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Plant Stress As Initiated By Environmental and Biological Factors - A Review

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Abstract: Plants are affected by environment during all phases of growth and development. The impact of selected environment factors is discussed with emphasis on the definition of stress, stress and disturbance, metabolic flexibility in relation to the environment Abiotic and Biotic Environments cause stress, specific and unspecific Reactions to Stress ,water ,temperature, light, Atmosphere and Nutrients.
Keywords: Plant, stress, environment, water, temperature, light, abiotic and biotic factors

INTRODUCTION

Environmental stresses represent the factors which most limit agricultural productivity worldwide. These stresses not only have an impact on current crop species, but they are also significant barriers to the introduction of crop plants into areas that are not currently being used for agriculture. Stresses associated with temperature, salinity and drought, single or in combination, are likely to enhance the severity of problems to which plants will be exposed in the coming decades. Major efforts to breed for traits that confer tolerance of drought, cold, heat, nutrient, and salinity stress are already made each year throughout the world. An understanding of the mechanisms that regulate form and function, and the significance of those processes to plant physiology, ecology and agriculture must include knowledge of plant stress physiology. Metabolic, anatomical and morphological responses to stress are some of the primary processes of microevolution by natural selection. Therefore, one of the major forces that shapes the structure and function of plants is environmental stress. The significance of adaptive responses to environmental stress also is highlighted by the many cases of convergent evolution in plants. Similarities in form and function among phylo genetically unrelated plants are often a consequence of environmentally driven coevolution. Because the term stress is used, most often subjectively, with various meanings, the first aim of the present paper is to clarify the physiological definition, and the appropriate terms as responses in different situations. The paper will secondly summarise the Strasser’s state-change concept where stress, in the sense of the physiological state, is the condition caused by factors that tend to alter an equilibrum. The paper shows finally that this concept can be applied to situations encountered during plant tissue cultures.

Definition of Stress

The term 'stress' originates from experimental physics, where an object is under stress, when an external (usually mechanical) force, the stressor, is impacting it. Once stress is perceived by the object, its body will be under a certain strain. If the stressor's impact, and thus the strain it exerts, exceeds the resistance of the body, the object will undergo lasting deformation or break. This stress concept had later been adopted by medical sciences and by psychologists, from where it made its way to biology. Common stress situations in biology are drought or anoxia resulting from water logging, excessive low or high temperatures, excessive solar radiation loads, severe shortage of nutrients, high concentrations of certain chemicals (salts, heavy metals), infections by pathogens, mechanical stress (bending, tearing) etc.

Distinction between Stress and Disturbance although they are often not different in the net outcome for an organism (e.g. death or significantly reduced growth), it has become another established convention to make a distinction between stress and disturbance. Stress is normally considered an impact that affects the functioning of an intact organism. Disturbance is considered an impact that physically (mostly mechanically) removes parts of an organism or destroys it [1]. There are some impacts which can be both a stress and a disturbance. For instance, pathogens may first stress plants. Once their impact reaches an “outbreak” dimension and induces a loss of biomass or destroys a complete population, they become a disturbance. Classical examples for disturbance are grazing (both the removal of forage as well as trampling effects) or browsing by animals, fire or floods or the damaging impact of strong wind on forests. Typical ground disturbances are also associated with the activity of burrowing animals.

Metabolic flexibility in relation to the environment

Plants, particularly in temperate climates, live in an environment that changes, not only seasonally, but also from one moment to the next. These rapid environmental changes largely involve fluctuations in light and temperature. Such plants grow over a wide range of temperatures and, apart from encountering large seasonal variations in temperature (including freezing), the aerial parts of the plant may face temperature variations of tens of degrees centigrade in a single day and smaller temperature changes in a matter of minutes.

Many of the environmental factors, which fluctuate, are associated intimately with metabolic processes. Variation in light, which supplies energy for photosynthesis, has immediate effects on metabolism, while water deficit decreases stomatal conductance and therefore limits carbon dioxide supply and changes the balance between photosynthesis and photorespiration. The source (nitrate vs. ammonium) and concentration of nitrogen influences the location (root or shoot) and rate of nitrogen assimilation into amino acids and therefore requires a dynamic balance between photosynthesis, carbon partitioning and nitrogen assimilation. Thus the environment around plants fluctuates regularly and predictably under daily and seasonal cycles. The flexibility of their metabolism allows plants to deal with their constantly fluctuating environment. Co-ordination of plant metabolic activity with the surrounding environmental factors (i.e. abiotics and biotics: temperature, water, light, UV radiation, mineral nutrient, oxygen supply, bacteria, myccorhizal fungi...) has major effects on plant growth. Stress arising from unpredictable environmental variations causes partitioning changes in the plant that are plastic, but the degree of response is under intraand inter-species genetic control. When the environmental stress is relatively predictable over the life span of a plant, responses to the stresses become genetically fixed in the plant, leading to evolution of ecotypes or landraces. Consequently stress responses will govern the level of tolerance, ultimately affecting productivity and temporal stability to less than optimal habitats.

Abiotic and Biotic Environments Cause Stress

The environment affects an organism in many ways, at any time. To understand the reactions of a particular organism in a certain situation, individual external influences, so-called environmental factors, are usually considered separately, if at all possible. Environmental factors can be of abiotic and biotic nature. Biotic environmental factors, resulting from interactions with other organisms, are, for example, infection or mechanical damage by herbivory or trampling, as well as effects of symbiosis or parasitism.

Abiotic environmental factors include temperature, humidity, light intensity, the supply of water and minerals, and CO2; these are the parameters and resources that determine the growth of a plant. Many other influences, which are only rarely beneficial to the plant (wind as distributor of pollen and seeds), or not at all beneficial or are even damaging (ionising rays or pollutants), are also classified as abiotic factors. The effect of each abiotic factor depends on its quantity. With optimal quantity or intensity, as may be provided in a greenhouse, the plant grows “optimally” and thus achieves its “physiological normal type” maximizing its physiological achievable performance. Plants almost never find the optimal quantities or intensities of all essential abiotic factors. Thus the “physiological normal type” is rather the exception and deviation from the rule [2].

It is very important to realise that growth is only one of many reactions of a plant to its environment. Flowering and fruiting determine the plant’s success in reproduction and propagation and might equally be used as a measure of the plant’s reaction to the environment. The value of the factors might, in this case, change but the principal behaviour would be similar. Deviations from the physiological normal type are regarded as reactions to suboptimal or damaging quantities or intensities of environmental factors, i.e. situations for which we use the term stress. Thus stress and reactions caused by it (stress reactions) can be used as a measure of the strength of the stress on a scale of intensity, ranging from deficiency to excessive supply. Environmental factors deviating from the optimal intensity or quantity for the plant are called stress factors. The optimal quantity can, in fact, be zero, e.g. with xenobiotics. Stress factors which could potentially influence the plant are listed. If the dosage is inappropriate, stress is caused, as is obvious with the effects of the following factors: light (weak light, strong light),temperature (cold, heat), water (drought, flooding), nutrients (lack of ions, over-fertilisation, salt stress), carbon dioxide and oxygen (photosynthesis, respiration/photorespiration, oxidative stress, an aerobiosis; Optimal intensities and concentrations of these may also differ not only for individual organisms, but also for particular organs of the same organism [3].

Environmental noxae are stress factors which trigger stress reactions when applied in any concentration or intensity: UV-B, ozone, ionizing radiation, xenobiotics, heavy metals and aluminium. In this context, electrical and strong magnetic fields can also be considered as stress factors. Endogenous stress may also occur, for example, by separating an organ from its water supply, as is the case during ripening of seeds and the desiccation of embryo and endosperm. Usually, an organism is subjected to several stress factors, e.g. lack of water and heat, or a “secondary” stress factor follows a “primary” one: When the plant lacks water and closes its stomata, internal CO2 deficiency occurs when the plant is illuminated, and as a further consequence oxidative stress ensues. Combination of several stress factors is the normal case and is referred to as multiple stresses.

WATER

Water is required by all living organisms. Plants can be stressed by lack of moisture as well as an excess of moisture. Brown reported that the availability of water was the most important environment factor limiting growth and survival of range plants. He indicated that water deficits developed in plant tissue when rate of transpiration exceeded that of water absorption. Risser (1985) [4] reported that the high positive correlations found between available soil moisture and forage production were related to a decrease in net photosynthesis as leaf water potential decrease. Hasiao (1973) [5] presented a sequence of events that occurred when a plant was growing in a moist situation and then encountered moisture stress. A slowdown of root and leaf growth was growth was listed first. In his discussion on the relation of water stress to long term growth and yield, he elaborated on the fact that cell growth was generally more sensitive to water stress than was stomatal opening and CO_2 assimilation. He further emphasized that mild moisture stress may not affect photosynthesis, but it can reduce the development of leaf surface area. Whether the reduction in leaf surface area affects dry matter yields to stress should be greater in a growing crop with a low leaf area index (leaf area per unit land area) that is limiting the crop's assimilation of co_2 than in a crop with a high leaf area index that is not limiting assimilation of CO_2

Slayer (1974) [6] reported that the most obvious effects of prolonged water stress on shoot development were reduced internode length and reduced leaf size. He stated that effects on leaf size, rate of leaf expansion, and rate of appearance of new leaves had profound effects on total dry matter production. Photosynthetic area increased less rapidly, and also stomata tended to become nonfunctional more quickly on order compared to younger leaves. Slayer (1974) [6] summarized the effects of water stress on annuals as; (1) reduced leaf size and internode length, (2) stunted tops of plants, (3) suppressed root growth in proportion to shoot growth, (4) delayed time of flowering and fruit set although they occurred at similar ontogentic stages as well watered species, (5) reduced seed number, size, and viability, and (6) halted growth and development with severe stress, following by death.

Slayer indicated that a similar general effect of reduced leaf size internode length could be expected on shoot development of perennial grasses. Root growth, however, could continue if roots were growing in moist soil. This continues growth resulted from the fact that root growth was controlled more by local levels of soil water potential than by mean plant-water potential. With increasing stress, reproductive development may be delayed, and floral initiation may not occur. With severe stress, shoot dieback may occur, but new tillers will develop from basal buds when water becomes available. Woody evergreens respond similarly to perennial grasses; shoot growth may cease, but root development will occur in moist soil (Slayer 1974) [6]. The pattern of shoot development may, however, be affected for long periods where growth is mainly seasonal and is based on development of over wintering buds. Water stress during bud development can affect subsequent vegetative and reproductive shoot development. Slayer suggested that the number of leaves and flowers will be controlled by water stress during bud development; but leaf size, shoot length, amount of fruit set, and final seed size may be more influenced by water stress during the post winter period.

Excess moisture is tolerated by some plants but not by others. One has only to look at the ecotones that occur between stands of big sagebrush (*Artemisia tridentata*) and silver sagebrush *(Artemisia cana*) or to look at the death of some plant species. Ganskopp (1986) [7] noted that several workers found excessive soil moisture detrimental to big sagebrush [8-10] and others have speculated that anaerobic conditions in some soils prevent successful colonization of big sagebrush [11]. In flooded environments, oxygen is absent or more often in short supply, and the normal exchange of gasses from roots to soil is frequently disturbed [12]. Kozlowski (1984) [13] reported that flooding rapidly depleted soil oxygen, altered plant metabolism, and thereby inhibited growth. He indicated that flood tolerance varied widely among plant species, cultivars, and ecotypes and was associated with both morphological and physiological adaptations.

TEMPERATURE

Scientists have long recognized the importance of temperature in regulating rates of physiological processes and influencing growth and development of plants. Larcher (1980) [14] stated that sufficient but not excessive heat is a basic prerequisite for life. Each vital process id restricted to a certain temperature range and has optimal operating temperature on either side of which performance declines. Laude (1974) [15] stated that temperature response is conditioned by the level of other factors of the environment. Two examples are the associations of temperature with moisture and radiant energy with temperature. Cooper and Tainton (1968) [16] reported that the optimum temperature for growth (dry matter increase or relative growth rate) occurs between 20^0 and 25^0C for most temperature Festucoid (C_3) grasses. Growth rate drops rapidly below 10^0C, but some growth occurs at 5^0C, and the plant remains healthy. Growth is reduced above 25^0C and may cease above 30-35^0C, even with adequate soil moisture. Sub-tropical, non-Festucoid (C_4) grasses have an optimum of 30-35^0C and grow extremely slow, if at all, at temperature below 10-15^0C. Exceptions occur in some species with optimum temperature shifting according to local conditions [17].

Berry and Bjorkman (1980) [18] reported unequivocal evidence that inhibition of whole leaf photosynthesis by high temperature is caused by a disruption of the functional integrity of the photosynthetic apparatus at the chloroplast level. They also reported that dark respiration is more heat resistant than photosynthesis occurs before any inhibition of dark respiration or other symptoms of high temperature injury can be detected in leaf tissue. Levitt (1980) [12] stated that when high temperature was the primary stress, a water deficit was induced which subsequently caused minerals nutrient deficiency.

Cold temperature can affect plant productivity by delaying initiation of growth I spring, restricting water movement to roots, decreasing permeability of the membrane on the root surface, and delaying opening of stomata on a daily basis, thereby reducing the duration of daily photosynthesis. Freezing temperature can also injure and kill plants. Smith (1964) [19] reported that winter injury and death of forage plants is a major hazard of grassland farming in many areas of the world; mortality occurred frequently where below freezing temperatures prevail for long periods. Winter injury can result from low temperature, smothering, and desiccation [19]. Soil or snow cover may provide some insulation for crowns of plants. Temperatures alternating above and below freezing can cause damage through raid freezing of plants cells, deacclimation or decrease on frost hardiness, and frost heaving.

Burke *et al.;* in 1976 [20] also reported that freezing injury is a major cause of crop loss and that low temperature is reputedly the single most that stresses of late spring and early fall frosts, low mid-winter minima, and rapid temperature changes cause various types of injury directly and indirectly associated with freezing of water in plant tissues. Injuries include crown kill in winter cereals, biennials, and herbaceous perennials; sunscald on thin-barked tree species; winter burn to evergreen foliage; blackheart and frost cracking in xylem of trees and shrubs; blossom kill; death of buds and bark in plants which lose hardiness rapidly during transient warm spells in winter; and out -right death of tender annuals. Low temperature responses of most pants appear to fall between the 2 extremes of either being killed at the moment they freeze or tolerating extremely low temperature (196^{0}C) in midwinter. Plant responses and freeze resistance, however, may change markedly with season and stage that plants growth.

Burke *et al.;* in 1976 [20] stated that plants varied in their ability to tolerate ice crystal formation in tissues. Some became acclimated extensively in response to endogenous factors and the environment factors of temperature and day length. Some acclimated only a few degrees, while others did not acclimate at all. Smith (1964) [19] indicated that hardiness developed most rapidly with shorter days and decreasing temperature and hardiness could be retarded by warmer temperature accompanied by abundant soil moisture. Factors reducing plant vigor such as defoliation, disease, and lack of nutrients all effectively reduced acclimation [19].

Smith (1964) [19] reported hat winter injury was usually more serious in a stand of old plants than in a stand of younger plants because: (1) old plants are likely to be weakened by invasions of disease and insects, (2) the fertility level of soil under an old stand is likely to be limiting, and (3) older stands have fewer plants per unit area than young stands. He indicated that evidence of injury to forage plants becomes apparent as growth begins in the spring. Injury plants begin growth slowly, are yellowish in color, and may have only a few stems per unit. Time is required for healing of tissue if plants are going to survive and regain vigor. Winter kill had been reported for several shrub species growing on rangelands. These include mountain big sagebrush (Artemisia tridentate subsp. vaseyana) [21], fourwing saltbush (*Atriplex canescens*) [22]. Bitterbrush (*Purshia tridentata*) [23], and showbrush (*Ceanothus Velutinus)* [24].

LIGHT

Photoautotrophic higher are dependent on light for survival [25]. The supply of light to an area of land is the most reliable environment resources for plant growth since cloud cover causes the only serious variation in light climate at any point on the surface of the earth [26]. Light varies in intensity, duration, quality, and angle of incidence in both daily and annual cycles. Decrease light can become a limiting factor to plant growth when shading occurs; one major effect of shade is to slow the rate of photosynthesis relative to respiration [26]. Thus, even an efficiently photosynthesizing plant may not grow if its respiratory burden becomes too large.

Solar radiation capture by individual's plants is a function of several factors including leaf size, angle of displayed, pubescence, age, and physiological condition [27]. Since leaf surfaces are primary radiation interceptors, the amount of leaf surfaces is closely related to rate of growth in forage plants. Maintenance of a high leaf area index is very important for sustaining maximum growth rate. Broughman (1956) [28] suggested that maximum growth results when leaves are sufficient to intercepts 95% of the radiation. Donald (1961) [29] referred to an optimum leaf area index where every leaf was making a positive contribution to increase dry weight. As leaf area per plant population growing within an environment of limited light resources adjust its structure and growth rate a plant population growing within an environment of limited light resources adjusts its structure and growth rate to the available radiation. Perfect adjustment, however, is impossible because environments change. He indicated that plant canopies are usually compromises and balances between respiratory costs and photosynthetic advantages.

Daylength affects plants through phonological responses (flowering, etc.) therefore; it is difficult to determine the exact effect of daylength on other factors [30]. Mccloud and Bula (1973) [31] suggested that knowledge of the photoperiod responses of the various forage species would facilitate development of management systems that are best adapted to different climatic regions.

Specific and Unspecific Reactions to Stress

An organism that is stressed, for example, by elevated temperature, not only increases its metabolic rate, but other reactions occur which are usually not observed in the unstressed organism, or take place only to a very small degree. An example of this is the formation of "heat shock proteins". The modification of the basic metabolism could be interpreted as an unspecific reaction, whilst the production of heat shock proteins would be considered a specific stress reaction of the organism. The differentiation of these two components of a stress reaction is based on the findings of Hans Selye, a Canadian general practitioner, who, in the 1970s, summarized the various complexes of stress reactions of human beings as follows: "Everything which endangers life causes stress reactions and adaptive reactions. Both types of reactions are partly specific and partly unspecific." Contrary to plants there is, in humans, also a strong psychic -humoral stress component. The concept of both components of the stress reaction is complicated by the fact that even the specific reactions often lack specificity: The abovementioned heat shock proteins also assist the folding of proteins during synthesis and after denaturing, not only by high temperature stress, but also under other stresses. They are produced in high amounts, for example, under stress by xenobiotics (e.g. heavy metals).This does not exclude that there are in addition more specific responses by which an organism differentiates between stress by heat and by heavy metal.

There is yet another facet to the question of specificity of stress reactions which is described by the term cross-protection. Previous drought stress or salt stress (osmotic stress) is known to harden plants against temperature stress, and particularly cold stress. Is this an unspecific stress response? The apparent lack of specificity of the adaptation is explained, on the one hand by considering the physiological effects of salt and drought stress on cells and, on the other, the effects of frost. All three factors lead to a partial dehydration of cells (in an ivy leaf at –7_C, ca. 90% of the total leaf water is frozen, forming ice, and thus is no longer available as free water; see Fig. 1.3.25). This causes problems with the stability of bio membranes in particular, as the lipid bilayers are stabilised by so-called hydrophobic interactions, which are disturbed if the availability of water, or the ion concentration at the surface of membranes, is drastically changed. If too much water is removed from the aqueous environment of the bio membranes (by evaporation or freezing), the concentration of solutes increases, e.g. in the cytosol or the chloroplast stroma. Increase in the ion concentrations in turn changes the charges at the surface of membranes, and as a consequence the membrane potentials. This usually leads to destabilisation of membrane structure. High charge densities, however, not only result from water deficiency, but also from excessive salt concentration. A general reaction to stress is the synthesis of hydrophilic low molecular protectants, so-called compatible solutes (sugars, sugar alcohols and cyclitols, amino acids and betaines, which replace water at the membrane surfaces and dislodge the ionic compounds upon loss of cellular water. Production of compatible solutes requires, of course, synthesis of respective enzymes, triggered by stress. Synthesis of these enzymes is often preceded by signals transmitted by certain phyto hormones – particularly abscisic acid (ABA) or the stress hormone jasmonate, but also ethylene, may transiently change their concentration. One ex- ample of such cross-protection is induction of frost hardening in wild potatoes by salt stress. Potato plants treated with NaCl are able to tolerate lower temperatures than untreated controls. A transient increase in ABA concentration mediates this hardening reaction.

Stress Concepts

Based on physical principles, Levitt (1980) published a theoretical understanding of stress reactions that is applicable to all groups of organisms, as illustrated by an abstract experiment.It is known as the physical stress concept. A body is deformed if it is stretched by a force (stress); this deformation is at first reversible ("elastic"), but upon intensifying the force it becomes irreversibly ("plastic") deformed and finally breaks. The change in the body caused by the force is called strain. The force required to produce a unit of change is the elastic modulus, M. In this sense, elasticity does not mean expansion in the sense of maximum elastic deformation. The modulus of elasticity M corresponds in principle to _, the elastic modulus of a cell wall, which is a measure of the cell wall's flexibility

$$M = \frac{\text{force}}{\text{deformation}} = \frac{\text{stress}}{\text{strain}}$$

According to this relation, M is also a measure of the resistance of the system to an externally applied force on the system. In biological systems, stress is not commonly a single physical force affecting the organism, but a load from many individual environmental factors. Primarily, metabolic processes are changed or deformed. The concept by Levitt convincingly explains the relation of stress and strain, but it can be applied to biological systems only to a limited extent, as the following, biologically important parameters are lacking:

Time factor: In a physical system, the amount of stress equals the strength of stress; in a biological system, the amount of stress is the product of the intensity of stress and duration of stress. For example, if one cools the tropical ornamental *Saintpaulia ionantha* (African violet) for a short time (6 h) to 5 _C and then returns it to the original temperature, some of the metabolic reactions may change their rates in accordance with their activation energy (Q10), but the increase or decrease in metabolite pools is not changed so dramatically that the plant is damaged. However, if the plant is left for a longer period (48 h) at 5 _C, metabolic chaos results, as individual metabolite pools empty whilst others grow disproportionally. The plant is damaged, in other words: Elastic strain has passed into plastic strain .

Repair: Plastic change or deformation is not completely irreversible. In most cases, the organism is able to repair the damage, if it is not too severe. One example is DNA repair after damage by UV irradiation. Plastic strain can change to elastic strain. Because of the open life form of plants, "repairs" can also be accomplished through premature Senescence or shedding of damaged.

Physiological responses

The duration, severity, and rate at which a stress is imposed all influence how a plant responds. Several adverse conditions in combination may elicit a response differing from that for a single type of stress. Features of the plant, including organ or tissue identity, development age, and genotype, also influence plant response to stress. At specific developmental stages, plants are either more or less sensitive to particular stressors. The sensitivity stages of development are called windows of sensitivity. A response may be triggered directly by a stress, such as drought, or may result from a stress-induced injury, such as loss of membrane integrity. Some responses clearly enable a plant to resist stressing, whereas the functional role of others is not apparent.

Do somaclonal variations and mutations simply represent accidents? Failure to compensate for a severe stress can result in somaclonal variation or mutation, in complete loss of organogenictotipotency, and ultimately in plant or cell death, directly or following a neoplasic progression. Mechanisms that permit stress survival are termed RESISTANCE mechanisms and can allow an organism to tolerate or avoid stress. Thus, physiological responses to stressors can be divided into three possibilities. In one case, TOLERANCE, plants have mechanisms that maintain high metabolic activity (similar to that in the absence of stress) under mild stress and reduced activity under severe stress. In contrast, mechanisms of AVOIDANCE involve a reduction of metabolic activity, resulting in a dormant. Strain as defined in the Strasser state-change concept state, upon exposure to extreme stress. Commonly, a plant species may have several tolerance or avoidance mechanisms, or a combination of both. For instance, drought stress may induce drought tolerance that can be followed by desiccation tolerance: in the later "dormant" state, the organism can survive the dry state for long periods, i.e. years. Notice that the ability to rehydrate without damage can be considered as a part of the desiccation tolerance. The other issue is immediate or delayed DAMAGES, through somaclonal variation, mutation, neoplastic progression, ultimate death via necrosis and/or apoptosis the intensity of stress (pressure to change exerted by a stressor) is not easily quantified. Stress could occur at a low level, creating conditions that are marginally non-optimal, with little effect expected. However, if this mild stress continues for a long time, becoming chronic stress, the physiology of plants is likely to be altered. In contrast, conditions could become difficult quickly, resulting in acute condition. This shock pattern of stress is likely to induce significant changes in a short time frame. Toxicologists, particularly those in the area of pollution studies, have developed the concept of dose. Dose is defined to be the magnitude of perturbation times the length of time the stress is applied. It thus accounts for the influence of both intensity and duration on physiological performance. Stress can be dramatic when it is applied for a short duration and high intensity, or when it is applied for a long duration at low intensity. Plant responses to chronic stress and acute stress may be very different even though the dose is the same. In plant stress physiology an important distinction must be made between ultimate (ADAPTATION) and proximal (ACCLIMATION) plant responses. Adaptation occurs by various mechanisms at the genetic level in populations over many generations. Micro evolutionary processes change gene frequencies of a population over time. In a stressful environment, it is logical to assume that specific genotypes with appropriate gene combinations (those that confer the ability to survive and reproduce) are dominant in the population. Those particularly favourable gene combinations in plants that inhabit stressful environments are called adaptations. Populations that have adapted through evolutionary processes acting at the genetic level to a particulars climatic regime are by no means static systems. On the contrary, plants have an incredible ability to adjust physiological and structural attributes on the scale of seconds or seasons within a single genotype: this is acclimation. In other words, during acclimation, an organism alters its homeostasis, its steady state physiology, to accommodate (further) shifts in its external environment. For instance, prolonged ex- Plant responses to environmental stress in correspondence with stress and plant characteristics. Posure of chilling resistant plants to cold results in the adjustment of plant growth and metabolism to low temperature conditions and in the increased resistance of tissues to freezing temperatures. Freezing resistance is the ability of plants to survive formation of ice in tissues. Systematic acquired resistance (SAR) against pathogens is another form of acclimation. On a long-term scale, acclimation is enhanced in plants because of the modular nature of metabolism and growth. Plant parts can be abscised and re grown in a new morphology or anatomy, specific organs can be enhanced by increasing their numbers or size. On a short-term basis (i.e. seconds or minutes), protein populations can ebb and wane, growth regulators can be released or activated, or transcription and translation can be regulated up or down. Acclimation is a phenotypic response to different combinations of environmental characteristics. Phenotypic plasticity is an index of the amount of acclimation that is possible within one genotype.

Thus, adaptation at the population level, or acclimation at the level of the individual plant, occur through a combination of behavioural, morphological, anatomical, physiological and biochemical processes, which depend on processes at the molecular level. As another example, plants have evolved varied and multiple mechanisms that allow them to survive heat stress. These include limiting or avoiding direct absorption of solar radiation, dissipation of excess absorbed radiation, and physiological mechanisms that counteract the effects of heat stress on metabolism.

All three strategies of tolerance are equally important for survival. These strategies of tolerance have arisen through the evolution of specific development sin plant morphology, anatomy and physiology. What is said above also means that, contrary to the general opinion, stresses must not be automatically associated with adverse detrimental effects. That is like the breathless and fatiguing training of a sportsman that prepares him for a greater performance.

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