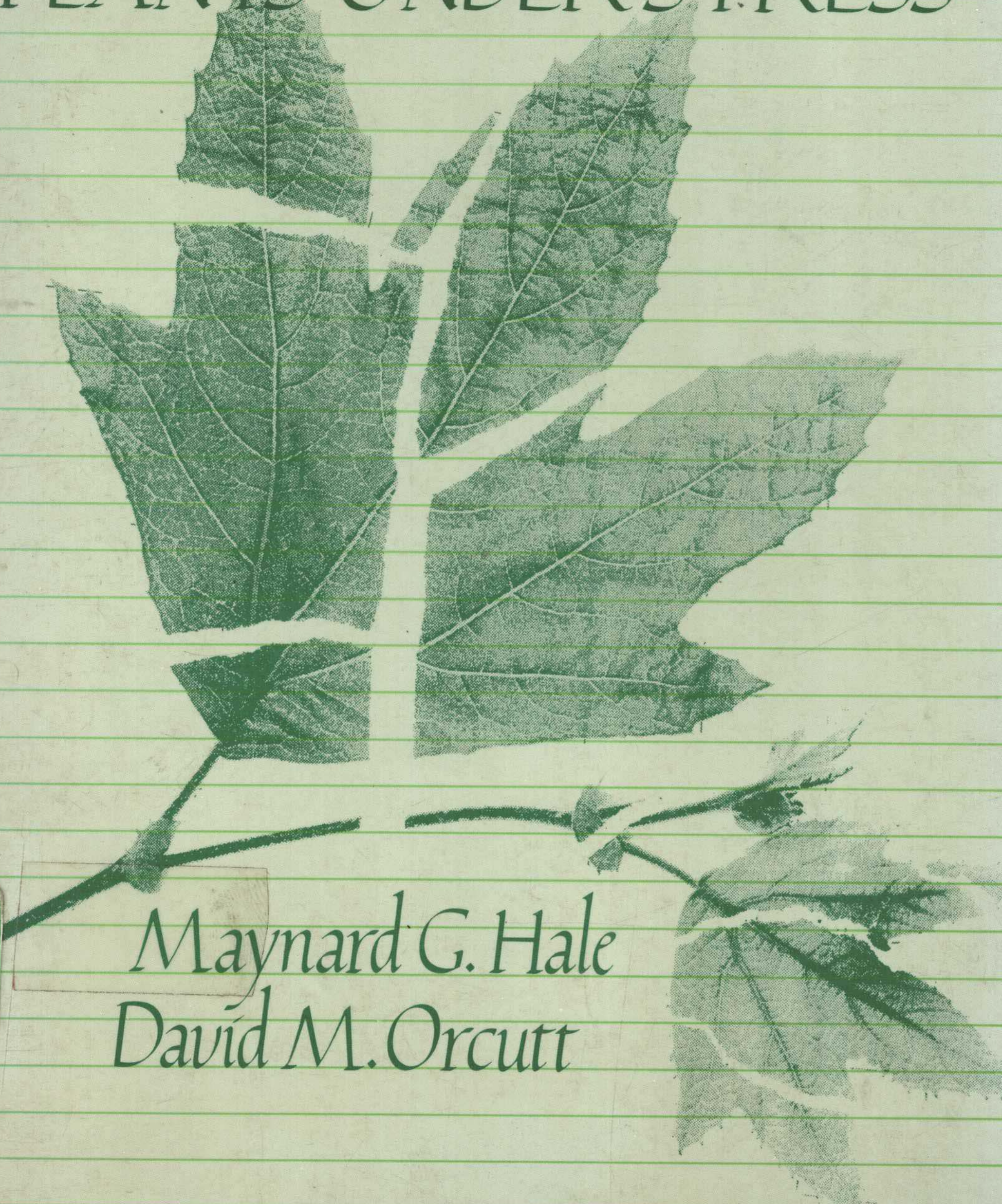
The PHYSIOLOGY OF PLANTS UNDER STRESS



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PREFACE

As the human population of the world increases and utilizes more land area for housing and industrial activities, agriculture is being forced into marginally productive areas. Drought, nutrient deficiencies and toxicities, salinity, temperature extremes, air pollution, and chemical interference are stresses often encountered. Alteration of environments and climates may also result from human activities that increase the stressful conditions under which plants must grow and survive.

Knowledge of the effects of various stresses on the physiology of plants is essential to an understanding of resistance and survival mechanisms and to breeding for stress resistance. Selection by humankind is more rapid for crop plants than the natural selection of evolution. Development of new cultural practices using technology to alleviate stress effects also depends upon a knowledge of the physiological reactions of plants to stressful conditions. Plants have characteristics that may enable them to survive aberrant metabolism, hormonal imbalances, and membrane disfunctions. The processes of tolerance and avoidance of the effects of stress are not completely known but there is a large body of knowledge accumulating, which we have attempted to summarize for those students in plant science who have a basic understanding of plant physiology.

For a number of years, the senior author has successfully taught a graduate level course in plant stress physiology, and the authors collectively have many years of experience in organizing and teaching courses in various aspects of plant physiology for all levels of students in agricultural curricula. This experience has been useful in writing with the student in mind.

The questions at the ends of chapters should be useful in stimulating discussion and thought. General and specific references have been carefully chosen from the vast literature for their clarity and pertinence to the state of knowledge.

We acknowledge the inspiration of all those students who have passed through our courses and who left something of themselves with us. It has been their enthusiasm and quest for knowledge that has encouraged us to attempt this textbook. We also thank our colleagues who have continued to encourage us and critically listen to our expositions of stress concepts and principles.

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TERMINOLOGY

It is important to understand the terminology that has evolved concerning plant stress, and we might begin with the question "What is stress?" What do we mean when we say a plant is under stress? Stress results in an aberrant change in physiological processes brought about by one or a combination of environmental and biological factors (Table 1.1). An inherent connotation in the term is that stress has the potential to produce injury. Injury occurs as a result of aberrant metabolism and may be expressed as reduction in growth, yield, or value, or death of the plant or plant part.

TABLE 1.1 Sources of Environmental Stress for Plants

Physical	Chemical	Biotic
Drought	Air Polution	Competition
Temperature	Allelochemicals (organic)	Allelopathy
Radiation	Nutrients (inorganic)	Lack of symbioses
Flooding	Pesticides	Human activities
Mechanical	Toxins	Diseases
Electrical	Salts	Insects
Magnetic	pH of soil solution	
Wind		

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Equally important is the question "When is a plant not under stress?", which leads to the concept of zero stress. Zero stress is that level of exposure to an environmental factor that leads neither to injury nor to reduction in growth, yield, or value. The concept of zero stress is related to the concept of optimum conditions for growth of individual species. Variations from optimum environmental conditions might result in stress. Therefore, there are degrees of stress ranging from zero to moderate to severe and the degree of stress is related to the amount of energy entering into the change of processes within the living systems. Zero stress seldom if ever occurs but it is an important theoretical concept.

A number of stresses cause injury without producing visible symptoms. Accordingly, stress injury can occur at a subclinical as well as at a clinical level. Diagnosis of stress effects is made more difficult as a result.

Whole plants can be resistant and survive stress injury, or some parts of a single plant may be resistant (seeds, buds, dormant cells) while other parts (meristems, succulent organs, seedlings) are susceptible. Through the processes of evolution a plant species can become fit or adapted to an environment in which it thrives. Natural selection causes those paths of evolution that are successful to survive and those that are not to perish. Survivors have a tolerance of injury from environmental factors that enables them to overcome partially or completely any adverse effects. Tolerance to a stress is the capacity of a plant to survive and grow even though subjected to an unfavorable environment; the plant can sustain the effects of stress without dying or suffering irreparable injury.

Such tolerance or resistance may change as a plant grows and develops so that at one stage of development a plant may be susceptible to stress induced injury but at another stage it may be completely resistant. In addition, a stress may change metabolism, a process called acclimation, and through such changes alter the morphology and render the plant resistant to that stress. Plants that become acclimated are hardened and can survive in the new environment.

Because of the timing of development in relation to the occurrence of a stress, some plants escape injury.

Levitt (1980) divides resistance to stress into tolerance and avoidance. Stress avoidance occurs if a plant does not come to thermodynamic equilibrium with the stress or can exclude the stress by means of a physical or metabolic barrier. Stress tolerance occurs if the plant comes to thermodynamic equilibrium with the stress but no injury occurs or injury that does occur is repaired. In the process of evolution, the selection has been toward avoidance mechanisms that are more efficient than tolerance mechanisms in causing resistance to stresses. Levitt's concepts, which involve an analogy to stress-strain relationships as used in physics, have not come into widespread usage and are somewhat confusing primarily because of the difficulty in recognizing the category of strain involved.

Examples of resistance to individual stresses are:

1. *Temperature.* Plants, with few exceptions, attain the temperature of the ambient environment. They are poikilotherms. Because of this, they must have some form of tolerance to temperature stress.
2. *Drought.* Terrestrial plants are normally turgid and, thus, resistance results from avoiding loss of turgor. Drought resistance should probably be divided into dehydration avoidance or postponement and dehydration tolerance (Kramer, 1980).
3. *Irradiation.* Because of the penetrating nature of radiation, plants cannot escape it. Tolerance of irradiation stress depends upon the intensity and duration of the radiation and the amount of energy absorbed.
4. *Salts.* Plants that grow with root systems in soil of high salt content have low osmotic potentials as a result of an increased concentration of solutes and are salt tolerant. Some plants are resistant because they have mechanisms by which they exclude salt or by which the salt is concentrated in vacuoles.
5. *Nutrient deficiency.* Tolerance of deficiency of a nutrient may depend on the ability of the roots to exude metabolites enabling them to obtain more of the nutrient from the soil, as with iron, or to use substitute ions such as sodium for potassium.
6. *Nutrient toxicity.* Much of the tolerance of toxicity is the result of the processes of exclusion at the root or by concentration in vacuoles of leaf cells. Either process prevents the toxic concentration from interfering with metabolism.

The reaction of plants to stress conditions may be pathological. It has been estimated that more than 50% of all plant diseases are caused by improper environmental, nutritional, or physical conditions. Such diseases are distinguished from those caused by infectious organisms or viruses and are referred to by terms such as noninfectious, abiotic, or physiogenic. Organisms that cause diseases in plants are called pathogens. Perhaps the term physiogens should be used for those conditions of the physical environment that cause disease and the process of development of such diseases is physiogenesis as distinguished from pathogenesis. The study of the physiology of plants under stress thus becomes the study of physiogenesis.

Additional terminology is included in the glossary. Because your concepts may change, you are encouraged to further develop the description of the terms as your knowledge of stress physiology increases and your circumspection of the terminology broadens. Understanding terminology is the key to understanding a new subject and in the rapidly expanding subject of stress physiology there is still disagreement on the usage of terms. We have tried to be consistant in the use of terms in the chapters that follow.

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2

DROUGHT STRESS

Drought is a meteorological term that means a lack of precipitation over a prolonged period of time. Sometimes physiologists refer to the resulting effect on plants as water stress but water stress may also occur over relatively short periods of time. Because ecologists have used drought stress frequently in their writings it is used in this chapter with water stress as a more specific term with the understanding that sometimes it is difficult to separate the two and they are often used interchangeably.

BASIC WATER RELATIONS CONCEPTS

Much has been written about the water relations of plants and the factors affecting them. General references at the end of this chapter may serve to review the subject. The diurnal cycles of water potential and osmotic potential have been described extensively in these references. Our purpose is to build on the fundamental knowledge of the physiology of water relations and to describe the chemical and physical changes in processes in plants that result when water loss is greater than water absorbed over extended periods of time. A summary of some of the salient concepts of plant-water relations will help establish a basis of understanding.

Water comprises 85 to 90% of the fresh weight of most living herbaceous plants. In higher plants, water is absorbed by roots from soil and is translocated to the shoots as a result of pressure gradients developed either from root pressure or transpiration. Whenever the rates of water loss by transpiration exceed the rates of water absorption by roots, water in the conducting tissues is subject to a tension (negative pressure), that is, its potential is lowered and competition for water among the various tissues and organs of the plant takes place because the equilibria among the separate water potentials have been disturbed.

The water potential (Ψw) in plants is the sum of turgor potential (Ψp), osmotic potential ($\Psi \pi$), and matric potential (Ψm). The relationship is given by the equation: $\Psi w = \Psi \pi + \Psi p + \Psi m$. Osmotic potential is created by dissolved particles, either molecules or ions, and is lowered in proportion to the number of particles in solution. Matric potential is the result of water adhering to surfaces and interfaces where the molecules of water become more ordered in arrangement and give up some of their kinetic energy. Activity of the water molecules is lost and the kinetic energy may be dissipated as thermal energy.

Turgor potential is created by water molecules bombarding the surfaces of membranes and cell walls retaining water in a closed system such as a vacuole. Turgor pressures are usually positive and are opposed by the membranes, the cell walls, or hydrostatic pressure caused by gravity in columns of water in the xylem tissues. Maintenance of turgor is necessary for growth and, if turgor decreases, wilting of parts of the plant may be visible. Turgor potential is the first component of water potential to be affected by water or drought stress.

A brief review of the status of water in the soil and how water moves through the soil may be useful in understanding how water reaches the surface of the root where it may be absorbed. Soil is composed mainly of particles and aggregates of various sizes interspersed with spaces filled with gases and water vapor or, under conditions of saturation, with liquid water. As water is removed from the soil by drainage, evaporation, or absorption by roots the continuity of the liquid water is interrupted. Some water remains on the surface of soil particles and some changes into vapor in the soil pore spaces. As more and more water is removed from the soil, that which remains is more tightly held on the soil particle surfaces. One can say that the water potential becomes lower and lower until it reaches a point at which a plant root can no longer remove enough water to overcome the deficit imposed by the loss in transpiration or other water-using processes. The plant may wilt and not recover even if transpiration is stopped by placing the plant in an atmosphere of high humidity. The plant has permanently wilted and the amount of water in the soil is at the permanent wilting point (PWP). The water potential in the soil at this point is somewhere between −1.0 and −2.0 MPa (megapascals, 1 MPa = 10 bars). Frequently, crop plants exist in a soil moisture range between −0.03 MPa and the permanent wilting point (−1.5 MPa) (Figure 2.1).

Water contacts roots in two ways: (1) the water may move to the root or (2) the root may grow and intercept moist soil. Movement of water in soil is most easily accomplished at saturation and follows Darcy's law for saturated flow. Darcy's law may be stated as

$$V = K \frac{\text{change in total } \Psi\text{w in soil in cm } H_2O}{\text{change in depth or distance}}$$

where K is the coefficient of hydraulic conductivity. Remember that Darcy's law is an expression for liquid water flow. As the water potential decreases to −1.5 MPa, the value of K decreases more rapidly to 10^{-3} that of the saturated soil value.

At low soil moisture content, the continuity of water films is broken and liquid flow no longer occurs. The contribution of the matric potential to water potential becomes higher in relation to the contribution of osmotic potential. Under these conditions, water vapor movement becomes important. Water may move along the surface of a soil particle, vaporize into a pore space, condense onto the surface of another soil particle, and move long distances by repeating the process. Temperature gradients in soil aid such movement and account for water vapor movement upward in winter and downward in summer.

The root–soil interface is a dynamic region. That portion of the soil that lies near the surface of the root and is influenced by chemicals and pressure from the growing root is often referred to as the rhizosphere. The rhizosphere is a dynamic ecosystem in which populations of microorganisms are often much greater than in the bulk soil. The root processes that result in exudation of chemicals, ions, and CO_2 into the soil, as well as those that result in water and ion absorption, occur here. However, the interface near the root tip is different from the interface some distance from the tip

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