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# Stress Physiology and the Distribution of Plants

*The survival of plants in any ecosystem depends on their physiological reactions to various stresses of the environment*

C. B. Osmond, M. P. Austin, J. A. Berry, W. D. Billings, J. S. Boyer, J. W. H. Dacey, P. S. Nobel, S. D. Smith, and W. E. Winner

In plant physiological ecology, as in many other subdisciplines of biology, the term *stress* has general connotations rather than a precise definition. By defining stress as any factor that decreases plant growth and reproduction below the genotype's potential, we make the term measurable and thus meaningful to ecology and agriculture. Most plants

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## Nearly every perturbation of a plant community results in stress

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undergo some form of stress during the various stages of their life cycle. Nearly every perturbation of a plant community or ecosystem results in stress and so affects the performance and survival of individual plants. Although we understand fairly well some of the cellular mechanisms of stress physiology, in order to predict their ecological impact we need to understand the temporal and spatial variation of a particular stress, genetic variation in stress responses, the plants' potential to acclimate to stress, and stress-factor interactions.

One motivation for studying stress in plant physiological ecology is to account for patterns of plant distribution and performance along environmental gradients. Such gradients can be described on almost any scale, ranging from degrees of latitude to millimeters. At points along these gradients, environmental factors can become stressful for certain physiological functions of particular plants or plant organs. Some of the finest studies of plant physiological ecology have compared physiological responses to stress in related plants from locations characterized by extremes of single environmental factors. But in nature, covariation of and interaction between major stress factors is the norm.

Figure 1 illustrates the interacting stress factors for the Northern Hemisphere, the most prominent of which are temperature and water availability. Superimposed on and related to this are very complex gradients that may arise from too little or too much light and such biological stresses as herbivory and diseases. The stresses introduced by shade or excessive light stem from many interacting factors including latitude, elevation, season, atmospheric composition, density of plant cover, and leaf properties.

The quantitative impact of excessive light is greatest in high alpine environments in the tropics and middle latitudes, and lowest at ground level in dense forests. The biological stresses of herbivory by vertebrate and invertebrate grazers and diseases caused by fungi, bacteria, and viruses tend to be greatest in tropical forests and least in polar deserts. These biological stresses vary over time, depending on environmental requirements of the predators and pathogens. Competition among plants is another form of biological stress. How much the biological factors, as opposed to environmental stresses, constrain species distribution along gradients remains one of plant ecology's central issues. Resolving these difficult questions will depend on imaginative integration of physiological and population ecology.

In stressful environments, plants show two types of adaptive behavior: tolerance or avoidance. Tolerance mechanisms permit plants to maintain high metabolic activity under mild stress, and reduced activity un-

der severe stress. Avoidance mechanisms permit plants to reduce autotrophic activity and become dormant in the face of extreme stress. Agricultural plant breeding, to the extent that it is concerned with mitigation of plant stress effects, has principally selected crop species for improved avoidance of stress (e.g., by appropriate seasonal phenology). This strategy may already have had its maximal effect, and further selection in this direction may give only a limited, or perhaps even negative, impact on productivity in stressful environments.

Boyer (1982) estimated that environmental stress effects still limit overall US agricultural productivity to 25% of its potential. We suggest that considerable scope remains for improved productivity based on marginal advantages conferred by stress tolerance mechanisms. Plant physiological ecology is providing key insights into these mechanisms. In this review we concentrate on abiotic stresses and their impact on vascular plants.

### Natural vegetation along gradients

Vascular plants have occupied moist, warm, abiotically nonstressful environments in the tropics since the mid-Paleozoic. Of the approximately 250,000 species that have evolved, about 95% are angiosperms. Species diversity is greatest in the low tropics, falling more or less logarithmically as a function of decreasing temperature with increasing latitude. While this observation clearly implicates temperature as a major factor, it is difficult to relate distribution along a climatic gradient to quantitative physiological differences. Limits to distribution may result from rare occurrences of unusual weather, which are seldom adequately documented, and also may have differential effects on specific steps in the life cycle.

There are many, albeit incomplete, illustrations of the complex fabric of environmental and biotic factors affecting plant distribution. For example, Shreve (1911) proposed that the northern geographic and elevational limits to the distribution of saguaro (*Carnegiea gigantea*), the giant cactus of the Sonoran Desert, are determined by infrequent winter freezing tem-

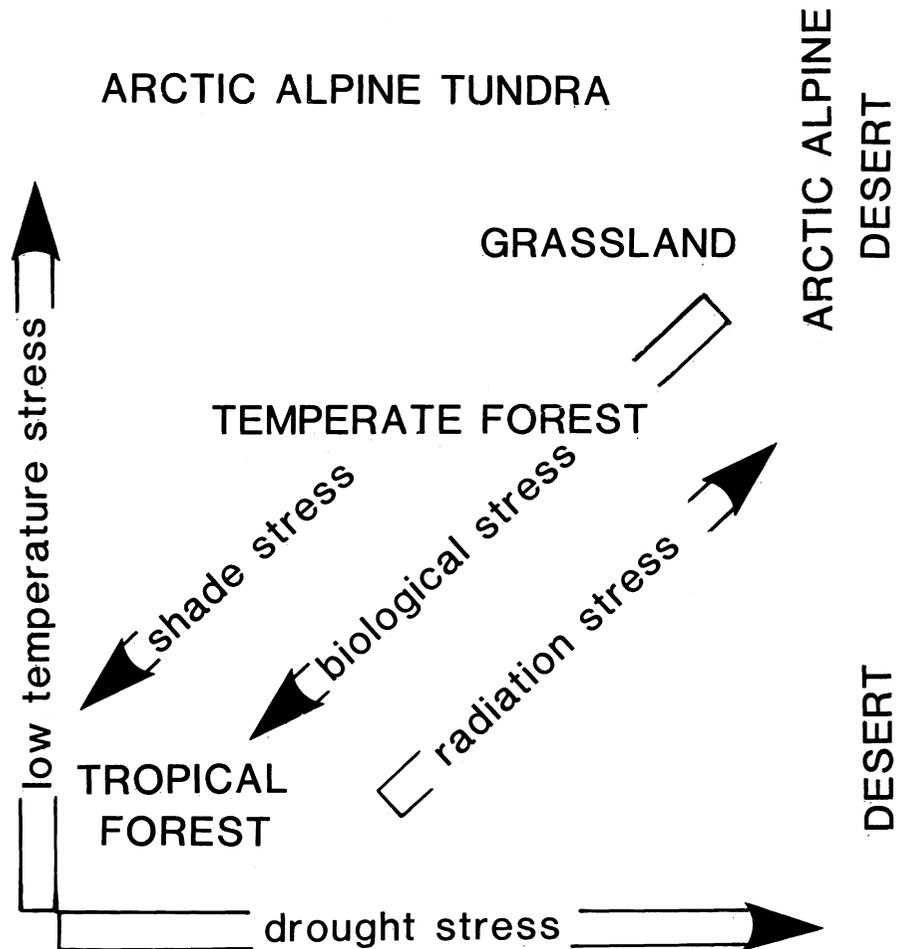


Figure 1. Schematic gradients of environmental stress in relation to major vegetation types. The X axis is a gradient of decreasing temperature, and the Y axis represents decreasing water availability. Adapted from Billings (1974).

peratures persisting for more than 24 hours. Niering et al. (1963) noted that such a freeze in January 1962 reduced the established population's density, rather than its spatial distribution. At some sites, large, exposed saguaros suffered higher mortality than did smaller individuals sheltered by rocks and adjacent "nurse" plants. Indeed, instead of being exposed to the cold night sky, seedlings received radiation from the nurse plants' branches, which had much higher effective temperatures. These microhabitat factors plus specific morphological characteristics of small saguaros enhance their survival (Nobel 1980).

Factors other than frost kill of mature plants may be important in determining saguaro distribution. Only 0.1 to 0.5% of naturally or artificially sown seeds germinate, largely because of bird and ant predation and the patchy distribution of favorable sites,

with sufficient soil surface moisture. Only 10–20% of germinated seeds survive the first summer; survival is least likely in rocky habitats. However, rocky habitats favor survival in the subsequent winter because they provide protection against frost (Steenbergh and Lowe 1969) and predation. In terms of plant stress physiology, saguaro distribution seems to be dominated by water and moisture tolerance limits during establishment and low temperature tolerance at maturity. The significance of its unusual mechanism of photosynthesis (crassulacean acid metabolism or CAM), which permits extraordinarily efficient carbon and water-conserving metabolism, is less clear.

In one of the few attempts to quantify environmental gradients, Austin et al. (1984) analyzed the distribution of *Eucalyptus* species at 1286 sites in southern Australia. With a general-

ized linear model using mean annual temperature, rainfall, and radiation as predictors, they examined the variability associated with species distribution. The distribution of snow gum (*E. pauciflora*), for example, can be clearly distinguished from that of *E. rossii* on the basis of temperature alone (Figure 2). These methods strengthen the conceptual base of Whittaker's (1967) direct gradient analysis and link it to earlier functional, factorial approaches to the differentiation of vegetation (Major 1951).

Defining gradients in vegetation and environment has led physiological ecologists to evaluate which aspects of temperature stress physiology play the most important roles in the distribution of snow gum. Seed germination in *E. pauciflora* is controlled by dormancy mechanisms resulting in germination and emergence when seedlings are least likely to be exposed to snow, drought, or high temperature (Abrecht 1985). Seedling establishment after germination depends on the "nurse" effect of neighboring grass tussocks that provide shade and frost protection, but these tussocks subsequently compete with the snow gum for water. Harwood (1980) concluded that while the seed-

lings in marginal environments (e.g., valley bottoms) are tolerant to temperatures well below mean monthly minimums, their tolerance limits are perilously close to the absolute minimum temperatures recorded (Figure 3).

Studies of the productivity of mature *E. pauciflora* have shown that the photosynthetic performance is remarkably plastic (Slatyer 1977). Laboratory work shows about 10° C adjustment, or acclimation, on the temperature optimums for photosynthesis when the plants are grown in cool rather than warm conditions. This temperature range corresponds to seasonal changes in the optimal temperatures for photosynthesis under natural conditions (Figures 3 and 4). The photosynthetic temperature optimum closely tracks the long-term mean monthly air temperature (Slatyer and Morrow 1977). Such highly tuned responses may determine productivity and reproductive success, and hence abundance and competitive ability, especially in the face of extensive herbivory (Morrow and La Marche 1978).

### Temperature stress

For the most part, plants experience

the highest and lowest temperatures near the soil surface. Thus, the mortality of juveniles during establishment usually determines the ecological impact of temperature tolerance limits. Recent studies show that the smallest seedlings suffer the most extreme thermal stress (Nobel 1984), but in established plants, especially succulents (Nobel and Smith 1983), morphological attributes mitigate stress to some extent. Consequently, if the thermal stress on the seedling is too great, a species may be unable to take advantage of a microhabitat well-suited to the adult plant.

**Heat.** The observed thermal limits for survival of metabolically active tissues in vascular plants range from about -60° C to about +60° C in different species. Lower plants and some vascular-plant tissues, such as seeds, can tolerate a wider range of temperatures. Species differ substantially within these limits as well as in the seasonal adjustment of temperature tolerance. This tolerance is generally greater when metabolic activity is negligible. Larcher and Bauer (1981) have reviewed instances in which leaves of mature evergreens are able to lower their freezing tolerance by 40° C or 50° C. Desert cacti may raise their heat tolerance by 10° C to 20° C (Smith et al. 1984).

Desert succulents display the highest tissue temperature tolerances (Downton et al. 1984, Smith et al. 1984). Their low surface-to-volume ratio, low stomatal frequency, and large mass help conserve water but impede transpirational cooling. Although succulents tend to mitigate overheating with an array of special properties, including reflectance of shortwave radiation in certain *Agaves* (Nobel and Smith 1983) and shading by spines on barrel cacti (Nobel 1983), tissues are often subject to an hour or more of temperatures above 60° C, on days when air temperature may exceed 40° C.

Perhaps the hottest environments occupied by growing vascular plants are found in summer in Death Valley, California. With daytime air temperatures approaching 50° C, rapidly transpiring leaves of the summer-active perennial desert honeysweet (*Tidestromia oblongifolia*) are cooled to 40° C to 45° C, at which tempera-

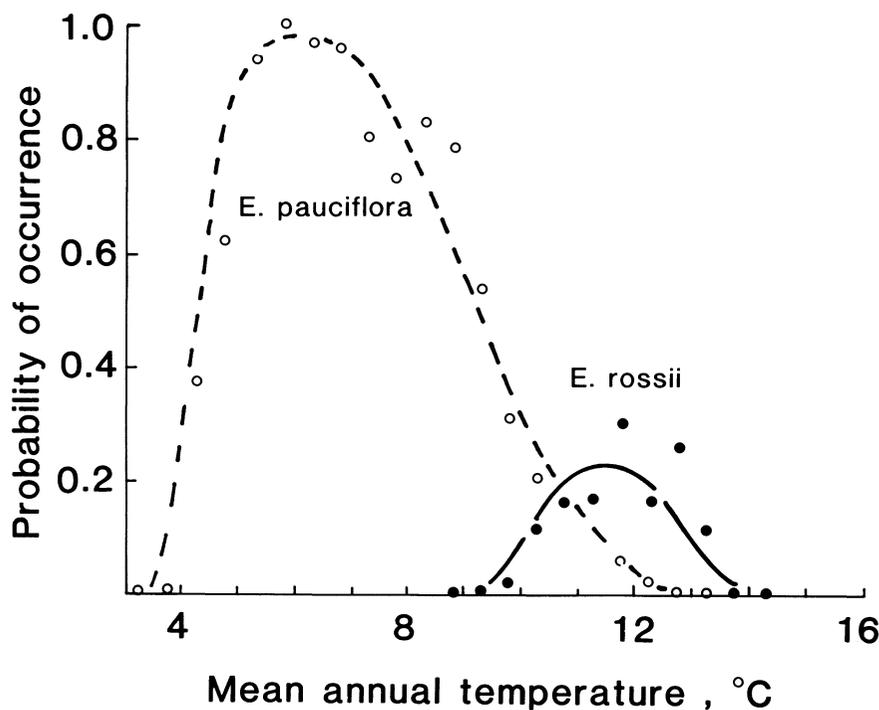


Figure 2. *Eucalyptus* distribution in relation to temperature. Adapted from Austin et al. (1984).

tures they are capable of extremely high rates of photosynthesis via the  $C_4$  pathway (Berry and Björkman 1980). This species can only maintain high productivity if its leaf temperatures are within this range. However, temperatures approaching  $50^\circ\text{C}$  are lethal. Other species with lower metabolic activity (and less transpirational cooling) can tolerate temperatures approaching  $55^\circ\text{C}$  (Downton et al. 1984).

Metabolically active plant tissues are limited in how well they acclimate to temperature change. Whether one considers alpine snow gum (Figure 3) or desert creosote bush (Mooney et al. 1978), the limit to acclimation of the optimal and maximal temperatures for photosynthesis is approximately  $10^\circ\text{C}$  (Raison et al. 1980, Seemann et al. 1984). Billings et al. (1971) established that acclimation of photosynthesis and respiration of *Oxyria digyna*, a widespread arctic alpine species, is genetically controlled. They related acclimation ability to performance of populations in changeable alpine summer climates and in colder but more stable arctic climates.

**Chilling.** Plants of lowland tropical origin can suffer chilling, a sensitivity to nonfreezing temperatures between  $0^\circ\text{C}$  and  $15^\circ\text{C}$  that can impair key physiological functions. This phenomenon is of great interest to agriculturalists since many crop species are of tropical origin. In wild relatives of the tomato, the effect of chilling on seed germination, seedling survival, and greening of cotyledons closely correlates with elevation of their origin (Patterson et al. 1978). Differences in the thermotropic properties of plant membranes and proteins have been implicated as mechanisms underlying the sensitivity of some plants to chilling temperatures (Berry and Raison 1981). However, the significance of these mechanisms in the natural distribution of plants has received little attention.

Although many  $C_3$  plants are sensitive to chilling, the complex physiology and biochemistry of the  $C_4$  photosynthetic pathway has been considered especially vulnerable to cold temperature (Slack et al. 1974). Minimum growing-season temperature has been used in the past to

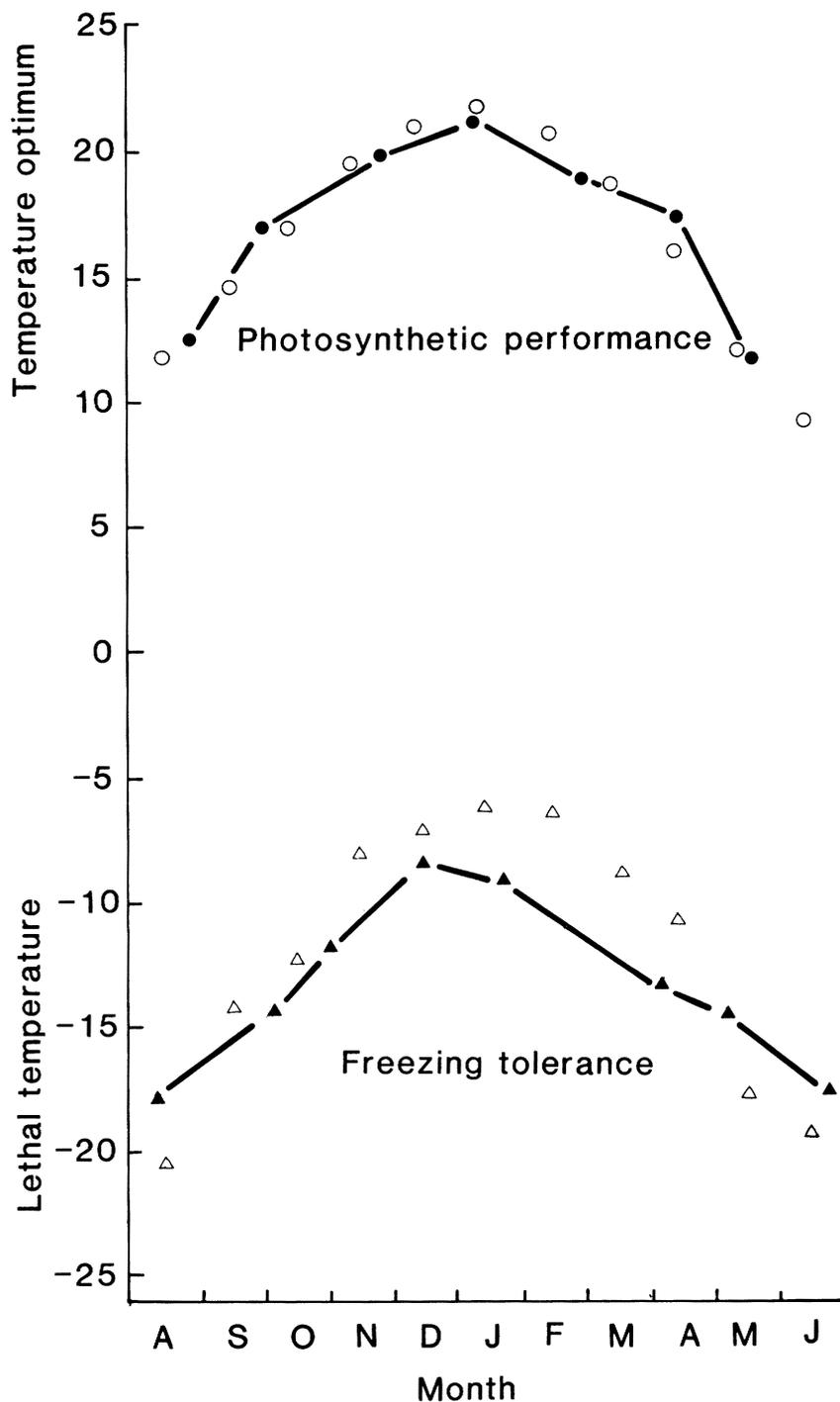


Figure 3. Thermal tolerance and photosynthetic performance in *E. pauciflora* in relation to temperature (in degrees C). The frost resistance of seedlings ( $\Delta$ ) closely follows the absolute minimum temperature ( $\blacktriangle$ ) recorded between 1897 and 1974. The temperature optimum of photosynthesis in air ( $\circ$ ) closely follows the long-term mean monthly maximum temperature ( $\bullet$ ). Source: Slatyer and Morrow (1977), C. E. Harwood unpublished data.

predict the presence of  $C_4$  grasses (Teeri and Stowe 1976, Hattersley 1983). However, the correlation may reflect in part the tropical origins of most  $C_4$  plant families. Some  $C_4$  spe-

cies are very tolerant of low temperatures (Osmond et al. 1980), suggesting that  $C_4$  photosynthesis per se does not necessarily lead to chilling sensitivity.

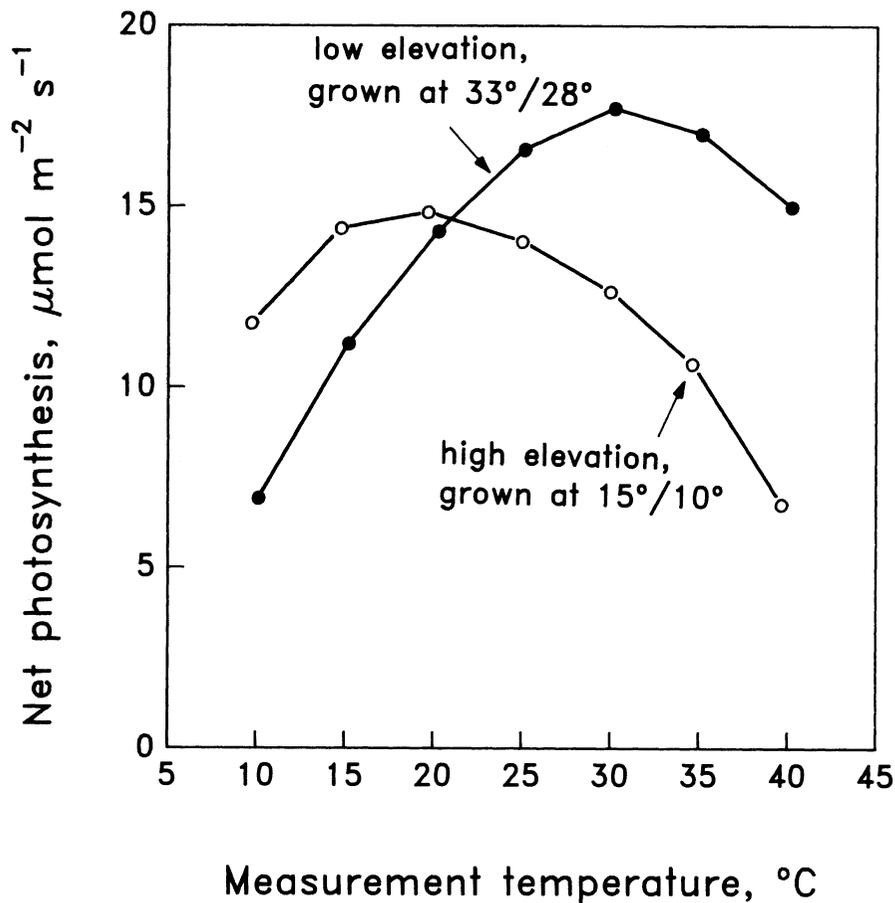


Figure 4. Maximum photosynthetic acclimation in high and low elevation populations of *E. pauciflora* grown at different temperatures. Adapted from Slatyer (1977).

### Water stress

It is likely that water stress, like temperature stress, has a major influence on plant distribution during seedling establishment. The most rapid changes in water availability take place at the soil surface, and several studies show that seedling mortality during drought is higher than adult mortality (Schlesinger et al. 1982, Wellington 1984). However, most studies have considered the impact of water stress on adult plants. Among desert perennials, for example, removing inter- and intraspecific competitors increases the water availability to remaining individuals and may stimulate their leaf area, growth, and reproductive output (Ehleringer 1984, Robberecht et al. 1983). While water stress is often associated with high temperatures, cold or frozen soils can reduce water uptake and thus produce water stress (Oberbauer and Billings 1981, Tranquillini 1976).

Unlike temperature stress, water

stress is largely determined by a plant's own control of its water relations, and a wide range of regulatory mechanisms has evolved (Lange et al. 1982). In general, the tolerance limits for metabolic activity in vacuolated cell tissues seem to require a small, positive hydrostatic pressure (turgor) of about 0.05–0.5 MPa (one megapascal approximately equals ten atmospheres) against a background of negative water potentials commonly ranging from –0.5 to –15.0 MPa. Tolerance limits for relatively inactive tissues, such as seeds or the leaves of desiccation-tolerant plants (Gaff 1980), are not related to turgor.

Not surprisingly, the means by which desert plants avoid and tolerate water stress represent extremes of physiological differentiation among vascular plants (Jones et al. 1981). Avoidance mechanisms include stomatal closure, leaf movement, and leaf shedding. Like many other plants, succulent plants can close their stomata and, at the same time,

cease water exchange through their roots; their succulent form serves to buffer tissue water potential. However, it is significant physiologically that they can maintain metabolic integrity by means of CAM in the absence of net CO<sub>2</sub> and water exchange (Osmond et al. 1982). The ability to rapidly resume water uptake when it is again available is also a key property of desert succulents (Nobel and Sanderson 1984).

Desert annuals, and indeed many crop plants, can acclimate somewhat to water stress by maintaining turgor with osmotic adjustment, accumulation of a wide range of organic and inorganic solutes in the vacuole and cytoplasm (Jones et al. 1981, Morgan 1984). High electrolyte concentrations in the cytoplasm interfere with normal metabolic function, and a special class of neutral organic compounds, such as betaine, may be involved in cytoplasmic osmotic adjustment. The maximal acclimation is usually about –2 MPa. Osmotic adjustment presumably prolongs the period of water uptake, transpiration, and hence carbon gain in the face of declining water availability. It also tends to preserve cell water relations and mitigate direct effects of water stress on nonstomatal components of photosynthesis.

Just as the potential for acclimation to temperature is limited, so even the most drought-resistant desert shrubs, such as *Hammada scoparia*, have a limited capacity for osmotic adjustment, despite their already low water potential (Kappen et al. 1976). The maximum extent of water stress tolerance in desert perennials is about –10 to –15 MPa; many of these plants are halophytes in which vacuolar salt accumulation is responsible for osmotic adjustment and turgor maintenance at low water potential (Osmond et al. 1980).

Research on water stress has focused on the loss of photosynthetic productivity due to CO<sub>2</sub> deprivation from stomatal closure. But water stress also impairs nonstomatal components of photosynthesis. It may be important to consider the daily excursions in leaf water potential, which are also associated with excursions in temperature and light intensity. Because plants must lose water in order to remove CO<sub>2</sub> from the air, they are

in constant peril of dehydration.

The higher water-use efficiency associated with  $C_4$  photosynthesis has prompted many analyses of its significance in water-limited environments. Comprehensive studies by Caldwell et al. (1977) and Schulze et al. (1980) suggest that under increasing water stress,  $C_4$  plants, such as *Atriplex confertifolia* and *Hammada scoparia* remain productive longer than comparable  $C_3$  plants. A combination of higher water-use efficiency and greater capacity to retain turgor at low water potentials is responsible. Other studies show that the potentially advantageous water relations associated with higher water-use efficiency in  $C_4$  plants tend to be expressed during hotter and drier periods of the year, when chilling limitations to development in  $C_4$  plants have passed (Monson and Williams 1982). But frugal water use is not the only avenue to ecological success in water-limited environments. Water-stress-tolerant *Acacia* is displaced from Australian coastal dunes by *Chrysanthemoides*, a less tolerant South African species that is successful because it develops leaf area and extends roots more rapidly than *Acacia*, thus achieving higher reproductive output through profigate use of, and competitive preemption of, the available water supply (Weiss and Nobel 1984).

### Flooding stress

Too much water is as drastic a stress to most terrestrial plants as too little. Because the diffusion of gases through solution is about  $10^4$  times slower than in air, diffusion of oxygen to the root system becomes limiting in waterlogged soils. Anaerobic conditions around the roots inhibit water uptake and can actually induce water stress in the shoot. Flooding also results in anaerobic metabolism in root tissues, leading to production of toxic products. The consequences of waterlogging depend both on its duration and the chemistry of the inundating water, particularly its salinity.

Most plants growing in permanently waterlogged soils avoid anaerobiosis by transporting  $O_2$  to the roots. Wetland plants typically have large, interconnected gas spaces throughout their leaves and roots, occupying as much as 50% of the tissue. Generally,

$O_2$  diffuses from the shoots, where it is abundant, to the roots, where it is consumed (Armstrong 1978).

Some aspects of metabolic theories of flooding tolerance are controversial, for example, the role of alcohol dehydrogenase, an enzyme that is rapidly induced in tolerant species when roots are exposed to anaerobic conditions (John and Greenway 1976). However, morphological properties of waterlogging-tolerant species also seem to prevent development of anaerobic conditions. Although most studies have focused on roots, the leaves are most susceptible to  $CO_2$  and  $O_2$  deprivation following submergence, especially if illuminated. Leaf surfaces of deep water rice (a variety selected for the ability to survive immersion) trap an air layer that ensures rapid gas exchange to photosynthetic tissues (Raskin and Kende 1983). Hollow leaf, stem, and root systems in some cold, wet, alpine meadow plants provide  $O_2$  to the roots and  $CO_2$  to the leaves for photosynthesis (Billings and Godfrey 1967, Keeley et al. 1984).

### Salt stress

Physiologically, salt stress is difficult to distinguish from water stress, since dissolved salts reduce the effective concentration of water. In agriculture, salt stress almost invariably arises as a consequence of irrigation with water of poor quality or irrigation on unsuitable soils. Plant susceptibility to salt stress depends on soil and atmospheric factors influencing plant water relations. In all but the most extreme situations, salinity stress tends to develop over time in parallel with water stress and to affect adults rather than seedlings. Salt-sensitive plants, such as avocado, tend to slow their growth in response to 20 to 50 mM salt, whereas growth of desert halophytes and some mangroves is insensitive to 10- or 20-fold higher salt concentrations (Greenway and Munns 1980). The direct toxic effects of high electrolyte levels probably dominate the physiology of salt-sensitive plants, but the contribution of these electrolytes to osmotic adjustments and favorable water relations determines the success of halophytes (Munns et al. 1983, Osmond et al. 1980).

There is little evidence that fundamental metabolic processes in salt-tolerant halophytes and in nonhalophytes differ in their response to electrolytes (Ball et al. 1984, Flowers et al. 1977). Salinity tolerance appears to depend on controlled salt uptake and compartmentation, especially in leaves. In salt-sensitive plants, inadequate compartmentation can lead to salt accumulation in the cytoplasm and chloroplast, which drastically impairs photosynthetic function (Seemann and Critchley 1985). Salt-accumulating, salt-tolerant halophytes maintain relatively low electrolyte concentrations in their cytoplasm and organelles (Robinson et al. 1983) but high salt concentrations in the vacuole. Death of salt-sensitive tomato cultivars in 50% seawater occurs following a sixfold increase in salt concentration in the leaves, but a related salt-tolerant species accumulates, and presumably effectively compartmentalizes, much higher salt levels (Rush and Epstein 1976). Cytoplasmic and organelle osmotic adjustment appears to depend on the accumulation of compatible solutes (Storey and Wynn-Jones 1979), although evidence for specific compartmentation of these solutes is thin. By such means, leaves of halophytes maintain turgor and unimpaired metabolic activities under a high salt load.

The ion transport processes that lead to regulated salt accumulation in the shoots of halophytes, and fail in salt-sensitive plants, are not clearly understood. The presence of salt glands in the leaves of many desert halophytes and mangroves is one important mechanism for regulating leaf salt load (Winter et al. 1981). Mechanisms that permit plants to exclude or excrete salt are particularly important because terrestrial plants must permit water loss (transpiration) in order to obtain  $CO_2$  from the atmosphere. Once within the plant, salt may accumulate to a much higher concentration than that in the environment. Effective control of transpirational water loss is especially important for plants under salinity stress.

One of the most spectacular consequences of salinity stress is the induction of CAM photosynthetic metabolism in the ice plant *Mesembryanthemum crystallinum*, and other salt-

tolerant succulents (Winter et al. 1981). This shift to a water-sparing, but slower, carbon assimilation pathway is a response to altered water relations under saline conditions and permits these plants to complete reproductive development.

## Light stress

Because all plant life depends on solar energy, it seems anomalous that light can become a stress factor. For the most part, light benefits plant performance, but abrupt changes in light intensity, like those occurring after a gap has formed in a rainforest, may exceed the tolerance limits of plants that developed in the shade. Also light may become damaging when high light occurs together with another stress (e.g., water stress).

The photosynthetic organs of vascular plants function in a wide range of light environments, with typical photon flux densities ranging from full sunlight (about 2,500 micromoles photons/m<sup>2</sup> · sec of photosynthetically active light), in such high albedo habitats as snow, sand dunes, and salt pans to less than 5 micromoles photons/m<sup>2</sup> · sec on the deeply shaded floor of tropical rainforests.

Leaves in low light—leaves of plants on the floor of rainforests, leaves deep in the canopy, or the shade leaves of herbs—have very different photosynthetic properties from leaves grown in high light (Björkman 1981). The shade leaves are able to maintain a productive balance between respiratory loss and photosynthetic gain at lower light levels than can leaves normally exposed to full sunlight. However, shade leaves are also more easily damaged by stressful high light levels.

Adaptation of the photosynthetic apparatus to different photon flux densities generally involves adjustment of the relative proportions of light-harvesting, energy-transducing, and energy-consuming components of the photosynthetic apparatus, so that the quantity of light absorbed is in balance with the capacity for using the products of the photochemical reactions. It is when this balance is disturbed that there is excess photochemical capacity and damage occurs (Björkman 1981). Thus, if shade-grown plants are exposed to high

photon flux densities, they suffer light-dependent damage to the photosynthetic apparatus, or photoinhibition. Sun-grown plants are normally unaffected, but these may also encounter photoinhibition if a stress factor damages the photosynthetic apparatus, impairing effective transduction of light energy (Osmond 1981, Powles 1984). Then continued irradiation exaggerates the extent of damage.

There are undoubtedly significant, genetically determined, quantitative differences among plants in their potential to adjust to a range of light regimes. Such acclimation occurs readily in the leaves of some herbaceous plants, provided they have adequate nitrogen (Osmond 1983), but only extremely slowly in the seedlings of rainforest trees (Langenheim et al. 1984). The significance of acclimation in leaf photosynthetic properties for net carbon balance in the sun and shade is obvious from simple models (Osmond et al. 1980).

In a rainforest, the succession of species is closely tied to the changing light environment. Plants whose photosynthetic properties allow them to thrive in bright sunlight appear early, while those tolerant of shade dominate later in the succession (Oberbauer and Strain 1984). However, plants normally found in deep shade may persist in bright light without acclimation (Langenheim et al. 1984), indicating that factors other than photosynthetic acclimation need to be considered in accounting for resistance to high light stress.

High-temperature, water, and salinity stress in plants all tend to coincide with highest photon flux densities. It is therefore not surprising that evidence is growing for photoinhibition associated with these stress responses. Björkman and Powles (1984) have quite clearly established that the loss of photosynthetic activity following water stress in sun-grown oleander (*Nerium oleander*) is light dependent (Figure 5, top).

A spectacular example of interaction among stress factors is found in *Macroptilium atropurpureum*, an important introduced pasture legume in Australia. In this species, leaf movement is a very effective means of avoiding high light stress and high temperature damage associated with

water stress. Ludlow and Björkman (1984) restrained leaves that would have otherwise moved, and the researchers established that the sun-avoiding (paraheliotropic) movements reduce the damage caused by high light intensity at high temperatures (Figure 5, bottom). No photoinhibition occurred when leaves moved, whether or not they were water stressed. When not water stressed, the leaves move to maximize, rather than minimize, the quantity of light absorbed.

Chilling stress also interacts with light stress to damage plants. Chilling usually first occurs under clear night skies and is quite likely to be followed by bright daylight. Experiments have shown that damage to the photosynthetic apparatus occurring when leaves are chilled increased in the presence of light (Öquist 1983, Powles et al. 1983). In chilling-sensitive rice varieties, no damage can be detected unless the leaf is illuminated after chilling. Chilling-resistant varieties can withstand many cycles of dark chilling followed by high light intensity during the day (Osmond, unpublished data). Winter stress, the progressive loss of photosynthetic activities in the leaves of evergreens, is almost certainly a consequence of the interaction of low metabolic activity at low temperature, to which the leaves are acclimated, and light (Öquist 1983).

Until recently, investigators paid more attention to the effects of light quantity than to the effects of light quality. But they are now also considering UV radiation at high elevation in low latitudes and far-red enrichment in shaded habitats. Plants from the high Andes of Peru have notably higher epidermal UV absorption than those from sea level in the Arctic (Robberecht et al. 1980). The relatively few studies of the ecological impacts of light quality in the shade (Grime 1966, Morgan and Smith 1981) indicate a wide range of effects on germination, establishment, and morphological properties.

Although ecological observations have indicated preferred light regimes for different species, and modern techniques permit quantitative analyses of light environments (Chazdon and Fetcher 1984), few quantitative analyses of gradients in light regime

and vegetation have been done (Waring and Major 1964).

### Present trends and future objectives

Research should now begin to integrate cellular aspects of plant stress physiology to account for plant tolerance limits and performance in a way that is sufficiently pragmatic for ecological applications. For example, studies with infrared gas analyzers provide us with the basis for estimating seasonal production in many ecosystems (Bunce et al. 1979, Oechel and Mustafa 1979), but offer relatively little insight into the relationships between production and reproduction or tolerance limits.

The challenge is heightened by the accelerating rate of human changes in the environment. The chronic increase in global atmospheric CO<sub>2</sub> concentration is likely to modify the stress responses discussed above (Strain 1985). Primary effects on carbon acquisition and water loss may be modified by secondary physiological processes and lead to changes in growth rate, morphology, and reproduction, which may in turn modify the ecological relationships of individual plants and plant communities. Regionally, other anthropogenic trace gases, such as SO<sub>2</sub> and O<sub>3</sub>, are now recognized to have adverse effects on crops and forests (Heck et al. 1982, McLaughlin 1985). These atmospheric pollutants directly affect leaf metabolism (Lendzian and Unsworth 1983) but also modify many aspects of plant responses to stress.

The need for vertical integration from cellular to ecosystem processes must be balanced against the traditional reductionist quest for underlying mechanisms. Plant stress physiology is now considering the molecular targets for stress responses.

One focus of this quest is membrane systems, which serve to separate, organize, and transduce much of the plant cell metabolic activity. The integrity of membranes determines and reflects the state of cells following stress, as well as acting as stress sensors, because many of the crucial relationships between lipids, proteins, pigments, and carriers are sensitive to changes in temperature, water potential, and local ionic activity (Raison et

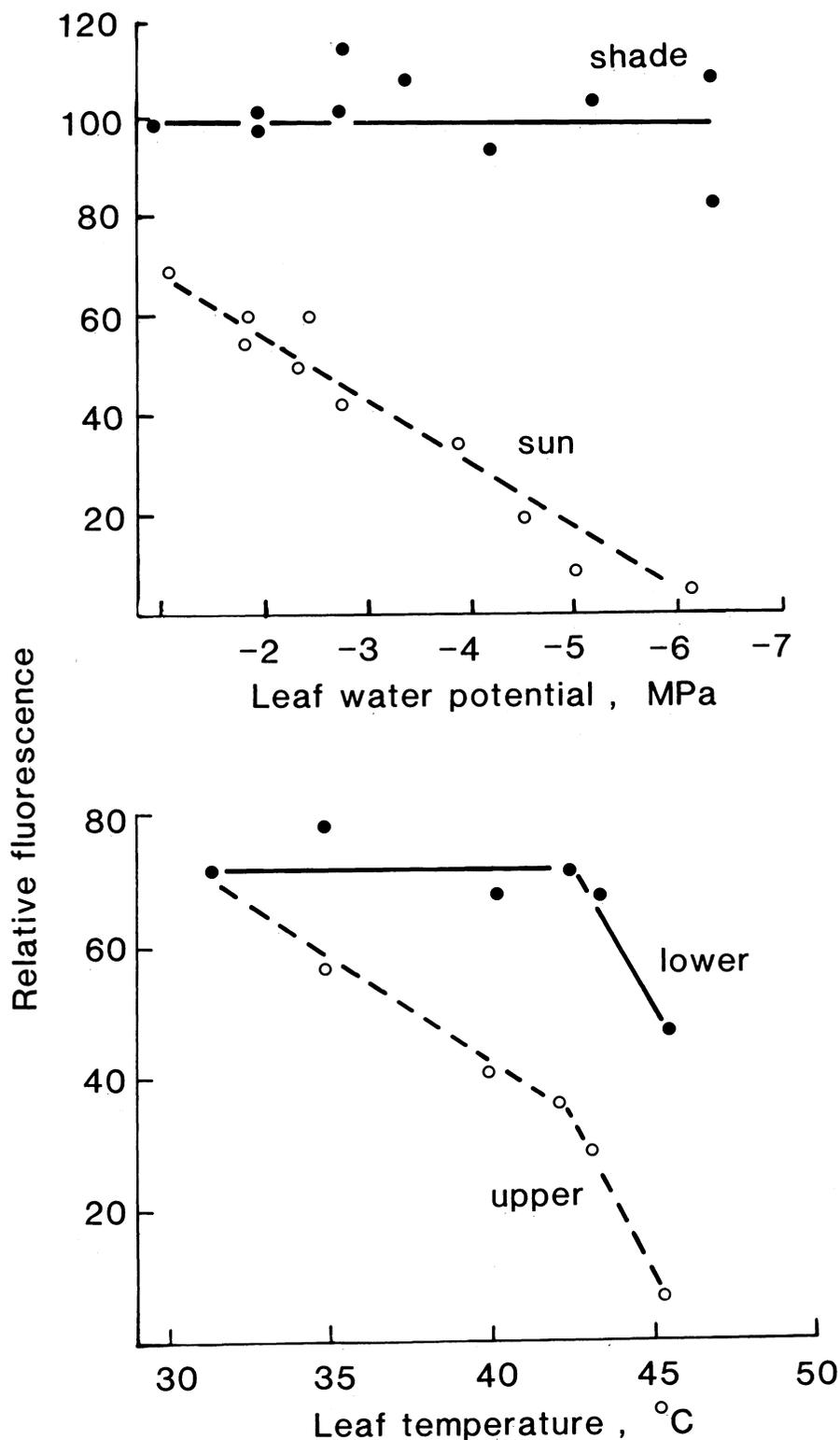


Figure 5. Light-dependent aggravation of stress effects on photosynthesis shown by decline in chlorophyll fluorescence measured at  $-196^{\circ}\text{C}$ . *Nerium oleander* (upper graph) shows no evidence of damage to the primary photochemistry at very low water potentials (high water stress) provided leaves remain in the shade. In mildly water-stressed *Macroptilium* (lower graph) high temperatures precipitate damage to primary photochemistry only on the upper, sun side of the leaf. There is no change in fluorescence on the shade side, until the thermal tolerance limit is exceeded. Source: Björkman and Powles (1984) and Ludlow and Björkman (1984).

al. 1980). Studies of the molecular basis of thermal stress have considered some specific components of membrane lipids that control fluidity and phase separation (Murata and Yamaya 1984). The effects of stress on cell membranes can be monitored by following changes in a cell's ability to retain electrolytes or to accumulate vital stains (Smith et al. 1984), by fluorescent probe studies of isolated lipids, by spin probe studies using electron spin resonance spectroscopy, and by differential calorimetry.

Another intrinsic indicator of stress is fluorescence from chlorophyll in the chloroplast thylakoid membrane (Smillie 1979). A variety of fluorescence techniques have been used to assess thermal limits to photosynthetic integrity (Raison et al. 1980) and photoinhibition (Critchley and Smillie 1981). Interpretation of these results is controversial because they reflect a complex of photochemical and biochemical activities. The conformation of chloroplast coupling factor in thylakoids seems particularly sensitive to water stress (Younis et al. 1979), causing inhibition of photosynthesis at low water potential. This may lead in turn to increased sensitivity to photoinhibition (Osmond et al. 1982). Studies of light-aggravated stress responses demonstrate impairment of the photosystem II reaction center (Powles 1984), and one of the polypeptides of the O<sub>2</sub>-evolving complex seems particularly sensitive to salinity (Andersson et al. 1984).

The genetic basis for controlled synthesis of chloroplast lipids and polypeptides is within the reach of molecular biology. Substituting and modifying some of these molecules might alter stress tolerance. For example, heat shock proteins, a suite of low molecular weight polypeptides of unknown function, are produced by seedlings under heat stress (Lin et al. 1984). These conditions approximate the extremes of environment seedlings meet during establishment at the soil surface. Manipulating heat shock protein genes may provide a way to extend the tolerance limits for high temperature.

Changed tolerance limits, if they can be extended even marginally, are likely to be reflected in increased production in agriculture and increased species area in natural ecosystems. To

have an impact on ecology, however, progress at the molecular and physiological level must occur together with corresponding increases in our capacity to relate physiological properties of plants to their growth, productivity, and reproductive success in complex natural environments. We need to develop the capacity to study and model plant performance with sufficient resolution to address problems of marginal advantage among competing plants. New technologies for measurement of environmental conditions and vegetation dynamics by remote sensing are emerging (Greggor 1986), and crop physiologists are developing more sophisticated growth models. If we can come to grips with the greater complexity of natural environments, then a new ecological understanding can follow.

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