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Review Article

Strategies of adaptation and injury exhibited by plants under a variety of external conditions: a short review

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Abstract

A wide variety of favorable or disadvantageous external conditions affect the growth, development and productivity of plants. Plants cannot avoid adverse environmental conditions (such as soil salinity, drought, heat, cold, flooding, heavy metal contamination, predators and pathogen infections) due to their sessile nature. Nature's wrath in the form of various biotic and abiotic stress factors adversely affect plant growth and productivity causing the loss of crop yield. These abiotic and biotic stress factors are a threat for plants, prevent them from reaching their full genetic potential and limit crop productivity worldwide. Stress cause injury, disease or aberrant physiology by imposing a constraint or highly unpredictable fluctuations on regular metabolic patterns of plants. These fluctuations are mainly associated with altered metabolic functions; one of those is either loss of or reduced synthesis of photosynthetic pigments. This results in declined light harvesting and generation of reducing powers, which are a source of energy for dark reactions of photosynthesis. Thus, this review article describes some induced changes in morphological, physiological and pigments composition in crops due to stresses and research progress in plant responses to abiotic stresses and biotic stresses is summarized from the physiological level to the molecular level.

Keywords: Abiotic stress, biotic stress, environmental stress, oxidative stress, signals transduction

Estratégias de adaptação e injúrias demonstradas por plantas sob diferentes condições ambientais: uma curta revisão

Resumo

Uma grande variedade de condições externas favoráveis ou desfavorável afeta o crescimento, desenvolvimento e produtividade das plantas. Plantas não podem evitar condições ambientais adversas (como a salinidade do solo, seca, calor, frio, cheias, infecções de contaminação, predadores e patógenos de heavy metal) devido à sua natureza séssil. Ira da natureza sob a forma de vários fatores de estresse biótico e abiótico afectar negativamente o crescimento das plantas e produtividade, causando a perda de rendimento da colheita. Esses fatores de estresse abióticos e bióticos são uma ameaça para as plantas, impedi-los de alcançar seu potencial genético completo e produtividade de culturas de limite em todo o mundo. Estresse causa lesão, doença ou fisiologia aberrante, impondo uma restrição ou imprevisíveis flutuações em padrões regulares de metabólicas de plantas. Estas flutuações são principalmente relacionadas com as funções metabólicas alteradas; um desses é a perda de ou reduzida síntese de pigmentos fotossintéticos. Isso resulta na colheita de luz será recusada e Générati. Portanto, essa revisão descreve modificações morfológicas, fisiológicas e de composição de pigmentos em culturas causados por estresses e os progressos da pesquisa quanto a resposta das plantas aos estresses abióticos e bióticos, sumarizados em nível fisiológico e molecular.

Palavras-chave: Estresse abiótico de, estresse biótico, estresse ambiental, estresse oxidativo, transdução de sinais

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Introduction

The reaction of a biological system to extreme environmental factors that may cause significant changes in the system depending on their intensity and duration is usually understood as stress (Nilsen & Orcutt, 1996; Godbold, 1998). The term "strain" is used as a substitute of the term "stress" in the cases where plant growth or reproduction is not significantly inhibited by the physiological changes happened due to extreme environmental conditions (Levitt, 1980, 1982).

There is a diversity of types of stressors that may affect plants. Stressors or stress factors are classified as extreme environmental conditions that induce functional changes in plants to such a level which lead to inhibited growth, reduced bio production, physiological acclimatization, adaptation of species or some combination of these changes (Schubert, 1985, Nilsen & Orcutt, 1996). An organism is affected by its environment in many ways, at any time. Nature of environmental factors can be of abiotic and biotic. Interactions with other organisms for example, infection or mechanical damage by herbivory or trampling, as well as effects of symbiosis or parasitism are consequences of biotic environmental factors. The parameters and resources that govern the growth of a plant such as temperature, humidity, light intensity, the supply of water and minerals, and CO_2 are comprised in abiotic environmental factors. Abiotic factors also include many other influences, which are only seldom beneficial to the plant like wind as distributor of pollen and seeds, or not at all beneficial or are even damaging such as ionizing rays or pollutants. The effect of each abiotic factor is determined by its quantity. In a greenhouse with optimal quantity or intensity, an organism achieves its "physiological normal type" maximizing its physiologically achievable performance. Study and understanding of the physiological and biochemical mechanisms of plant stress and the resistance of plants to stress is significant for maintaining the balance of ecosystems and their efficient economic use.

Plants have to be substantially more adaptable to stressful environments and must acquire greater tolerance to various stresses than animals and humans since they are bound to places. This sessile nature of plants is responsible for limitations in the distribution of particular types of vegetation for example, the tree line on mountains. Tolerance or resistance to adverse growing seasons can determine the ability of plants to adapt and live in a changing environment.

Damage in cell membranes, changes in enzymatic processes, and subsequent deviations in cell structures and metabolism are the primary responses of a plant cell. The duration for occurrence of the biochemical reactions and changes in plants depends on the quantitative and qualitative character of the stressor. Sequentially the resistance of the organism to the stressor and its further development is determined by the extent and character of these reactions. Restoration of metabolic homeostasis in a plant is decided by the short time period used to repair or compensate for the stress, and the small amount of energy used for repair and maintenance of the metabolic pools. Selection will favor genotypes with the least metabolic destabilization when metabolism is impaired. Consequently the genetic composition of the population will change (Ernst, 1993). The extinction or changes in the plant community may be caused by the sensitivity of the plant species towards stressors.

Thus, the objective of this short review was to compile scientific information about plant responses to their diverse environmental, abiotic and biotic stresses.

Development

Plant Responses to Environmental Stresses

A number of mechanisms are present in plants to cope with stresses in their environment which include such physical conditions as water (too much as well as drought), temperature (hot and cold), saline soils and oxygen deprivation, as well coping with biotic stresses such as predators and pathogens. Recently, focus on the interaction between the responses of plants to biotic and abiotic stresses have been started by more researchers. This approach has enforced researchers to compare the eco-evolutionary and the physiological frameworks both conceptually and methodologically. In this review some of the biotic and abiotic factors that will be studied simultaneously include drought, flooding, frost, heavy metals and wind as abiotic factors, and infection by plant pathogens (rusts, wilts, smuts, viruses, etc.), herbivores (including miners, gallers, aphids, chewers, seed parasites), and pollinators as biotic factors.

The environment is rarely optimal for plant growth in both natural and agricultural communities. The over-all productivity of US agriculture is limited to 25% of its potential by the environmental stresses (Boyer, 1982). The plant is continuously encountering new combinations of environmental stresses due to large seasonal fluctuations in light, moisture, temperature, and nutrients, often to levels that are suboptimal for plant growth. Moreover, most natural environments are continuously suboptimal with respect to one or more environmental parameters, such as water or nutrient availability. It is of particular interest to understand the nature of controls over plant growth in suboptimal environments, because these are the solitary territories into which agriculture can grow in most developing countries, and alteration in the suitability of most terrestrial habitats for plant growth may occur by the forthcoming global climate change. Consequently, it is essential to understand the physiological mechanisms that enable plants to survive and reproduce under suboptimal conditions. To date, additional emphasis has been started on the responses of plants to specific stresses in the most researches comprising the physiological responses of plants to environmental stress (Osmond et al., 1987). For example, salt and water stress may cause initiation of osmotic adjustments in plants (Morgan, 1984), nutrient stress may increase the potential to absorb nutrients (Lee, 1982), and shade or light stress can alter the quantity and balance of photosynthetic enzymes in plants (Evans, 1983). However, two lines of research suggest about the existence of a centralized system of stress response in plants which enable them to respond to any physiological stress, regardless of the nature of that stress. First, ecologists have noted that plants develop certain suites of traits such as slow growth, low photosynthetic rate, and low capacity for nutrient uptake in low-resource environments for e.g., deserts, tundra, shaded understory, and infertile soils (Chapin, 1980; Grime, 1977; Parsons, 1968). Second, physiologists have observed that most environmental stresses cause alteration in hormonal balance of an individual plant like frequent production of more abscisic acid and often less cytokinins (Chapin et al., 1988). Recent research suggests that these hormonal changes are the trigger for the direct stimulation of reduced growth in response to environmental stress; this stress response system is basically activated by the low availability of a resource. Thus plant growth in response to environmental stress is regulated through a basic physiological framework. This framework comprises a complex mode of reactions such as changes in hormonal balance, water relations, carbon balance, and nutrient use. ,

Plant Responses to Abiotic Environment

Normal physiological functions of all plants including economically important cereals are altered by the abiotic stresses (drought, salinity, radiation, high temperature, oxidative stress or freezing etc.). All these stresses cause reduction in biosynthetic capacity of plants and damages that can destroy plants. Intricate interactions between stress factors and various molecular, biochemical and physiological phenomena affecting plant growth and development are reason for the complex nature of tolerance mechanisms to abiotic stresses. Alleviation of the stress through irrigation, soil reclamation, fertilizer use and others has been main strategy used in the past to deal with environmental stress. However, these practices are associated with economic as well as ecological limitations thus the interest in searching for plant genetic resistance to environmental stresses have been encouraged. Stress-responsive mechanisms to re-establish homeostasis and protect and repair damaged proteins and membranes are initiated by the primary stress signals (e.g. osmotic and ionic effects, or temperature, membrane fluidity changes) which in turn trigger the downstream signaling process and transcription controls. Irreversible changes of cellular homeostasis and destruction of functional and structural proteins and membranes may be caused due to inadequate response at one or several steps in the signaling and gene activation which ultimately results in cell death.

Water Stress

Crop growth and yield is adversely affected by water deficit which is one of the major abiotic stresses encountered by the plants. Water stress is of common and wide occurrence in nature. It happens whenever evaporative demand of the atmosphere is more than the water absorption by the crop. In mild drought conditions the photosynthetic capacity of plants shows no or little changes while regulation of water loss and uptake is induced by allowing maintenance of their leaf relative water content within the limits. But in severe drought conditions unfavorable changes are induced in plants leading to inhibition of photosynthesis and growth. Desiccation is the most severe drought stress. The mechanisms of protection are different based upon the presence or absence of bulk water. The replacement of water by molecules that form hydrogen bonds is basic mechanism for desiccation tolerance. The roles of stomatal and non-stomatal limitation, the behavior of photosystem PS2, specific proteins and Rubisco, lipids and sugars, as well as mechanisms of acclimation lead to stress tolerance in droughty plants. During desiccation, in drought-tolerant species carbon fixation is endorsed through the control of stomatal function to improve water use efficiency and stomata open rapidly, when water deficit is relieved. Drought resistant reactions also include non-stomatal responses of carbon fixation such as photosystem (PS2) energy conversion and the dark reaction of Rubisco carbon fixation (Chaves, 1991; Dickson & Tomlinson, 1996). Water stress results in stomatal closure and reduced transpiration rates, a decrease in the water potential of plant tissues, decrease in photosynthesis and growth inhibition, accumulation of abscisic acid (ABA), proline, mannitol, sorbitol, formation of radical scavenging compounds (ascorbate, glutathione, a-tocopherol etc.), and synthesis of new proteins and mRNAs. Morphological changes are also produced in addition to these physiological responses of plants. Adaptation of plants and chloroplasts to high light (sun) and low light (shade exposure) is one of the largest morphological responses produced due to water stress. Many other stress factors including drought are responsible for the induction of this sun-type or shade-type chloroplast adaptation (Lichtenthaler et al., 1981).

Oxygen Stress

In flooded soils the major abiotic stress is oxygen limitation encountered by plants. Plants can experience waterlogging during winter or the raining season in poorly drained soils which cause scarce root oxygenation and leading to a hypoxic stress. Plants adjust their metabolism to minimize energy losses, the most important changes produced are regarding to glycolysis. Activation of specific anaerobic enzymes and over-expression of their transcripts induces with the reduction of oxygen availability. Potentially toxic metabolites like ethanol are accumulated into anoxic tissues due to induction of fermentation. Oxygen deficiency also strongly affect nitrate metabolism among the metabolic pathways. Oxygen deficiency cause up-regulation of the enzymes involved in nitrate assimilation and reduction. It has been estimated that there is an effective role of intracellular nitrates and nitrites concentrations in maintaining cellular pH homeostasis, limiting cytoplasmic acidosis deriving from fermentation and thus contributing to survival. In waterlogged soils specialized roots called pneumatophores have been developed in many swamp trees to obtain oxygen. In some experimental situations, air spaces within the stem tissue of plants have been developed in response to water-logged substrate.

Heat Stress

Crop yield is also severely limited by high temperatures. Plant development is accelerated due to high temperature and the floral organs, fruit formation, and as well, the functioning of the photosynthetic apparatus is specifically affected. Transpiration is the primary mechanism for energy dissipation to avoid heat. Maintaining transpirational cooling is main strategy induced in a good heat avoider crop. Enzymes are protected from denaturation by the excess heat through the synthesis of a class of proteins called heat-shock proteins (hsps). Heat shock transcription factors (HSFs) regulate the enhanced expression of hsps.

Cold Stress

Cold stress is a serious threat to the sustainability of crop yields. Indeed, cold stress can lead to major crop losses. Cold stress induces various phenotypic symptoms in plants like poor germination, stunted seedlings, yellowing of leaves (chlorosis), reduced leaf expansion and wilting, and subsequently death of tissue (necrosis). Severe membrane damage is the major negative effect induced by cold stress. During cold stress, acute dehydration is associated with freezing lead to membrane damage. In response to cold stress the receptor at the cell membrane switch on cold-responsive genes and transcription factors through the signal transduction for facilitating stress tolerance. Thus it is important for crop improvement to understand the mechanism of cold stress tolerance and genes involved in the cold stress signaling network. Membrane fluidity in cold temperatures is maintained by the production of more unsaturated membrane fatty acids for transport of proteins. Most cold tolerant plants drop their fragile parts prior to the cold onset, and undergo into dormancy through the lowering water content in cells. Plant health is seriously affected by the sudden frosts. Significant cell damage and death to fragile parts is caused by the formation of ice crystals below freezing point. Growth of ice crystals within cells is retarded by the production of antifreeze proteins in some cold tolerant plants.

Salinity Stress

Agricultural yield throughout the world is negatively affected by the salinity stress. Multiple biochemical pathways that facilitate retention and/or acquisition of water, protect chloroplast functions and maintain ion homeostasis determine the ability of plants to tolerate salts. Those are essential pathways that lead to synthesis of osmotically active metabolites, specific proteins and certain free radical enzymes to control ion and water flux and support scavenging of oxygen radicals. Water potential is affected and water absorption is decreased by the high concentrations of mineral salts in soil. Some mineral salts, such as sodium, in high concentrations are directly toxic to plants. In some plants, water movement from soil into the root is facilitated through the production of organic solutes for distribution in root cells that maintain more-negative water potential in the root cells. There are some plants, called halophytes that live in saline soils. Leaf epidermal cells of most halophytes contain active salt glands that excrete salt for e.g. Nolana plant of very arid regions uses salt glands to obtain water. Salt secreted on the surface of the leaves condenses water from the atmosphere which leads to active transport of water into the leaf tissue. It has been also found that there is a close negative correlation between the salinity resistance and Na/K ratio in the grains.

Plant Responses to Biotic Environment

Various predators constantly attack plants in field. Plants defend them from mechanical damage through the function of dermal tissues, but their ability to do so is inadequate. Plants are munched by sharp mouthparts of predators or penetrated through vulnerable spots. Plants also afford limited mechanical protection by spines, thorns and other offensive surface structures. Stomatal openings of leaves offer an easy passage for fungal spores to enter in spongy mesophyll leaf tissues for rapid spread. Nematodes, being infamous root parasites, bite through the epidermis. Plants use a chemical offense mechanism with secondary metabolites for response to many predator attacks; a strategy that follows the concept of best defense is a good offense.

Chemical Toxins – Secondary Metabolites

Plants produce hundreds of toxic alkaloids some of which, such as nicotine, caffeine and morphine, have worked their way into human culture. Predators are also potentially repelled by aromatic terpenes. Plants store their secondary metabolites in vacuoles isolated from the rest of the plant cell to prevent the toxin from killing the plant, but predator's digestive tract will be damaged by chewing on the plant. In some cases, non-toxic form of the produced secondary metabolite gets converted into a toxic form, often by bacteria, in the predator's digestive tract. Secondary metabolites are also used to prevent competition from other plants. Root growth of other plants may be prohibited through a chemical secreted by roots of one plant. Such allelopathy is found in black walnut tree roots. Germination and growth of potential competitors are inhibited by the toxins leached from leaves onto soil. Paint surfaces can be oxidized by the acidic eucalyptus secretions. This form of allelopathy is exhibited by many desert plants, such as sagebrush.

The Predator Retaliation

It has been revealed that some insect predators can incorporate secondary metabolites into their bodies to protect them from their predators thus making themselves resistant to these secondary metabolites. The best example of taking advantage of a toxic to protect itself from being consumed is the monarch butterfly. A tropical butterfly heliconius can convert the glycosides to no harmful molecules for nitrogen synthesis making it resistant to the cyanogenic glycoside of its “host” passion flower. Some beetles feast on the tasty parts in leaves and destroy the toxin-containing lactifers.

Induced Chemical Defenses

In addition to the always-present secondary metabolites, the action of the predator or pathogen also induced rapid responses in plants including activation of transduction pathways for the production of chemical (and other) deterrents to predation and wounding.

Genetically Determined Pathogen Response

Specific gene recognition is a strategy of many plants to evolve some pathogen resistance, in which a plant can permit some "munching" but prohibit virulent infestations. Genes that code for receptor proteins exist in both plant and non-virulent pathogens. The plant genes are called "R" genes and the pathogen's genes.

The Hypersensitive Response

In the hypersensitive response (HR), plant produces antimicrobial agents, called phytoalexins, and PR proteins (pathogenesis related proteins) in the infected tissues through the usual response mechanism with an Avr-R interaction. Arabidopsis synthesize a phytoalexin called camalexin from the amino acid, tryptophan. The cell walls of bacterial and fungal pathogens are degraded by the enzymes known as PR proteins. The chitin walls of fungi are degraded by such a PR protein called chitinase.

- The wound areas often instantly synthesize hydrogen peroxide and nitric acid that trigger events leading to cell death of the affected plant cells. These chemicals are often toxic to the pathogen as well.
- The plant typically seals off the infected area forming a necrosis after the success of gene specific defense which lead to destroying of both its own tissue and the pathogen.

The Systemic Acquired Response

In addition to mount a defense in the infected area plant expresses systemic acquired response (SAR) through the production and translocation of chemical signals in the infected area to other parts of the plant to provide resistance to infection, as mentioned as one job of the PR proteins. It has been observed that a systemic acquired response may be activated through the functions of salicylic acid which is produced as a part of the hypersensitive response to wounding. Pathogen resistant protein (PR) synthesis may also be initiated in other parts of the plant through the export of salicylic acid. Some virus infections are mainly affected by salicylic acid. A volatile methyl salicylate is produced in some plants which travels through air and functions as a warning signal for both parts of the affected plant and to neighboring plants. Resistance by SAR may be short lived, or last as long as a growing season, and non-specific, but effective.

Among the most common plant pathogens, RNA viruses are able to infect both vertically (passed from generation to generation) and horizontally (through direct infection). In some plants specific Immunity to RNA viruses is acquired through the enzymes that can form double-stranded RNA from the viral RNA, and chop the double-stranded RNA into siRNA (small interference RNA), to degrade the viral mRNA before it can be transcribed.

Jasmonic Acid and Wound Response

Another plant wound response includes activation of signal transduction pathways through a small peptide, systemin, produced in the wound area in response to the predator's saliva. Systemin was first isolated from tomato plants. Systemin stimulates conversion of plasma membrane fatty acids into jasmonic acid. The signal transduction pathways, to produce proteinase inhibitors that bind to the digestive enzymes of predator, are activated by passage of jasmonic acid through the plasmodesmata to phloem sieve tubes throughout the plant.

Dietary Defense

An amino acid (canavanine) is produced by some plants that get incorporated into larvae and cause death of larvae during the substitution of canavanine for an amino acid needed in protein synthesis.

Using Proxies

Plants also take advantage of other organisms to destroy and/or deter the plant predator.

Volatile chemicals can be secreted by some plants to attract larvae parasites in response to a larval predator. In one example, the parasite, a wasp, lays its eggs on the larva. The developing wasp larvae feed on the plant pest for their own development, saving the plant from destruction.

In an intricate symbiosis, the Acacia tree feeds and hosts ants, which protect the tree from potential predators and competitors. If a pest (or a clothes pin) touches the tree, the ants swarm to deter it or destroy it.

A volatile chemical is secreted by beans during injury by predators that are detected by adjacent plants, which sequentially activate synthesis of defense molecules through the signal transduction pathways.

Effect of metals to defend plants against biotic stress

It has recently been suggested that high concentrations of metals are absorbed by plants from the substrate as a self-defense mechanism against pathogens and herbivores. On a molecular basis, metal defense against biotic stress seems to imply common and/or complementary pathways of signal perception, signal transduction and metabolism. One or several of the following conditions are needed for plant protection by metals: the metal should be more toxic to pathogen or herbivore than to the plant; the metal should hamper the virulence of the pathogen or herbivore; and/or the metal should be able to increase the resistance of the plant to the biotic stress factor.

A wide range of mechanisms to cope with biotic and abiotic stresses have been evolved in Plants. To date, the molecular mechanism involved in each stress has been revealed rather independently, and so our understanding of convergence points between biotic and abiotic stress signaling pathways remain rudimentary. However, several molecules, including transcription factors and kinases have been revealed as promising candidates for common players that are involved in crosstalk between stress signaling pathways. Emerging evidence suggests that hormone signaling pathways regulated by abscisic acid, salicylic acid, jasmonic acid and ethylene, as well as ROS signaling pathways, play key roles in the crosstalk between biotic and abiotic stress signaling.

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