

Engineering Climate-Change-Resilient Crops

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Environmental adversities, particularly drought and nutrient limitation, are among the major causes of crop losses worldwide. Due to the rapid increase of the world's population, there is an urgent need to combine knowledge of plant science with innovative applications in agriculture to protect plant growth and thus enhance crop yield. In recent decades, engineering strategies have been successfully developed with the aim to improve growth and stress tolerance in plants. Most strategies applied so far have relied on transgenic approaches and/or chemical treatments.

cyanobacteria

photosynthesis

volatile compounds

gene expression

metabolites

plant protection resources

macro- and micronutrients

1. Overview

Environmental adversities, particularly drought and nutrient limitation, are among the major causes of crop losses worldwide. Due to the rapid increase of the world's population, there is an urgent need to combine knowledge of plant science with innovative applications in agriculture to protect plant growth and thus enhance crop yield. In recent decades, engineering strategies have been successfully developed with the aim to improve growth and stress tolerance in plants. Most strategies applied so far have relied on transgenic approaches and/or chemical treatments. However, to cope with rapid climate change and the need to secure sustainable agriculture and biomass production, innovative approaches need to be developed to effectively meet these challenges and demands. In this review, we summarize recent and advanced strategies that involve the use of plant-related cyanobacterial proteins, macro- and micronutrient management, nutrient-coated nanoparticles, and phytopathogenic organisms, all of which offer promise as protective resources to shield plants from climate challenges and to boost stress tolerance in crops.

2. Environmental Stresses

Environmental stresses and nutrient limitation are among the major causes of crop losses worldwide, a trend that will likely worsen if current models of global warming prove correct ^[1]. Adverse environmental conditions for plant growth, e.g., poor soil conditions, nutrient deficiencies, drought, and pathogen attack, constitute the most relevant factors in agricultural yield reduction ^{[2][3]}. All these hardships cause oxidative stress in higher plants; oxidative stress is defined as a shift of the balance between pro-oxidative and antioxidative reactions ^[4], and results in the abnormal accumulation of excited and partially reduced forms of oxygen such as singlet oxygen ($^1\text{O}_2$), the

superoxide radical ($O_2^{\bullet-}$), and hydrogen peroxide (H_2O_2), collectively known as reactive oxygen species (ROS) [4][5]. Many adverse environmental conditions, including drought and salinity, are also accompanied by an associated osmotic stress resulting from a decrease in water availability [6][7][8].

When growing in their natural habitats, wild plants encounter multiple environmental constraints and have developed numerous strategies to survive and set seeds under unfavorable conditions. Selection of crop cultivars by breeding has been conducted with a bias towards high plant productivity within quite narrow environmental limits. During domestication, many traits mediating stress tolerance in wild ancestors were lost in modern bred cultivars. A comparison of the average yield of eight major crops indicates that the combination of biotic and abiotic stresses resulted in yield losses in the range of 60–90% (FAO, 2011, <http://www.fao.org/docrep/014/mb060e/mb060e00.pdf>, accessed on 21 July 2021) [2]. These observations indicate that there is a large potential for yield improvement and that engineering of stress tolerance could have a lasting impact in agricultural practice.

Traditional approaches to increasing plant stress tolerance have largely relied on the strengthening of endogenous protective mechanisms via the overexpression of the genes involved in their respective pathways and/or by limiting the key components of these systems. Endogenous responses are controlled by cascades of molecular networks involving stress perception, signal transduction, transcriptional regulation, and expression of specific stress-related effector genes [9]. Components of the signaling and transcriptional regulation pathways have been extensively manipulated. These include members of the dehydration-responsive element-binding (DREB) protein family, transcription factors (TF) involved in abscisic acid (ABA)-dependent pathways, and others belonging to the Nuclear Factor Y family and the ABA-independent AP2/ERF and NAC families [10][11][12]. Most attempts, however, have been directed towards the overexpression of effector genes acting downstream of the plant response cascade, including ion channels [13], enzymes involved in the synthesis of compatible osmolytes [14][15], ROS scavengers, and other antioxidant proteins [16].

Although increased stress tolerance has generally been achieved through these approaches under controlled conditions, translation to the field has met with considerable difficulties, in part due to the complexity of the endogenous regulatory networks governing these responses. Overexpression of genes that operate upstream of the response cascade (e.g., signaling factors or transcriptional regulators) often leads to growth and/or reproductive penalties, whereas boosting the levels of functional effector proteins confers tolerance to a limited set of stresses or even a single source of stress, which is of relative significance to field conditions, where the combination of concurrent stresses (for instance, heat plus drought) is the rule rather than the exception [9].

These limitations have prompted the search for novel, alternative approaches to improve crop productivity in suboptimal environments, and a number of new strategies are being explored to extend and diversify the toolkit of biotechnological resources. Within this context, manipulation of phytohormone levels has emerged as a most promising choice, since most of these signaling molecules have been shown to participate in plant responses to adverse environmental conditions—most conspicuously ABA, the canonical stress hormone. In addition, Xu et al. [17] performed a transcriptome analysis in creeping bentgrass under drought stress and showed that hormone

signaling and synthesis, particularly synthesis of cytokinins, play a crucial role. The relationships between phytohormones and secondary metabolites and their effects on drought tolerance in crop plants have been recently reviewed as indicating that they significantly contribute to better plant development under drought in crops [18]. Engineering of cell wall metabolism has also attracted considerable attention as a possible means to increase tolerance to multiple stresses via a physical barrier against abiotic and biotic onslaughts [19][20]. Exploiting plant interactions with beneficial microorganisms provides still another novel approach for improving growth and yield in adverse environments. Successful interventions based on these various strategies have been comprehensively addressed in a series of excellent reviews [18][21][22][23], and will therefore not be discussed here in great detail.

A critical and, until recently, relatively unexplored aspect of the survival and reproduction of plants exposed to environmental hardships is nutrient status. Specifically, improvements of the activity of energy and sugar metabolic pathways have been shown to correlate with increased plant development and tolerance to drought and other stresses [24][25]. Chloroplasts play a key role in this context, as the site of carbon, nitrogen, and sulfur assimilation and of phytohormone synthesis. At the same time, they are also primary targets of environmental hardships and oxidative stress. Preservation of chloroplast metabolic routes, especially photosynthesis, is thus of paramount importance for the survival and growth of stressed plants. While increasing the stock of antioxidant systems, as described before [5], provides protection against individual ROS, the use of alternative electron sinks has gained momentum in recent years as a way to prevent generation of all chloroplast oxidants and develop multiple stress tolerance [5].

A direct approach to improving nutrient availability is via exogenous supplementation, which is probably as old as agriculture itself. New findings, however, have revealed previously unknown links with stress tolerance and provided novel tools for both customized nutrient delivery and better assimilation via the manipulation of biochemical and morphological traits associated with nutrient uptake and mobilization. Finally, several studies have shown that plant–microbe interactions can influence abiotic stress tolerance, with significant impacts on growth and biomass accumulation. While the role played by endophytic microorganisms has been known for some time and is associated with their modulation of phytohormones production in the plant host [22][23], further discoveries have shown that beneficial effects are not restricted to rhizosphere microorganisms but also include phytopathogens, which act via entirely different mechanisms that mainly occur in the chloroplasts [26].

3. Conclusions

In recent years, a large number of beneficial approaches have been proven and recommended to improve plant growth and tolerance towards rapidly changing environmental conditions. Several strategies rely on purposeful breeding, chemical treatments, and/or modification of stress-related genes. Beside these strategies, there is an urgent need to develop and utilize the existing plant protection resources that cover plant cognate genes from the ancestors of plants and/or environmentally friendly biostimulants originating from various organisms including bacteria, algae, or fungi. The recent advances reviewed in this article demonstrate that it is reasonable to expect

successful outcomes for plant development and the resulting final yield that in turn secure food resources for the rapidly increasing global population of the future.

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