1.1

Environment as Stress Factor: Stress Physiology of Plants

Plants are bound to places. They, therefore, have to be considerably more adaptable to stressful environments and must acquire greater tolerance to multiple stresses than animals and humans. This is shown very clearly by the limitations in the distribution of particular types of vegetation, for example, the tree line on mountains. Extremely high light intensities, mechanical stress by wind, frequent periods of frost, and a winter period of many months have left their marks on these spruces and pines at about 3000 m altitude on Mt. Hood in Oregon (USA). Photo E. Beck

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1.1.1

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 CO_2; 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

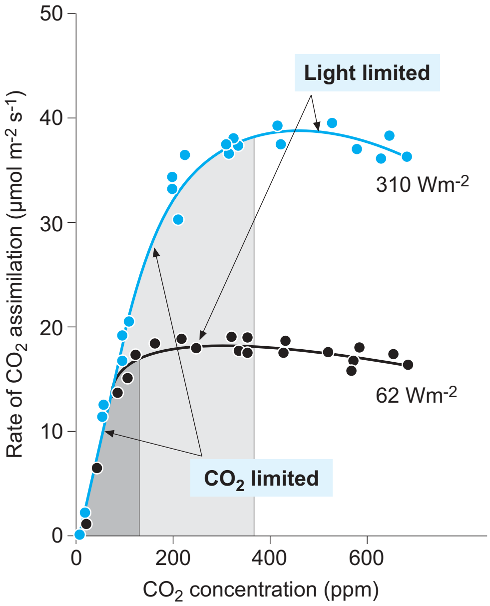


Fig. 1.1.1. Limitation of photosynthesis by CO_2 and light. The rate of photosynthesis of a sorghum leaf (*Sorghum sudanense*) is shown at different light intensities and CO_2 concentrations in air. (After Fitter and Hay 1987)

“physiological normal type”, maximising its physiologically achievable performance.

Plants almost never find the optimal quantities or intensities of all essential abiotic factors (Fig. 1.1.1). Thus the “physiological normal type” is rather the exception and deviation from the rule. 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 in Fig. 1.1.2.

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, anaerobiosis; Fig. 1.1.3). Optimal intensities and concentrations of these may also differ not only for individual organisms, but also for particular organs of the same organism.

Environmental noxae are stress factors which trigger stress reactions when applied in any concentration or intensity: UV-B, ozone, ionising 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.

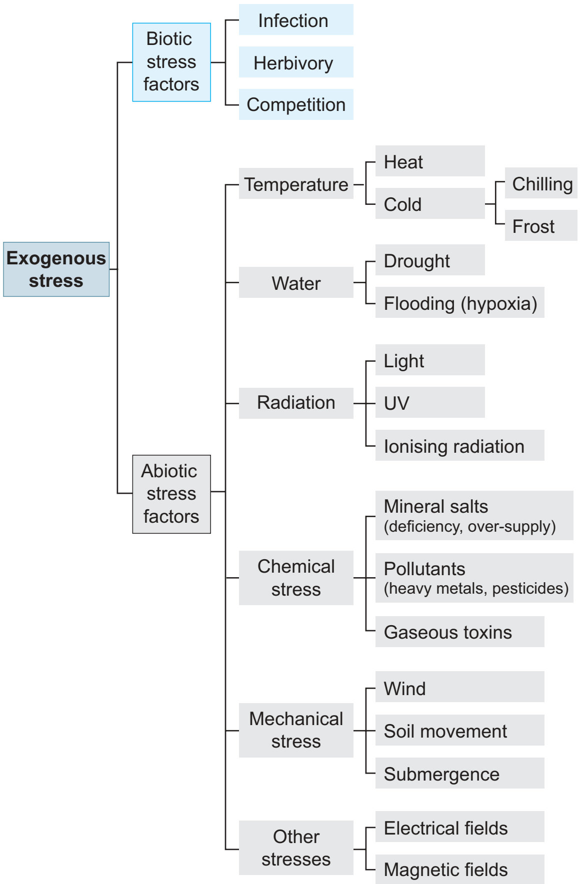
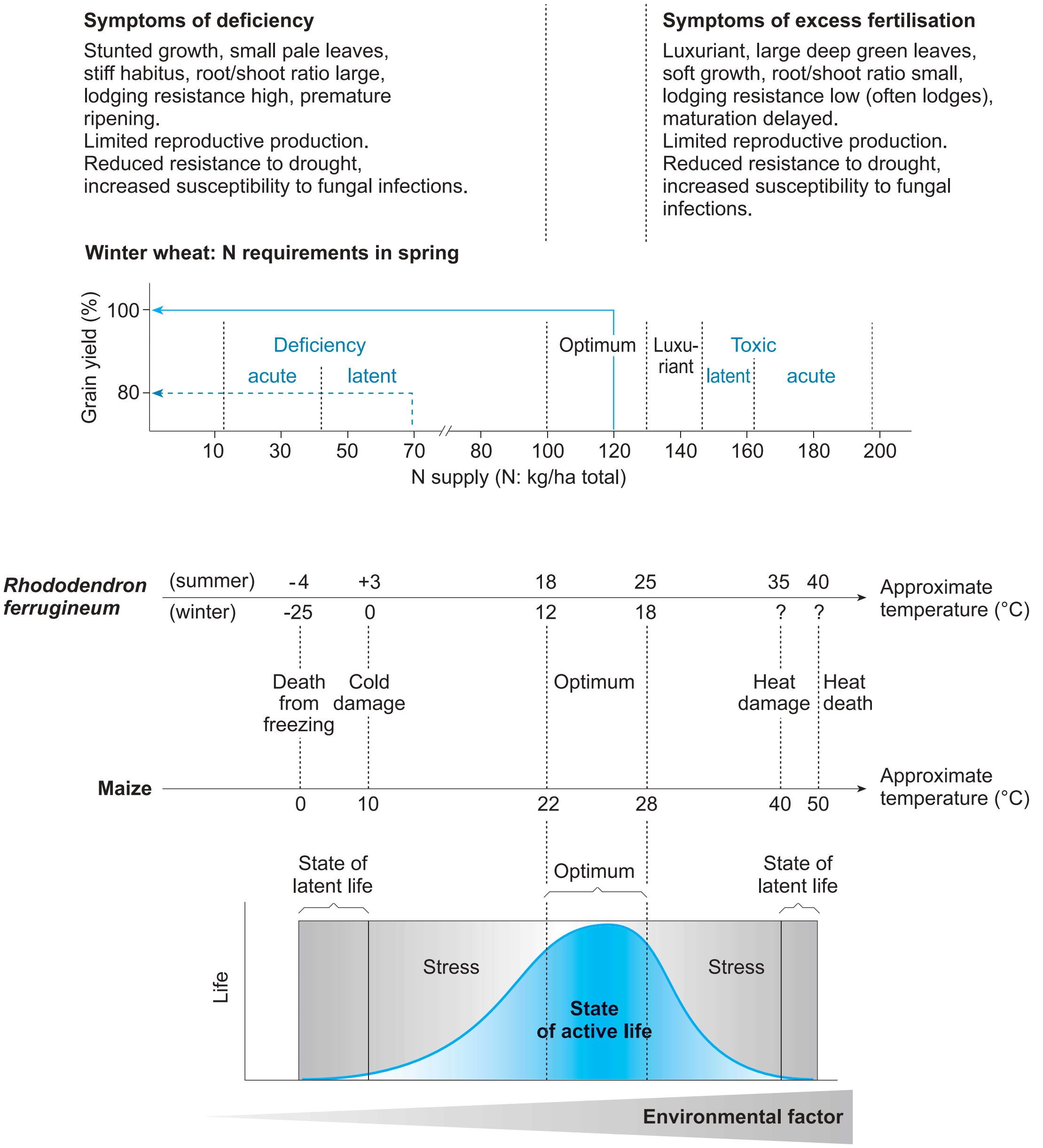


Fig. 1.1.2. Biotic and abiotic environmental factors creating stress for plants



Symptoms of deficiency

Stunted growth, small pale leaves, stiff habitus, root/shoot ratio large, lodging resistance high, premature ripening.
Limited reproductive production.
Reduced resistance to drought, increased susceptibility to fungal infections.

Symptoms of excess fertilisation

Luxuriant, large deep green leaves, soft growth, root/shoot ratio small, lodging resistance low (often lodges), maturation delayed.
Limited reproductive production.
Reduced resistance to drought, increased susceptibility to fungal infections.

Fig. 1.1.3. Life processes of an organism described as a function of an (abiotic) environmental factor. The **relative growth rate**, **R**, may be used as a measure of life processes:

$$R = \frac{\Delta \text{biomass}}{\Delta t} \times \frac{1}{\text{biomass}}$$

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 CO_2 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 stress.**

1.1.2

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” (see Chap. 1.3.4.2). 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 (1973), a Canadian general practitioner, who, in the 1970s, summarised 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 above-mentioned heat shock proteins also assist the folding of proteins during synthesis and after denaturing (see Chap. 1.3.4.2), 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 metals (see Chap. 1.7.5).

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 (Fig. 1.1.4). 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 biomembranes 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 (see also Chap. 1.3.5.2). If too much water is removed from the aqueous environment of the biomembranes (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, see Chaps. 1.5.2.6 and 1.6.2.3), 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 phytohormones – particularly abscisic acid (ABA) or the stress hormone jasmonate, but also ethylene, may transiently change their concentration. One ex-

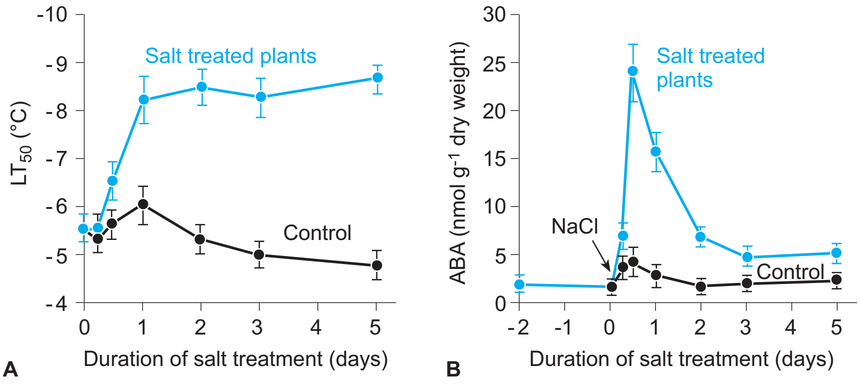


Fig. 1.1.4. Frost hardening through salt treatment. Cuttings of potato plants (*Solanum commersonii* Dun PI 458317) were grown in Murashige-Skoog medium to which NaCl was added (100 mM final concentration). A Frost hardiness of plants and B ABA content of plants. (After Ryu et al. 1995)

ample of such cross-protection is induction of frost hardening in wild potatoes by salt stress (Fig. 1.1.4). Potato plants treated with NaCl are able to tolerate lower temperatures than untreated controls. A transient increase in ABA concentration mediates this hardening reaction.

1.1.3

Stress Concepts

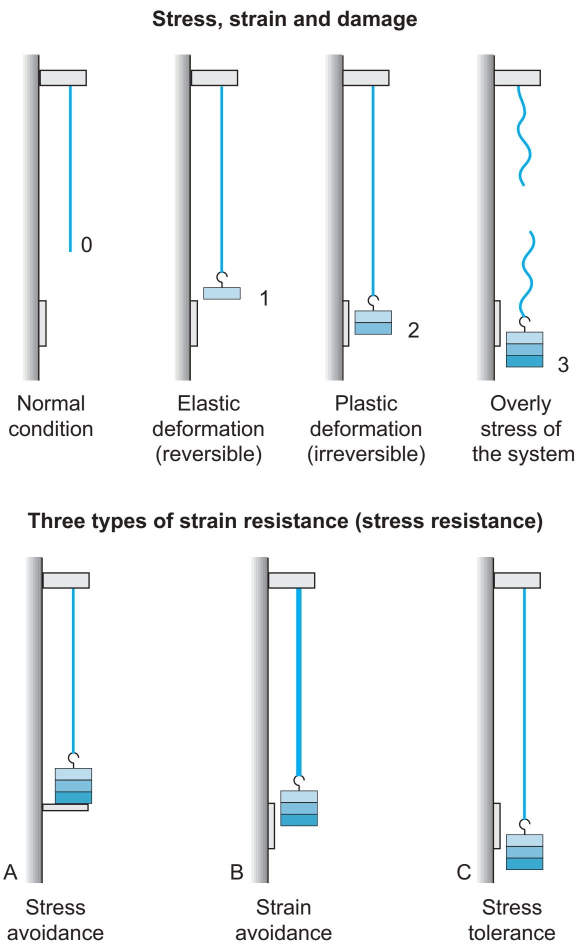
Based on physical principles, Levitt (1980) published a theoretical understanding of stress reactions that is applicable to all groups of organisms, as illustrated by an abstract experiment. It is known as the **physical stress concept** (Fig. 1.1.5). A body is deformed if it is stretched by a force (**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 ε, the elastic modulus of a cell wall, which is a measure of the cell wall's flexibility (see, e.g., Fig. 1.5.2)

$$M = \frac{\text{force}}{\text{deformation}} = \frac{\text{stress}}{\text{strain}} \tag{1.1 a}$$

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 (Q_{10}), 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** (Fig. 1.1.6).


Stress, strain and damage

Three types of strain resistance (stress resistance)

Fig. 1.1.5. The physical stress concept of Levitt (1980)

- **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** (see Box 1.2.4). Because of the open life form of plants, "repairs" can also be accomplished through premature senescence or shedding of damaged