important trends. Recent analyses show that some extremes in weather have increased in magnitude or in frequency, others have declined … and changes are nonuniform across regions, even changing in opposite directions (Easterling *et al.*, 1999, 2000a,b; Meehl *et al.*, 2000). The direct participation of climatologists and weather statisticians is mandated for the study of changes in spectra. This participation is also offered, by our own experience and as witnessed by joint publication of these researchers with ecologists (Easterling *et al.*, 2000b).

### 2. Scaling up in space and time

Scaling up is a topic that occupies a vast literature and that we can only address selectively here. Scaling in time itself invokes new processes: short times concern individual acclimation, longer times invoke community structure and ultimately evolution. We have already noted that acclimation, such as to seasonal weather changes, makes it necessary to de-trend climatic variables when defining extremes of, say, temperature or humidity or soil water content. However, acclimation capacity has limits (from several origins: Gutschick, 1987; this is so, even if plasticity may sometimes have low cost: Dorn, Pyle & Schmitt, 2000). Acclimation capacity necessarily weakens for greater extremes experienced at longer time scales. Long-lived perennial plants, compared with shorter-lived plants, experience greater extremes that recur at longer return times. They may acclimate substantially to most

interannual or even decadal weather trends, but the 100-yr extreme may exceed the acclimatory capacities of almost all individuals. Currently in the Western US, extensive death of dominant trees from drought and coupled insect attack is occurring (D. Breshears, N. Cobb, pers. comm.). Individual acclimation gives way to adaptation via population-genetic changes.

Such genetic changes are far less often accounted in predicting responses of populations, ecosystems, and the biosphere than are responses from better-known fixed physiologies of species. These changes alter our own definitions of extremes. Consider the microevolutionary changes and possibly the speciations induced by aboriginal use of fire for 60 000 yr in Australia (Bowman, 1998) or for a few millenia in North America (Lorimer, 2001; Boyd, 2002). Fire became the norm and not the extreme in these cases, for the new genetic composition. Vegetation has come to tolerate and even require fire for dispersal or even completion of life cycles (Taylor *et al.*, 1998), as also in pine species in North America (Schwilk & Ackerly, 2001). Only under special conditions of extent or repetition interval does fire attain very extreme status in these systems.

The evolutionary responses at long times have rate limitations, just as do acclimatory responses in individuals at short time scales. The limitations are known by the engaging name of the Red Queen effect (van Valen, 1973; Stenseth & Maynard Smith, 1984), which expresses lags in adaptation by all organisms in response to changes in the environment, particularly but not exclusively in the biotic environment (that is, in coevolution). Costs of acclimation are also quantifiable, as excess genetic deaths needed to replace an allele (Wallace, 1981; Kimura, 1983). The analogy with acclimation in the individual is rather strong. The nature of selection by extreme events in contrast with normal events that endure much longer is a subject of much interest in itself; it will be addressed in Sections V.5 and V.6 below.

At the ecological scale in between, there is no simple description or terminology for acclimation or adaptation in a population, community, or ecosystem. Some changes in the way that an ecosystem operates after any event or interval include changes in soil nutrient levels or soil compaction, or in age structure of plant and animal populations that alter their responses to opportunities for colonization or recruitment. Community-scale effects in responses have been documented. One expects altered competition and altered diversity from extreme events that selectively reduce fitness of individuals and species. Neighbor effects vary with the type of disturbance, driving the community along different trajectories of species composition and function (Frelich & Reich, 1999). Nonetheless, a comprehensive framework on the ecological scale is elusive. It remains difficult to conceptualize costs and benefits that apply to a whole population, community, or ecosystem.

The frequencies to which we must pay attention are spatial as well as temporal. Mathematically, events of great spatial extent are of low spatial frequency. Romme *et al.* (1998) argue that large spatial events are fundamentally different in origins and effects from small events. Formation and recolonization of gaps, mostly smaller ones, in vegetation cover caused by fire, death of old dominant trees, etc. have been studied extensively (Bugmann, 2001). Even within this subsampling of events, size is important. For one, large gaps bring into play the limitations on dispersal mechanisms for seeds and other propagules, and differentially so among species. Extremes of dispersal events, such as by large eddies in the atmosphere then become important (Nathan *et al.*, 2002).

Spatial extremes and temporal extremes are commonly the purviews of different groups of researchers. This situation may often be satisfactory – for example, in climatic changes, the temporal sequence may demand more attention than the spatial structure. In complementary fashion, spatial events may be described with only a simple temporal scale – one specifies the time interval in which a hurricane felled trees, for example, but it is not important to know the exact sequence for each treefall. However, spatial and temporal scales interact, such as in outbreaks of herbivorous insects: large-scale outbreaks often involve population cycles of longer duration. Large-scale spatial disturbances create gaps large enough that dispersal into the gap is limited; this raises the importance of seed banks, which represent a coupling to more remote times. In any case, a common framework for considering spatial and temporal events is needed.

## 3. Quantifying stochastic costs and benefits

Not all stochasticity is problematic. Some stochastic excursions in a driving variable such as water potential generate deterministic responses amenable to description within the individual organism. Returning to the example of xylem cavitation in Section II.2, we note that the response may be quite reproducible between repeated stress cycles. However, stochastic costs and benefits that accrue to only some individuals in a population are impossible or not useful to evaluate in a single organism. Rather, they must be evaluated in a population average. This takes us to the ecological and evolutionary scales.

We propose that stochastic responses, with their stochastic costs, are most pronounced when the organism uses surrogate signals of risk. A clear example is photoperiodic control of development, especially of anthesis. Frost is unpredictable from the immediate environmental conditions but it is commonly terminal; terminal drought acts similarly. The balancing of deterministic benefit (continued growth for providing seedfill) against stochastic risk of death has been the subject of rewarding theory and some experiment to date (Cohen, 1966, 1971; Paltridge & Denholm, 1974; Paltridge *et al.*, 1984). In photoperiodic control of anthesis, we note that the stochastic risk of large damage (by early frost or drought) is reduced by enforcement of a conservatively early flowering date. The

organism bears a contrary stochastic risk that growth will cease prematurely, not making maximal use of resources. This latter risk has a different probability distribution, with persistent small risks each growing season. It contrasts with the distribution of risk of damage, dominated by a few large values.

Stochastic risks are changing, as with climate change. Consider photoperiodic responses of plants for germination, flowering, dormancy, and physiological hardening. A photoperiod that in preindustrial times indicated a low risk of late-spring frost in the so-called temperate zones now comes at a time that is warmer. It may be even safer physiologically to break dormancy than in past climates … but the plant has forgone yet earlier breaking of dormancy that is advantageous compared with competitors. In past climatic cooling, a static photoperiodic response had the converse disadvantage, an increased risk of frost damage. These changes are considered in some analyses or models of responses to global climatic change (Saxe *et al.*, 2001).

Both acclimation and evolution can ameliorate the risk. Turning to acclimation first, we consider two types of acclimatory responses. First, changes in developmental programs of plants (more branching when flowering is early) may compensate for reduced time for seed fill, thereby largely preserving seed set (Preston, 1999). Second, organisms respond as well to the immediate environment. They partly override photoperiodic controls, risky as this is with such stochasticity in weather. For example, the photoperiodic response can be modified by current mean temperature or water potential. The latter responses are complex (Heide, 1994). They may be in the wrong direction for climate change, hastening development at higher temperature (Slafer & Rawson, 1996), so that even less of the usable season is exploited. Considerable changes in relative competitive status of species can be expected. The consequent changes in biogeography of species will be much more diverse than those predicted simply (and often inappropriately: Loehle & LeBlanc, 1996) from climatic optima alone.

Some predictions have been made of climatic change effects mediated by photoperiodic responses, excluding evolutionary changes (Heide, 1993; Hanninen, 1995; Beuker *et al.*, 1998). Tropical plants may be substantially unaffected (Corlett & LaFrankie, 1998), but temperate plants should be much affected – already a concern of crop breeders (Koski, 1996). On the empirical level, it is found that, globally, vegetation now greens up earlier (Myneni *et al.*, 1997), British plants flower earlier (Fitter & Fitter, 2002) and phenologies in many taxa are advanced globally (Parmesan & Yohe, 2003; Root *et al.*, 2003).

Given the limitations of phenotypic acclimation just noted, we expect that photoperiodic responses must evolve as the climate changes. A fascinating and perhaps disturbing story in physiology, development and their genetic bases is due to unfold in this century. Photoperiodic responses show genetic diversity (Weinig *et al.*, 2002); they can be altered in

populations by selection. However, evolutionary genetic responses are constrained in effectiveness by rapid rates of climatic change – 'rapid' in evolutionary terms may mean a century (Thompson, 1998). The evolutionary responses are also constrained by the loss of genetic variability for photoperiodic responses over the millenia between climate excursions, and by genetic linkages. These conditioning factors are little understood to date.

## 4. Difficulties in describing biotic dimensions in process-based models

Many responses of organisms, populations and communities involve biotic interactions such as competition, disease, or herbivory. Biotic events are even more challenging to define than climatic events. Some biotic events such as eruptions of insect herbivores are readily visible once developed. Proceeding beyond description to quantitative assessment and prediction is far more challenging. The dynamics of their triggering, development and abatement must be put into a comprehensive model. If mean air temperature rises with climate change, can we expect greater activity of herbivorous insects (Zhou *et al.*, 1995; Cannon, 1998), and therefore greater herbivory as well as disease vectoring? More importantly, the projections need to account for changes in plant quality, particularly for the decrease in leaf nitrogen content. Such characteristics may be critical in response to this biotic extreme event and the recovery from it. Other global changes, particularly socio-economic changes in land use and agricultural technologies, may be more important (Coakley *et al.*, 1999); these are clearly more difficult to model. Social scientists must be active participants. Some concrete research plans have already been proposed (Ayres & Lombardero, 2000).

## V. Evolutionary dimensions

### 1. Responses depend upon evolutionary history

We noted in Section III.3 that genetic linkages affect responses to extreme events. Etterson & Shaw (2001) showed that genetic traits of leaf function and allocation in a native North American forb (*Chamaecrista fasciculata*) are linked. The correlations are antagonistic to the direction of selection in each trait that is most adaptive for climate change. More generally, very broad classes of organismal responses may become maladaptive under large-scale, persistent extremes such as climate change (both natural an anthropogenic), or the introduction of exotic species (Kokko & Sutherland, 2001). Schlaepfer *et al.* (2002) describe these responses as ecological and evolutionary traps. Some genetic linkages are likely to be functional or adaptive, of course, even if not yet analyzed as such. Extreme events themselves must have selected some allocation patterns that should detract measurably from other organism functions in normal times. One candidate is
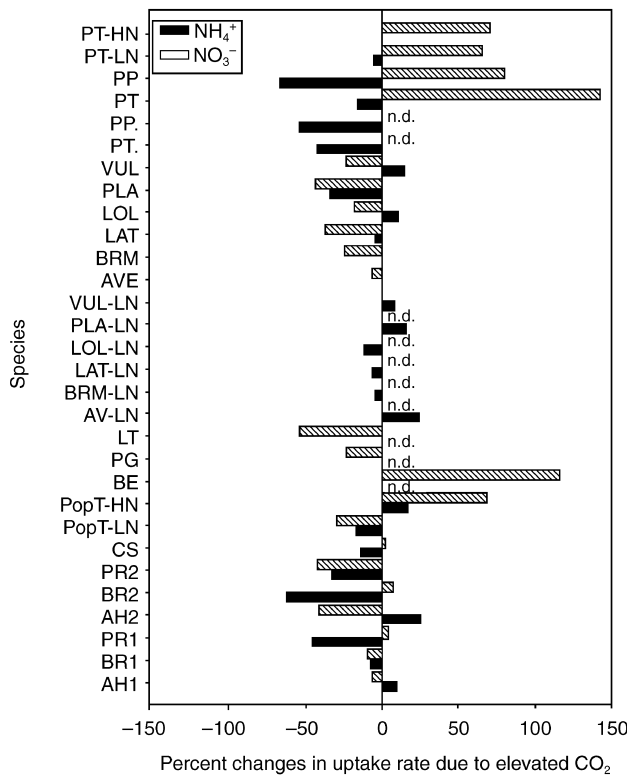
**Fig. 5** Wide variation among plant species in responses of N uptake rate (nitrate and ammonium) to elevated $CO_2$. Species identities are given in original publication of BassiriRad *et al.* (2000; Fig. 2); woody and herbaceous species are represented, as are annuals and perennials.



**Fig. 6** Diversity in growth responses of 156 plant species to elevated $CO_2$, as biomass at elevated $CO_2$ (600–720 µmol/mol) relative to biomass at ambient $CO_2$ (300–360 µmol/mol). Data from Poorter (1993, Fig. 1).

wood development for wind stress in trees that far exceeds in amount (and in metabolic cost of construction) what is needed in the vast bulk of the time at moderate windspeed (Coutts & Grace, 1995). We may also consider some costly constitutive chemical defenses (Hartley & Jones, 1997), and adhesion devices of tidal-zone organisms for extreme wave forces (Denny, 1994). Many more may be unapparent to us.

Long-term genetic responses are known to very limited extents. It is clearly difficult to conduct real-time evolutionary experiments on long-lived organisms, in contrast to some successes with bacteria (e.g. Lenski & Travisano, 1994) or fruit flies and other short-generation-time organisms (even these experiments have caveats: Harshman & Hoffmann, 2000). In long-lived organisms, we do see signatures of some of the major selection events of the past. Textbook examples include the rise of the $C_4$ pathway in plants (Ehleringer *et al.*, 1997) and swings in $C_3/C_4$ abundance ratios at individual locations (Monger *et al.*, 1998), or the earlier origins of heat-shock proteins and of dehydrins among many kingdoms (Feder & Hofmann, 1999). However, many more of important genetic changes surely remain invisible as yet. How did some extreme stress-tolerating organisms (e.g. perennials in hyperarid zones) get their extensive suite of tolerance characteristics?
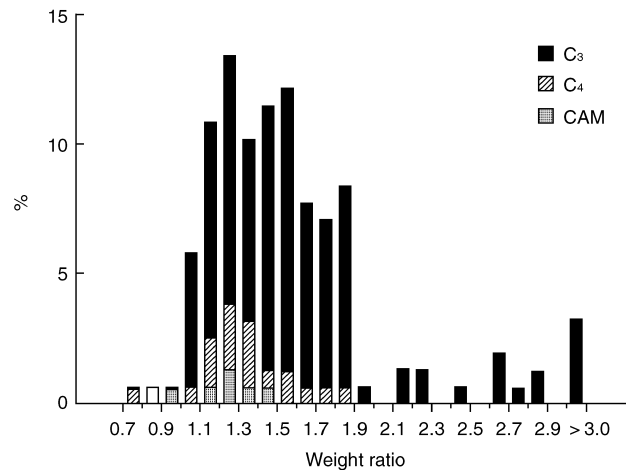
Has genetic variability for performance at elevated $CO_2$ and the attendant changes in climate been largely lost since the Eocene? This will be important for near-future responses of native plants, exotics, and crops, particularly if the extents of loss differ markedly between species. Such variable losses may underlie the still-bewildering spectra of responses to elevated $CO_2$ among plant species, in their photosynthetic acclimation (Curtis & Wang, 1998; Peterson *et al.*, 1999), mineral nutrition (BassiriRad, Gutschick & Lussenhop, 2000; Fig. 5 here), and net growth rate (Poorter, 1993, Fig. 6 here), or the differences between biomes in responses of nutrient cycling at elevated $CO_2$ (Schimel, 1995).

By what methods might we seek, systematically, these genetic changes, which may be termed the genetic signatures of extreme events past?

Attempts to quantify the genetic variability and constraints by reciprocal transplantation, common gardens, and breeding in controlled environments are problematic. The very structure of such experiments radically changes the spectra of events whose actions we think are important. There is a critical need for ability to trace gene flow and frequency in undisturbed field conditions. Fortunately, some new techniques of population genetics may help materially (Milligan, 2003). The same techniques useful for studying evolutionary constraints are useful here; section VIII.4 details these.

## 2. Are extreme events themselves strong(est) agents of natural selection?

We may expect that the strong responses of organisms, populations and communities driven by extreme events lead to marked changes in fitness, thus to strong selection. We argue first the corollary, that in normal times, most trait

variations are functionally neutral and therefore not subject to significant selection. This is not a simple argument to make, as it involves optimizing selection (flatness of the fitness function near the mean phenotype), alternating selection (acting to largely cancel episodes of directional selection that are observed), and balancing selection (strong fitness variations by genotype, with allele frequencies maintained by heterozygote superiority). Despite this near-neutrality, strong selective events do occur – extreme events, in fact. These events may be responsible for much of trait fixation and also of speciation. Linkages of traits at these times carry along many other traits, even some maladaptive traits, because selection occurs on the whole organism with its full phenotype and genotype. We close with suggestions of which kinds of traits – physiological, developmental, and ecological – are most likely the subjects of selection by extreme events.

## 3. Arguments for functional neutrality of most trait variations in normal times

To initiate a discussion, we propose that almost all traits (physiological, developmental, and ecological) are selectively neutral in normal times. Two lines of argument can be followed, which we may call top-down and mechanistic. The top-down argument consists of two parts. First, if directional selection were significant and persistent on any one trait, its value should go to fixation rapidly; however, trait variation, genetic and phenotypic, is abundant. Second, if selection were strong on many traits simultaneously, net selection would be intense. The fraction of surviving individuals would be very small; the 'excess genetic deaths' would be an intolerable load (see, e.g. Kimura, 1983; elaboration by Hughes, 1999; elements in Gould & Lewontin, 1979). This argument may apply even for very fecund individuals such as trees that produce millions of seeds. Most of the deaths of seeds or seedlings are random or nonselective. In addition, fecundity is often traded off against survival capabilities, at least in some clear examples from animals (fecundity vs. starvation resistance in fruit flies: Leroi *et al.*, 1994).

We concentrate now on the mechanistic arguments for effective neutrality. Several levels of effective or functional neutrality can be posited. At the DNA level, many base substitutions are silent, not affecting the amino acid sequence of final translation products. Other substitutions change amino acids for other amino acids that are functionally nearly equivalent (one aromatic amino acid for another, for example; *ibid.*). This concept of strict neutrality of most DNA changes is not without controversy (Kreitman & Akashi, 1995). Arguments for preservation of phenotypic trait values may need to proceed to higher levels, in many cases.

At the next level, genetic changes cause changes in the phenotype, but the latter have a neutral effect on fitness. We resolve several cases here and in Section V.3, which follows. One case is strongly optimizing selection, in which fitness is a

function of trait value that has a broad, flat optimum. This can arise if a trait (described in either genetic or phenotypic terms) affects primarily one measure of performance, such as photosynthetic rate, and performance exhibits a broad, flat optimum as a function of trait value. Such behavior is apparent in a number of physiological traits that the authors have studied. We detail a few of these cases here, because the mechanistic bases of performance tradeoffs have not been discussed systematically to date. In Section V.4, which follows, we consider more general cases of environmental variation altering the fitness function, and of a trait affecting multiple measures of performance.

One example is biochemical, in which major changes in protein function have little effect on net photosynthesis, which we can take as one major fitness contributor. Variant isozymes for photosynthetic carboxylation (rubisco) differ in maximal carboxylation rate and, in opposite directions, for selectivity for $CO_2$ over $O_2$ (Spreitzer & Salvucci, 2002). Rubisco variants with high turnover have lower selectivity and more losses from 'photorespiration' (photosynthetic carbon oxidation); they prove to have no significant net advantage. A second example of a virtually continuous or quantitative trait is specific leaf area, or SLA (Garnier & Laurent, 1994; Garnier *et al.*, 2001). Thin leaves trade an enhanced light capture against a lower efficiency of using intercepted light. This occurs because light-saturated rates of photosynthesis are closely proportional to leaf thickness, as seen for example by Dornhoff & Shibles (1970); this is true for leaves of comparable water content and density only, and thus not between some major functional groups such as trees, grasses, and forbs; see Niinemets (2001) and Roderick *et al.* (1999). The near-neutrality of the effect of SLA on whole-canopy photosynthesis is predicted to be quite strong at the whole-plant level (Gutschick & Wiegel, 1988).

## 4. Generalized neutrality: cancellation among fitness contributions in time or among different performance measures, and overdominance

This simple case of flatness of fitness in a single dominant measure of performance such as photosynthesis is not likely to be the predominant explanation for very weak net selection on traits. First, the shape and position of the fitness function depends upon the environment, which is constantly changing. If the shape moves such that there is now a significant slope at the current mean value of the trait, then directional selection should occur. Indeed, it may be common. Putting aside artificial conditions that change the fitness function with some often intentional bias, Kingsolver *et al.* (2001) reviewed 65 cases of directional selection, culled from over 2500 published studies by limiting consideration to natural populations and to studies meeting a number of statistical criteria. The selection differentials were distributed about 0 but had a modest absolute value of 0.16 – which is still adequate to drive

traits to fixation in a number of generations far smaller than a species persistence time. It may be telling that studies with very large sample sizes had very small selection differentials. Still, selection may occur, but to maintain genetic diversity (to maintain alleles), one may (must?) invoke alternating selection over time – positive now, negative later, and so on (Futuyma, 1998). None of the studies that were reviewed were repeated to test for alternating selection. We may point to some classic cases of alternating selection, including selection for beak size in Galapagos finches between repeated cycles of El Niño and La Niña years (Grant & Grant, 1995; Grant *et al.*, 2000).

Second, most traits affect multiple measures of performance. One need not even invoke pleiotropy. A change in stomatal control (for conductance, $g_s$) alone, without changes in any controls over expression of photosynthetic enzymes, will change photosynthetic $CO_2$ assimilation (A), transpiration (E), water-use efficiency (WUE) and nitrogen-use efficiency (NUE), to name a few changes. The changes often have contrary effects on fitness. Section II.3 presented notional estimates of the changes in A, E, and WUE. We add here that a decrease in $g_s$ also decreases NUE. The net effect on fitness is smaller – probably much smaller, in general – than the effect contributed by the change in any one of the four performance measures. The exact degree of cancellation depends upon the relative weighting of A, E, WUE, and NUE in determining fitness. Is nitrogen in shorter supply than is water? Is growth competition and thus A more important than saving water in a current period of relative abundance? Travis (1989) presents a number of other examples of opposing forces of direct selection.

Other examples of tradeoffs in multiple performance measures are readily cited. The trait of specific leaf area can be analyzed for tradeoffs of canopy photosynthetic rate against, first, ability to shade competitors and, second, water-use efficiency, or WUE. The superior shading ability of thin leaves was suggested by Gutschick & Wiegel (1988) to account for SLA being somewhat larger than would be optimal in a stand of cooperatively growing single genotypes. Schieving & Poorter (1999) provide a comprehensive model for this tradeoff. Regarding WUE, we note that thin leaves have lower assimilation rates per area; because stomatal conductance scales closely to assimilation (Wong *et al.*, 1985a,b,c; Ball *et al.*, 1987), thin leaves transpire less. The lesser cooling means that they operate at higher temperatures than do thick leaves and thus at higher vapour-pressure deficits and lower WUE (Osorio & Pereira, 1994).

Physiological tradeoffs are also apparent in leaf nitrogen content. A high leaf N content confers high assimilation rate, linearly at low N and tending toward saturation at high N (Field *et al.*, 1983). High leaf N also confers high WUE (Gutschick, 1999; Wright, Reich & Westoby, 2003). A simple version of the argument is that intrinsic WUE at the stage of leaf $CO_2$–$H_2O$ exchange is proportional to the differential between ambient and internal partial pressures of $CO_2$

(Farquhar & Richards, 1984). All else equal, and particularly if stomatal conductance is unchanged, the higher the assimilation capacity, A, the more that leaf-internal $CO_2$ pressure ($C_i$) is drawn down. However, the efficacy of using N itself decreases (Field *et al.*, 1983). First, the trend of saturation of A at high N means that A/(N content) is a decreasing function. Second, a decrease in $C_i$ results in a lower carboxylation rate per rubisco enzyme and thus per unit mass of N. This is readily seen in standard formulas for carboxylation rate in terms of $C_i$ (Farquhar *et al.*, 1980 *ff.*). The tradeoff of WUE against NUE within a single species has been observed by Patterson *et al.* (1997) in boreal trees.

We offer one more among the many examples of physiological tradeoffs. Stomatal control balances high assimilation rates against loss of xylem hydraulic conductance. High stomatal conductance maximizes use of investment in photosynthetic capacity, while the accompanying high transpiration rate draws down water potential. The drawdown can cause xylem cavitation with partial loss of hydraulic conductance. In turn, this causes yet-greater decrease in water potential. Tyree & Sperry (1988) proposed that plants operate near the point of catastrophic failure. Sperry *et al.* (1998) have developed a very quantitative approach to infer that this is nearly optimal. A comprehensive mechanism by which leaves can sense the loss of xylem conductance may be complex (Matzner & Comstock, 2001) and of multigenic origin. Multiple measures of performance are involved (photosynthesis, use of water, use of N) and are challenging to convert to a single measure of lifetime fitness. Many tradeoffs may pose such challenges, we concede.

Developmental rather than physiological tradeoffs are also apparent in a number of cases. One might take SLA in the discussion above as a developmental trait as well as one related to physiology. Another example may be afforded by variation in plant height. Greater investment in stem growth reduces allocation to leaves and current photosynthetic potential. The tradeoff is primarily temporal, current photosynthesis by leaves on short stems against future photosynthetic potential if the plant can overtop competitors. Schmitt and coworkers (Dorn, Pyle & Schmitt, 2000) have provided very informative studies of these costs and benefits, with genetic bases. Many life-history traits such as flowering time may be viewed as developmental tradeoffs. Much variation in flowering time is likely to be plasticity in response to environmental variation, but intraspecific genetic variation exists. Tradeoffs may be occurring with early flowering between such performance indicators as pollinator access and flower number (Zopfi, 1995) or between male and female function of flowers (tested but not supported in studies of Robertson *et al.*, 1994). The analyses are complicated by the multigenic control commonly found (Laurie *et al.*, 1995; Kole *et al.*, 2002). Many other developmental variations such as photoperiodic control of flowering most likely trade off performance in normal times against performance in extremes.

Some performance tradeoffs might be deemed more ecological than simply physiological or developmental, although the lines are blurred. We may cite here the intraspecific variations in allocation to defense compared with growth (Hartley & Jones, 1997; Ohnmeiss & Baldwin, 1994). Herbivory and disease are very much in the ecological realm, involving other members of an ecosystem. They commonly occur at a 'background' level, and, exclusive of explosive outbreaks, may be considered as a normal event.

Alternating selection may combine with tradeoffs in performance measures to generate strong neutrality of traits. The tradeoff of photosynthetic rate against WUE when stomatal control varies may not be very close to neutral in any one time interval but it may attain near zero effect on fitness when averaged over a sequence of environments. For example, WUE may be more valuable than photosynthesis in a dry interval.

One more mechanism for maintaining genetic diversity in a trait and trait values is overdominance, in which the heterozygote is superior to both homozygotes (in a simple 2-allele case as an example) (Hughes, 1999). Fitness varies widely between genotypes but significant selection for the heterozygote maintains allele frequencies. This behavior generalizes to the case of many alleles, in pleiotropic overdominance (Travis, 1989).

## 5. Some traits, and trait combinations, do get strongly selected and fixed

Neutrality is not universal; traits do get fixed, such as woodiness vs. herbaceousness. These traits had to be nonneutral on their way to fixation, barring founder effects. Intriguingly, the nonneutrality may arise in interaction with many other traits and/or in genetic linkages. The role of directional selection in speciation has support in evolutionary biology (Rieseberg *et al.*, 2002). In particular, the constraints on trait combinations resulting from directional selection are strongly related to speciation and are worth much study (Ricklefs & Wikelski, 2002).

Up to here, we have been considering traits singly, in effect. This is legitimized in many cases by their additive effects on fitness. However, it is whole organisms that are selected, with their unique trait combinations that are genetically linked (in proximity on a given chromosome). An interval of intense directional selection – such as might occur in an extreme event – generates 'selective sweeps' (reviewed by Amos & Harwood, 1998) that preserve unique combinations of traits found in a relatively few individuals. Selection over a short time leaves little time for genetic recombination. Traits subsequently remain correlated in occurrence. Any two traits might be related in different ways. A strongly selected trait might carry along a nearly neutral trait. This can confuse the analysis of relations of traits to fitness: we may see a correlation of the nearly neutral trait with fitness but only from its linkage to the strongly selected trait (Travis, 1989). Even maladaptive traits may be

linked to adaptive traits, provided that selection is stronger on the adaptive trait. A caveat to this viewpoint is that Kingsolver *et al.* (2001) found evidence that such indirect selection is typically weak.

Such correlations from selective sweeps may underlie marked trait combinations within species that may not be adaptive. Of course, concurrent positive selection on multiple traits should bolster the likelihood of various trait combinations occurring similarly in many species. For plants in particular, Meinzer (2003) hypothesizes that 'there are a limited number of physiological solutions to a given problem of plant adaptation to the environment.' We may paraphrase these ideas as expressing that the adaptive landscape has isolated peaks at certain discrete combinations of traits (Wright, 1931). To this we add that extreme events may be the most important selective agents on the landscape, enforcing strong directional selection. They also are likely to select for phenotypic plasticity as the counterpart of directional change (Trussell, 1997; Srgo & Hoffmann, 1998).

Examples of traits that combine in fairly repeatable fashion include leaf N content, leaf lifetime and leaf thickness (Reich *et al.*, 1997; Ackerly & Reich, 1999). Commonly, these nearly fixed traits occur with each far from the mean among all species. These combinations appear to be akin to tradeoffs of traits within an individual, although the analogy is broad: the traits once fixed among discrete species cannot recombine and generate intermediate variation. In the restricted sense, however, we can say that Wagner *et al.* (1998) found that xylem-vessel diameter trades off hydraulic conductivity (largest for wide vessels) against vulnerability to implosive cavitation from wall failure in drought stress. Fernandez & Reynolds (2000) found maximal relative growth rate traded off against drought tolerance among eight arid-zone grasses. Polley *et al.* (2002) found that elevated $CO_2$ reinforced these same tradeoffs in five woody legumes. Walters & Reich (1996) found tradeoffs between shade tolerance (considering shade as an extreme event for intolerant species) and high growth rate in high light. Water-use efficiency, at first surprisingly, appears to be traded off against drought tolerance (Thomas, 1986; Grieu *et al.*, 1988).

Fixation of traits can occur with quite small selection differentials over many generations. Some extreme events only recur after a great number of generations. in this category we may place elevated atmospheric $CO_2$, in which the current levels may have last occurred in the Miocene. Alleles that were adaptive in high (or low) $CO_2$ have probably been lost over millions of years. There are indications that genetic capacity to adapt to high $CO_2$ may be limited already in short-generation plants such as annuals (Bunce, 2001). The paucity of genetic variation for adaptation to low $CO_2$ may constrain adaptation to rising $CO_2$ (Sage & Coleman, 2001). Signatures of lost genetic variation should be sought in genes for climate-responsiveness. Particularly we might focus on alleles for $CO_2$-responsiveness in which so many differences are observed

among species (meta-analyses or reviews by Curtis & Wang, 1998; Peterson *et al.*, 1999; BassiriRad, Gutschick & Lussenhop, 2000; many others).

In addition to affecting responses to new means – and to new extremes – the correlations or constraints affect our ability to predict directions of microevolution from comparing phenotypes in populations along current environmental gradients. These populations evolved with multiple, concurrent gradients of which we are unaware. Tools to deal with this challenge are presented in Section VII.

## 6. Which traits are likely to be selected by extreme events?

We believe that documentation in some detail is merited in order to properly delimit the discussion for traits that seem clearly nonneutral. Traits for competitive acquisition of resources (water, nutrients, light) are candidates here. One would expect benefits to exceed costs in almost all circumstances in traits that we have analyzed for nutrient uptake. We have given detailed analyses of traits for nutrient uptake capacity per area of root, root allocation, and root thickness in other publications (Gutschick & Kay, 1995).

Our previous analyses did not consider extreme events. This may underlie our inability to explain why the magnitudes of these traits appear to be fixed even when the fitness function has no optimum, no peak. One expects that uptake rates as high as physically possible would only enhance competitive status. Despite this, most plants are restrained in uptake (Chapin, 1980, BassiriRad *et al.*, 2000). Among tradeoffs that have been considered (Gutschick, 1987; Gutschick & Kay, 1995; Gutschick, 1999; BassiriRad *et al.*, 2000) are limitations on the density of uptake carrier proteins on root-cell membranes, costs of nitrate reduction and ion balance, risks of herbivory at high N content, lowered drought tolerance of leaves with high water content that is necessary (Roderick *et al.*, 1999) to use N in soluble proteins, and damage from uptake of chemically analogous nonnutrients (such as arsenate for phosphate). Other authors have suggested that high uptake capacity is deleterious to tolerance of stress (Vanderwerf *et al.*, 1993; Aerts, 1999; Busso, Briske & Olalde-Portugal, 2001; – even if the genetic distance between high-uptake and stress-tolerating plants may not be large in some cases: Chapin *et al.*, 1993).

None of these costs or barriers are convincingly large or so widely occurring as to counterbalance photosynthetic benefits. Rethinking the value of these traits in the context of extreme events leads us to propose that they, and many other competitive traits, have been directionally selected by their fitness value in extremes. In particular, we would argue that high nutrient availability (the only condition in which high uptake capacity has a large benefit: Gutschick & Kay, 1995) is a positive extreme. It occurs in patches limited in both space and time. Persistence in time and dispersal in space through

intervening low-nutrient conditions strongly dilutes selection for most species and only fixes high-acquisition traits in ruderals. In these species, the traits are necessarily combined with high dispersal ability. The net result is a diversity among species in degrees of capacity for resource use and resultant growth potential. There is evidence for analogous fixation of animals' growth potentials at diverse levels (Gotthard, 2000).

The same nonneutrality between normal and extreme events may appear in development. Photoperiodic responses in flowering time have been noted earlier as possibly neutral for within-species variation. Similar photoperiodic responses in bud dormancy and germination act mainly to reduce risk of damage or death in extremes of temperature or water availability. Vallardes & Pugnaire (1999) investigated foliage orientation in arid-zone grass and shrub species as a means to balance light interception for photosynthesis in good conditions against avoidance of photoinhibition in drought. They did not quantify intraspecific variation in particular. It is noteworthy that interspecies variations are commonly strong, as if the traits have been largely fixed by directional selection that led to speciation. Developmental tradeoffs have been reviewed in a number of animal taxa (Doughty & Shine, 1997; Zera & Harshman, 2001), with specific attention to intraspecific tradeoffs that we emphasize here.

In conclusion, the traits of resource acquisition and usage efficiency are clearly important in plant performance during the recovery from an extreme event. We propose that the role of these traits be studied as strong contributors to fitness in extreme events. They may explain as much or more of fitness as do traits for survival and function (e.g. thermotolerance) during the extreme event itself.

## VI. The mandate for new conceptual tools for ecological and evolutionary prediction

The proper intellectual development of the disciplines of physiology, developmental biology, ecology and evolution requires that we improve our accounting for extreme events. Many practical applications of such knowledge are pressing. We in these fields are called upon for ecological prediction in the face of global change (Clark *et al.*, 2001). Climate change, driven largely by greenhouse gas emissions, is one major component, while land-use changes will have potentially much greater aggregate effects (Sala *et al.*, 2000). A wide range of ecosystem services should be expected to change, such as pollination (Boumans *et al.*, 2002), flood control by vegetation, biocontrol (or exacerbation) of pests and diseases by new abundance and geographic patterns of predators, parasites, and vectors. Extreme events are likely to have large roles in all such predictions. Current knowledge of the real nature of extremes merits greater application as well. For example, reforestation at higher elevations in Australia should employ shelter designs for tree seedlings planted out that differ strongly from common tent-like shelters. Protection is needed

against the combined photoinhibitory effect of high light and cold, without hindering convective cooling in midday (Holly *et al.*, 1994).

The limitations on genetic variability and the constraints within the variability will affect not only the fate of individual species but also of ecosystem function, including ecosystem services to humans. Will climate change substantially alter the frequency and geographic distribution of diseases that are strongly climate-related, such as fungal diseases or diseases spread by temperature-sensitive vectors (Djurle *et al.*, 1996; Sutherst, 1998)? How long will vegetation continue to sequester nearly 20% of anthropogenic $CO_2$ (Ciais *et al.*, 1995; Field & Fung, 1999)? Will this fraction change as natural selection proceeds for superior acclimator species? Models of C-sequestration currently use fixed physiologies (sometimes with acclimation capacities) for any given species or functional group (e.g. Lloyd & Farquhar, 1996; Luo *et al.*, 1996). Yet physiological and developmental limits are foreseen within the dominant vegetation and in nitrogen-cycling organisms (Schimel, 1995), and these will be affected by extreme events and by attendant microevolution. In addition to action in the C-cycle, vegetation and associated soil also act as a source of nitrogen oxides that varies notably with climate and with species composition (Schimel, 1995), both of which are being driven anthropogenically. Vegetation and soil are also a source of atmospheric water that is sensitive to the overall growth response of vegetation and to acclimation in stomatal control (Bunce, 1993, 1998); thus, they affect precipitation regimes down to mesoscales (Avissar & Pielke, 1991). Vegetation and soil also comprise a modest sink for carbon monoxide (10% of the total: Potter *et al.*, 1996). All these functions, and more, will change with the (constrained) microevolution of populations.

## VII. Tools in hand, and tools needed, to study extreme events

### 1. Tools for identifying extreme events in terms of organismal responses

We have offered arguments on a number of bases that extreme events are definable only in terms of organismal responses, not as tails of distributions of the remote driving variables such as weather variables. Hypothesizing as we do that extremes are defined by their exceeding acclimatory capacities, we take the first task as quantifying acclimation capacities in organisms. This task includes, first, quantifying the progressive onset of limits in rates and in total magnitudes and, second, quantifying the costs and benefits (in fitness terms) of acclimation on several time scales. We recall the discussion in Section II.3 of acclimation benefits differing on daily and seasonal scales; acclimation is definable then as adjustment of phenotypic traits that accrues a net benefit. Full acclimation accrues the maximal benefit. Some costs and benefits must be evaluated

in populations rather than in individuals or over several generation times, because costs in particular fall differentially in time and space upon various individuals (who share genes or genotypes), out of both deterministic processes (canopy microclimate processes) and stochastic processes (e.g. disease incidence).

Acclimation capacities, as well as performance measures and hysteresis in phenotypic traits, need to be expressed in the proper driving variables. For example, in cold-induced photoinhibition (Ball *et al.*, 1991, 2002), leaf temperature and irradiance are the direct leaf variables, which must be related in turn to the ultimate driving variables of solar flux densities (both PAR and thermal infrared), air temperatures and wind-speeds, and radiative properties of the underlying soil or vegetation. Process models exist for all these relations (e.g. King & Ball, 1998, for this photoinhibition process), and these must take precedence over simple statistical models. The use of process-based or mechanistic models guides the proper resolution of causation from correlation. Certainly, mechanistic understanding has its limits; we do not follow everything to its biophysical basis, or even to its basis in biochemistry and gene expression. Thus, statistical models must be incorporated, with due care again to resolving causation from correlation (Shipley, 2000). In between are models such as neural networks that allow very complex fits to data beyond the mathematical inventiveness of most researchers attending to the biological details. Even these are challenged to include detailed time series with contingent effects, so more work is needed to make these effective in studying extreme events.

From another hypothesis that most fitness effects of extreme events accrue in the long hysteretic or recovery period, we pose a second task as describing the hysteresis behavior quantitatively. This may be viewed as an extension of the acclimation process, or its reverse as deacclimation. In any event, the performance of the organism (e.g. $CO_2$ assimilation rate, water-use efficiency, etc.) and the consequent net benefit in fitness must be evaluated over the full time course of onset, extreme, and recovery.

A third task must be on quantifying the genetic variation in, first, measures of performance that are traded off, particularly in normal time; this allows testing of near-neutrality of most trait variation; and, second, acclimatory capacity in traits identified as important in particular extreme events chosen for study. Initially, such studies are case-specific (species, location, event type) of necessity, but generic methods should emerge, such as molecular probes for conserved sequences in the genes involved.

A bit more detail needs to be presented on process-based models. It will require some significant research on biological mechanisms to identify the most relevant driving variables in the environment, and the relevant statistics of those variables. Cross-correlations are often important, such as temperature and PAR flux density in cold-induced photoinhibition (Ball *et al.*, 1991, 2002). The temporal sequence may also matter.

Not all cases are as simple as thermal (fire-induced) death of cells in the cambium of tree trunks. Here, the probability $P$ of cells surviving this extreme event is characterized by a single variable, the cell temperature $T$. The data of Lorenz (1939) may be approximated well by a simple differential equation: $dP/dt = -k(T)P$. We can readily integrate this to express $ln(P) = \int dt\, k(T(t))$. Here, $T(t)$ is the time series of cell temperatures, and the order clearly is irrelevant. The case of leaf expansion as curtailed by episodes of water stress, low humidity, or low light illustrates the opposite case, in which the effects of stress are contingent on the temporal sequences. The relative cell division rate (RCDR) and the relative cell expansion rate (RLER) are affected by the three stresses in overlapping but distinct windows in thermal time (Granier, Inze & Tardieu, 2000). The final area of a chosen leaf is a primordium area multiplied by the exponential of the time integrals of both RCDR and RLER. The complications in expressing stress effects on plant leaf area are several: first, final area development is seen after a time lag; leaf development rate is not a function of current environment; second, the time is scaled as thermal time; third, only the logarithm of single-leaf area is linear in any stress variable; the sum of areas of all leaves is a sum of exponentials.

Such complications can be handled mathematically in a process-based model but are not apparent in simple regression analyses, especially those not resolving the contingency or importance of temporal order of stress. In cases where we have no such detailed mechanistic insight, we must develop 'geometrical insight' into the interaction (correlated, nonlinear) of driving variables in an extreme event. Also demanded are more comprehensive statistics of the ultimate driving variables. Let us continue consideration of basic weather variables as an important part of the set of driving variables. Field stations that record weather and soil water conditions hourly will allow construction of the properly correlated stress variables for leaf expansion (or many other events, normal and extreme). However, many geographic areas have stations recording only cruder daily averages of each variable, if any measurements are made at all; the patterns over shorter terms must be inferred from patterns at stations in similar climates. For coverage of large geographic areas, it is possible to turn to copious data analyses performed by climate analysts (e.g. Easterling *et al.*, 1999, 2000a,b). Climate analysts do appreciate the importance of correlations among weather variables (Katz & Brown, 1994; Wagner, 1996). Processing data from wide geographic areas to include such correlations demands considerable computing power (Kalvova & Nemesova, 1998; Park *et al.*, 2001), but it is practical to do such computation currently. Future extremes pose a similar problem. General circulation models (GCMs) are used to predict future climate scenarios but commonly run on daily time steps, not hourly. Hourly patterns must be estimated from patterns occurring in the weather 'type' of a given day (Schubert & Henderson-Sellers, 1997; Sailor & Li, 1999). These estimates are practical but introduce some error.

Additional detail is also needed on how traits must be defined or measured. Ultimately, the desired traits are genetic, especially individual genes. It is too much to ask such resolution for even one species currently. The steps toward a genetic resolution, or at least to phenotypic traits with strong genetic linkages, may be illustrated by considering stomatal conductance, $g_s$. It is not itself a fixed phenotypic trait, as it varies widely in one leaf with environmental conditions – it is a function of perhaps six or seven major environmental variables (irradiance, temperature, humidity, etc.). Kingsolver *et al.* (2001) offer nonparametric fits to describe such function-valued traits, as alternatives to using parameters of parametric models. The latter remain attractive for traits that are functions of many variables. A number of empirical models capture the environmental responses concisely in a few parameters, such as the Ball-Berry model (Ball *et al.*, 1987) or several alternatives (Dewar, 1995; Leuning, 1995). Even when extended to include response to root-derived signals of water stress, these models have only three or four parameters (Tenhunen *et al.*, 1990; Gutschick & Simonneau, 2002). Are these strongly determined genetically and thus usable as heritable traits? Systematic surveys within species to elucidate genetic links are essentially absent, but they are possible and should be very rewarding. Only pieces of more mechanistic models of $g_s$ are currently available (Assmann, 1999; Matzner & Comstock, 2001), so there is no inclusive model ripe for genetic analysis. We might jump directly to genes identified by their effect on $g_s$. Single genes affecting $g_s$ behavior are known but, again, nowhere near a full framework for expressing $g_s$ has been developed from the purely genetic side. For other traits, we must explore the best use of genetic, empirical and mechanistic models. The genetic analyses of critical traits are challenging, from any starting point: because of our emphasis on acclimation and recovery, we are considering the genetics of plasticity, an area deliberately avoided by the classical genetics developed by Haldane and Fisher (Kimura, 1983). Recent work is advancing the study rapidly (Jasienski *et al.*, 1997; Pigliucci & Schmitt, 1999).

## 2. Tools for sensing driving variables of extreme events

New sensors for variables not traditionally measured will be valuable. Many new sensors of biological materials (organic compounds, some proteins, etc.) are available or under active development (see the journal *Biosensors and Bioelectronics*, in particular). High-resolution cameras for field networks are being tested (http://hpwren.ucsd.edu/news). These might enable rapid detection of extremes affecting animals as well as plants – at first with monitoring by people and later with automated pattern recognition. In view of the need to determine some complicated correlations among even simple micro-meteorological variables in near-real time, it is important to improve in-field data processing capacity. Traditional dataloggers have low processing speeds and clumsy programming. Laptop

computers are moderately expensive but unreliable in the field, or else very expensive when field-hardened. Palmtop computers are much less expensive to field-harden, and some are specifically designed for field data acquisition, such as the Psion™ line.

Long-term baseline data are of great value for studying extreme events. The Long-Term Ecological Research (LTER) sites in the US, the International LTER sites in several other countries, many research sites of the European Economic Community, a number of networks to monitor surface-air fluxes of $CO_2$ and water vapor (AmeriFlux, EuroFlux, etc.) are natural choices for studies. The focal instrumentation at each site will need augmentation by sensors of wider ranges of variables.

At the level of communities and ecosystems, the uses of remote sensing can be expanded profitably. For large areas, aircraft and satellite remote sensing has evolved to resolve many functional groups of vegetation, and thus, any significant changes in composition and physical structure over time (Asner et al., 1998; Asner, 1998; Asner & Heidebrecht, 2002). Smaller-scale sensing, as from high-resolution sensors traversing communities on tramways (J. A. Gamon, pers. comm.), offers finer resolution.

### 3. Testing neutrality and nonneutrality of trait variations

This task will demand simultaneous measurement of suites of performance measures, such as photosynthesis, water-use efficiency and nitrogen-use efficiency. Quantifying acclimatory capacities will require frequent measurement until optimal sampling protocols can be developed. These data will be valuable only if accompanied by measurements of detailed time series of driving variables on the one hand and of fitness effects on long time scales. The genetic variability within species must be focused upon, to correlate with phenotypic performances. Fortunately, genetic profiling by a variety of techniques such as microarrays is becoming relatively simple and affordable.

### 4. Predicting ecological and evolutionary trajectories

The future environment is elusive but predictions are generated nonetheless. For climate, researchers continue to improve general circulation models (GCMs; monograph by Trenberth, 1992; review of recent progress by McGuffie & Henderson-Sellers, 2001). GCMs operate on large spatial scales and must be downscaled to small regions of more uniform elevation, slope, aspect, hydrologic status and soil type. Downscaling algorithms use the coarse GCM output as boundary conditions for 'within-cell' processes (Wilby & Wigley, 1997; Wilby et al., 1998). Some claim to operate down to the level of single plants (Seem et al., 2000). Their validations are very effort-intensive and incomplete but the models are promising. What is not known yet is how well GCMs and downscaling methods preserve the temporal and cross-correlations that should be critical for extreme events at the organismal level.

The genetic structures of populations will constrain the course of evolution, particularly the linkages among traits (Etterson & Shaw, 2001). It is very impractical to determine these structures by sequencing, even partially, adequate numbers of individuals in any population; more-indirect measures must be used. Even for a few traits at a time, the classic methods of breeding are laborious and slow. They are also misleading, in that breeding is not in field conditions or it disrupts field conditions; the very selection pressures we wish to track are skewed. There is thus great promise in new methods (Milligan, 2003) that use a modest number of markers (on the order of 20) in each individual. The marker sequences need *not* have their functionality known. The markers are used to estimate relatedness in undisturbed populations and then to estimate the genetic covariance matrices. Together with phenotypic-trait covariance matrices, these predict evolution of mean genotype and mean phenotype in the population under prescribed selection pressures estimated from the phenotype performance (the performance in resource acquisition and use and the translation into fitness).

## VIII. Conclusions

We have proposed many hypotheses about the definition of extreme events, about the loci of important changes in physiology driven by extremes, and about genetic changes that are driven by extreme events and that condition global responses to new patterns of extremes. We have also proposed a large agenda for research, addressing features of extreme events that are little appreciated today – the roles of contingent events, of correlations in environmental variables and of evolutionary constraints to responses. Joined with these features are challenges in statistical descriptions and in designing protocols to capture stochastic costs and benefits in plant responses. We propose many specific patterns of evolution driven by extreme events. One may ask if such a broad and deep research plan is doable. At the least, parts of the plan merit trying, in order to map out what is achievable. There are some sanguine trends in support for related efforts. Some of the work will require large interdisciplinary collaborations; in the US, programs to support these are growing, including the initiatives in biocomplexity at the National Science Foundation and a possible National Environmental Observatory Network. The key innovations, however, remain likely to come from individual investigators. The numbers of such researchers who attend to extreme events is currently small but growing rapidly. We remain hopeful that timely research will eventuate.

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