Environmental stress and survival strategies: an overview

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Abstract

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Adaptive responses to environmental stresses at family, genus, species, and population levels are examined, with emphasis upon the consequences of natural selection effected by grazing, temperature, and drought.

Stress factors vary from the obvious such as climatic, biotic, edaphic, and human-made factors, to the very subtle. Such is the extent of individual stress factors and combinations of factors which affect plant growth and survival, that it is neither possible nor sensible to try and consider other than a limited number of them in this paper. This paper will therefore be confined to three factors, the impact of grazing animals, the impact of temperature, and finally of water stress, which are of considerable importance for the conservation of wild species in Europe, because of their significance for plant breeders.

For plants living in a terrestrial environment, it is difficult to envisage any situation in which they are not at least to some degree, subjected to stress of one sort or another, or to combinations of stress factors. One might think that with all the expertise that farmer, agronomist, plant breeder, and agricultural chemist can bring to bear on the growing of crops, they would be free of stress. However, if we examine the response of wheat to increasing density in pure stands, it is clear that yields per plant at standard sowing rates (approximately 280 seeds m^{-2} for UK winter wheat) are considerably less than those at lower density, implying stress from competing neighbours which limits yield per plant, as illustrated by data from Puckridge & Donald (1967) for wheat. The same point can be illustrated in a different way using data from an experiment examining potential improvements in crop yield from growing cultivar mixtures of faba bean (*Vicia faba* L.). Pure stands of the cultivars "Danas" and "Minden" had lower mean seed yields per plant, than when they were grown in mixtures (Table 1). In fact mixtures outyielded pure stands by 22.5% at low density (Tarhuni & McNeilly 1989).

Table 1. Mean seed weight per plot for monocultures and three component-frequency mixtures grown at two densities of 25 (1) and 44 (2) plants m^{-1}·

Cultivar	Density 1 seed yield (g $plot^{-1}$)		Density 2 seed yield (g $plot^{-1}$)	
"Danas" (D)	427.7		566.0	
"Minden"(M)	389.7		534.3	
		% gain/increase over mean of components		% gain/increase over mean of components
3 : 1 [D + M]	514.2	23.0**	611.9	9.6*
1 : 1 [D + M]	519.5	27.1**	584.5	6.2
1 : 3 [D + M]	468.9	17.5*	582.9	7.5
X Monocultures	408.7		550.1	
X Mixtures	500.8	22.5**	593.1	7.8

*, and ** denote differences significant at $p< 0.05$, and 0.01 respectively.

Again one may conclude that the effects (stress) of neighbours of a different variety are (significantly) less than those from neighbours of the same variety. The kinds of stress that are imposed in a situation of this kind where plant interactions may be related to exploitation of limiting resources, are difficult to explain satisfactorily, although they may reflect subtle differences in plant morphology, in the timing of various stages of growth, or differences in requirements for abiotic factors.

The colonisation of land by plants some 400 million years ago occurred because of evolutionary changes which enabled them to withstand the stresses involved in that new environment. Evolutionary adaptations to stress have continued to the present day, and to a considerable extent modern floras and plant distributions reflect differences in ability to evolve stress tolerance. This can be seen for example, in conifers where there are considerable differences in winter hardiness between families, and genera within families. The *Pinaceae* and *Taxodiaceae* provide an interesting contrast. In the early Tertiary, the *Taxodiaceae* were present as far north as the Arctic regions, but they are now confined to relict areas in middle latitudes. At present the *Pinaceae* dominate boreal forests in the Northern Hemisphere, and occur in sub-Arctic and Arctic regions where other less cold tolerant conifers are excluded. Within the *Pinaceae*, species from four of its nine genera, *Pinus*, *Larix*, *Picea*, and *Abies*, have been shown to include provenances which survive freezing to -60° C (Sakai and Eiga 1985). Again considering response to low temperature and intraspecific adaptation to stress conditions, it has been shown for meadow fescue (*Festuca pratensis*) that the pattern of overwinter survival of different cultivars in northern Sweden correlates precisely with the latitudinal origin of those cultivars (Andersen 1971).

Probably the most obvious stresses to which plants are subjected are those which arise from their being widely exploited as food for animals. Some grazers such as the locust show little specialisation in their diet. Others can be quite specific, and have apparently arisen because of remarkable co-evolutionary events which allow certain animals to exploit highly toxic plant tissues. This can be seen in the case of the moth *Tyria jacobaea*, the food plant of which is the highly toxic *Senecio jacobaea*, avoided by all but a very few herbivores. Specialist feeders (pests) such as the corn borer in the United States, and the brown plant hopper on rice in parts of India and the Philippines, and many others, are major problems for farmers.

On the other hand many areas of the world have been dominated by grasslands which have been subjected to grazing by wild herbivores for thousands of years, as in the case of the semi-arid grasslands of Australia, the north American prairies, and the rangelands of Iran. The key to their survival lay in the naturally controlled grazing they were subjected to, where herbage availability determined the numbers of grazers. In present day agricultural grasslands, provided grazing intensity and grass productivity are kept in strict balance, similar degrees of stability can be maintained over long periods of time. This can be seen in the case of old pastures, dominated by *Lolium perenne* and *Trifolium repens*, on reclaimed saltings on the Romney Marshes in Kent, England, which have been grazed for at least 400 years (Kerridge 1967). Disruption of this delicate balance between grazing intensity and herbage availability can lead to sward deterioration, loss of native species, or whole communities. This has happened following the settlement by European farmers of lands previously supporting wild herbivores and inhabited by native non-farming peoples. In the semiarid grasslands of Australia a number of summer growing grasses were widespread until the introduction of sheep and cattle in the middle of the last century. Of the five main grass genera then present, only one, *Chloris acicularis* remains – as a sparsely distributed tussock grass. It is dormant in winter, and depends upon effective summer rain for vegetative growth and seed production. The dominant grass is now *Danthonia cespitosa* which differs from *Chloris acicularis* in its phenology, commencing growth in response to rain in all seasons. A long-term experiment (Williams 1970) showed that grazing by sheep tended to enhance the survival of *Danthonia*, despite its being preferred grazing for the sheep. In contrast, prevention of grazing caused a marked reduction in numbers surviving. In *Chloris*, whereas survival and plant numbers increased when grazing was prevented, plant numbers declined markedly with grazing because the plants grew whenever adequate summer rains fell, so that any growth was grazed off, and flowering was prevented. Where overgrazing or mismanagement does not eliminate communities, it may result in the rise to dominance of unpalatable species which are left largely ungrazed, with almost complete extinction of more palatable species, as has happened in the north west of the present USA where vast areas of mixed stands of the unpalatable *Aristida longifolia* and the palatable *Agropyron longifolia* have been replaced by almost pure stands of *Aristida* as a direct consequence of over-exploitation by cattle grazing (Evans & Tisdale 1972).

Pressures to increase food production to meet the demands of world population growth have had unforeseen effects in certain areas. For example high temperature stress has significantly limited the area available for growing rice in Pakistan, Iran, Saudi-Arabia, Egypt, and many parts of tropical Africa. In parts of S.E. Asia in order to increase rice production it is now widely grown as two crops per year whereas formerly it was grown as a single crop per year. In some areas this frequently results in the first of the years two crops flowering and maturing when high temperatures induce male sterility, rice spikelets having zero fertility when kept at a temperature of 41°C for one hour. IRRI has therefore examined the possibility of exploiting varietal differences in response to high temperature sensitivity. Of three varieties initially exposed experimentally to high temperatures, at 35°C two had 80% and 90% fertility, the third only 20% fertility and at 38°C one variety had 60% fertility, whilst the other two had less than 5% fertility. Breeding for improved high temperature tolerance thus seems possible.

It is not known why these particular rice varieties were heat tolerant. However there is rather convincing evidence that wild plants and animals which have wide geographic distributions may exhibit adaptive shifts in enzyme kinetics in response to specific environmental factors such as temperature. Primary metabolic processes may be adjusted to particular temperature regimes through differing thermal properties, and regulatory catalytic modifications of enzymes involved in carbon metabolism. Such developments may be the product of evolutionary changes which fit enzymes to a particular thermal environment (Hochachka & Somero 1973). Much of the evidence for such adaptations comes from work with fish and amphibian populations, but there is parallel evidence from several plant species. In *Lathyrus japonicus* populations collected in northern north America, from 55°50' N in Quebec to 46°05'N in New Jersey (Simon 1979) showed variations in NAD malate dehydrogenase (MDH) activity in response to temperature. Clones from each of 8 populations were grown (acclimatised) in three temperature regimes (night/day; 7°-15°C; 15°-25°C; 22°-30°C) to assess possible acclimation effects, and enzyme thermostability. Plants from warm summer temperature sites had higher MDH activation energies (twice those of plants from cooler summer sites), and greater levels of MDH activity at high temperatures, except when acclimatised at low temperatures. Warm summer plants also had enhanced MDH thermostability, suggesting an adaptive response to maintain catalytic efficiency over the temperature range of the growing season. Thermostability remained relatively stable despite experimentally manipulated temperatures during growth, suggesting a genetic component controlling enzyme thermal stability. Similar findings which show relationships in plants between enzyme thermo-kinetics and environment temperatures have been reported by Simon & al. (1986) in North American *Viola* species, and by McNaughton (1972, 1974) in *Typha.* Overall there is fairly convincing evidence for adaptation in these species at this level of organisation, suggesting perhaps much wider adaptation to high or low temperature stress.

At a more fundamental level of organisation it is known that across a broad range of organisms, a specific group of compounds, termed heat shock proteins, (HSP), are produced in response to heat stress, the product of stress-altered gene expression. Seedlings moved to a temperature 5 or more degrees above optimum growing temperatures, synthesise, transcribe, and translate a small number of these heat shock proteins with a response time of less than 5 minutes, whilst at the same time the synthesis of most normal proteins and mRNAs is repressed. This type of heat shock response is highly conserved across a very wide range of Eukaryotes and some Prokaryotes and the molecular mechanisms of heat induction of HSPs are also similar, suggesting that the production of HSPs is a fundamental adaptive process for surviving high temperatures. Perhaps the most compelling argument for that function comes from evidence that the temperature of maximum HSP synthesis in a group of species is positively correlated with their optimum growth temperatures. Elevated expression of many HSPs can be brought about by other stress conditions, such as ethanol, heavy metals, glucose starvation, and arsenite. HSP based selection may have some future role in breeding to increase heat tolerance in plants. However, the genetic control of HSP inheritance is not known. Inevitably perhaps, the author of a recent review article about HSPs (Vierling 1991) suggests that breeding can only be possible when the mechanism of HSP induction, and the roles of HSPs are known.

Perhaps the most obvious vehicle of stress for terrestrial plants is that due to lack of water, a major factor on a world scale affecting the zonation of natural vegetation – desert to tropical rainforest – and contributing in a major way to limited crop productivity and distribution. In desert areas mean primary productivity is less than 1 g m^2 y^{-1}, whereas when water is not limiting, productivity can be as high as 20 g m^2 y^{-1}. In south east England irrigation can result in 10-15% increases in barley yields due to reduced water stress in the crop. Maize as a grain crop in Europe is limited by water availability in the south, and by (low) temperature in the north. Predicted climatic warming may increase the water demands of maize, which may be critical for its exploitation as a crop grown almost entirely under irrigation in Spain and Greece. The problem may be particularly difficult in Spain where there is already concern about use of ground water for irrigation (Kenny & Harrison 1992).

Wild plants may drop their leaves in response to seasonal dry conditions, root systems may penetrate deeper into the soil in response to drought, whilst on a day to day schedule stomatal closure may control water loss. Water stress is another factor which has had a remarkable impact upon evolutionary diversification. The dwarf shrubs *Zygophyllum dumosum* and *Artemisia herba-alba* are a feature of desert areas in the Middle East with annual rainfall of between 26 and 90 mm y^{-1}. Both survive by conserving water. *A. herba-alba* sheds its leaves with petioles, whilst *Z. dumosum* sheds only its leaf blades. The epidermal cells of the petioles (which remain on the plant), begin to elongate, to divide, and to develope thickened outer walls, processes which result in sunken stomata unable to open fully. Both species successfully avoid water deficits, a strategy which promotes drought tolerance as an alternative to tolerance of water deficits by maintenance of cell turgor, the production of protective solutes, and mechanisms relating to efficient water use.

It is common knowledge that different crops are preadapted to different water availability regimes. However selection and breeding for drought tolerance within a particular crop is not simple. Whilst there are many possible characters which may be used as selection criteria – a list of 21 selection criteria has been produced for sorghum – problems arise because the best combination of characters to use depends upon the crop, the climate, and the farming system that will grow the end product. Use of whole plant response to drought, and particularly the development of desiccation tolerance tests on seedlings using PEG in hydroponic systems which allow the rapid screening of many thousands of seedlings, would seem to hold greater promise for drought tolerance breeding than the more sophisticated mechanism based tolerance tests that have been proposed. Successful selection of a group of barley lines with enhanced drought tolerance based simply on mature plant grain yield in trials under low rainfall conditions, was made from segregating F_2 generation material by Ceccarelli (1987). A second group of lines was selected for high yield under more favourable rainfall conditions. Grown at a low rainfall site, these selections had significantly lower yields than the lines selected at the low rainfall site, suggesting that genes for increased yield in favourable conditions differ from genes controlling yield in unfavourable conditions, these latter actually reducing yield in stress conditions.

It is clear from this brief account that adaptive responses to stress can differ broadly between families, and extend with increasing degrees of subtlety to differences between genera, species, and populations.

The fact that selection can bring about the evolution of such tolerance implies that adaptive variation must also exist at the level of individuals within populations, the raw material for evolutionary change.

It is variability at inter- and intra-population levels which are of greatest importance to the breeders of cultivated species, and hence requires the greatest efforts for conservation, and assessment. I stress assessment, because from a biological point of view, germplasm resources which remain permanently unassessed are of little more value than populations which have become extinct.

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