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SUSTAINABLE CULTIVATION OF DIFFERENT CROPS UNDER DROUGHT-STRESS CONDITIONS: BIOTECHNOLOGICAL STRATEGIES

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SUMMARY

Climate change and frequent droughts are assumedly one of the major constraints in crop production in the near future. Crop productivity has crucial threats from increasing environmental stresses and disruptions in the water and nutrient regimes. Drought reduces crop production and causes rapid soil erosion, with long-lasting effects on the soil microbiota. This also instigates environmental degradation under stressful conditions, increasing the soil microorganisms' role in the regulation of plant adaptability. In combating deleterious consequences of drought, the creation of new strategies for crop development is a challenging task because of the complexity of plant stress tolerance mechanisms. New technologies have emerged to enhance the drought resistance in crop plants and minimize the negative impact of water-deficit conditions. Selection of highly productive and drought-resistant crop cultivars, using integrative genetics, molecular biology, and microbiological approaches offers promising opportunities to mitigate the adverse effects of drought stress. The following review presents state-of-the-art biotechnological strategies and solutions based on recent advances in transgenic plant breeding, seed preparation, and the use of superabsorbent hydrogels as soil conditioners for sustainable crop production under arid conditions.

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Key findings: Drought is an environmental stress factor that affects crop plants at various phases and eventually negatively impacts the plant's metabolism, growth, development, and yield. The strategies to overcome drought effects are now intensively evolving. Therefore, the future research should address reproducible experiments under field conditions and the development of optimized protocols for commercialization of these new techniques.

INTRODUCTION

Approximately one-third of the Earth's land area is arid and semi-arid, and the continuously increasing part of the arable land sits in the risky farming zone. Climate change trends showed a long-term alternation in temperature and precipitation patterns; periodically unexpected climatic droughts often occur in most of the other areas (Mansour *et al*., 2020). Drought considerably reduces the soil organic carbon decomposition, lowers the microbial biomass, and causes less CO_2 production. Drought stress is one of the chief abiotic stresses affecting crop productivity worldwide, as most crops are highly sensitive to drought (Alikulov *et al*., 2022).

Water-deficit conditions can affect crop plants at different phases, interfering with the plant's normal growth and functioning, which eventually results in reduced yields. Similarly, drought crucially affects the seed germination and seedling stand, vegetative, and reproductive growth, as well as diminishes fresh and dry matter formation (Mukhtorova *et al*., 2024). Drought tolerance can be successful through the activation of adaptive traits. Plants' resistance to stress conditions results from numerous signal transduction and metabolic pathways that include protein kinases, i.e., mitogen-activated protein kinases (MAPK), calcium-dependent protein kinases, and protein phosphatases transcription factors (DREB, WRKY, bZIP, bHLH, NAC, MYC, and MYB gene families). Furthermore, proteins involved in the biosynthesis of osmolytes, water channels, ion transporters, heat shock proteins, and the proteins related to late embryogenesis affect plant resistance to stresses. Several pathways are highly conservative and activated in response to various abiotic stress conditions.

At the hormonal regulation, the crop plants' adaptive strategies are realized via cross-talk of auxin, cytokinin, gibberellins, and abscisic acid (ABA) signaling. Strigolactone, a plant hormone affecting physiological activities, such as shoot and root branch elongation and leaf senescence, is a signal molecule vital for drought stress tolerance in crop plants (Visentin *et al*., 2016). The ABA is also one of the most essential signaling molecules for drought signal transduction. The ABA synthesis, when triggered in root cells in response to soil water deficit conditions, continued the transfer to shoots until further induction for stomatal closure in leaves. The stomatal closure, aimed to prevent water loss due to transpiration, is the chief physiological reaction of crop plants to water deficiency (Aslam *et al*., 2022).

In plant cells and tissues, the reactive oxygen species (ROS) generation has served as a stress signal and occurs in response to drought conditions. ROS signaling has a connection with the Ca^{2+} increase and ABA signaling, and its excessive accumulation leads to lipid peroxidation and cell membrane deterioration. Specific metabolic reactions responding to drought have an association with the regulation of osmoprotectants, such as proline and soluble sugar content (trehalose and betaine). Osmoprotectants retain water potential, cell turgor, and membrane stability allowing them to avoid drought stress-induced damages. In crop plants, the proline aggregates under drought stress; however, this does not take place under heat stress conditions (Cohen *et al*., 2021).

The carbon fixation and nutrient availability are main metabolic parameters affected by drought stress. Chlorophyll content's net photosynthetic rate, maximal quantum yield, stomatal conductance, and transpiration significantly decline with decreased soil moisture conditions. The plants, which can maintain higher chlorophyll contents under water stress conditions, tend to use light energy more efficiently, and therefore, could have significant drought tolerance. Water deficit conditions also cause a considerable impact on the uptake of nutrients by the roots and their translocation to the shoots in crop plants. Drought stress causes an enhancement of N, decreases P content, and generally has no effect on the K content in crop plants (Farooq *et al*., 2009). Several enzymes mostly contribute to carbon fixation, i.e., phosphoenolpyruvate carboxylase, NADP-malic enzyme, fructose-1,6-bisphosphatase, NADP-glyceraldehyde phosphate dehydrogenase, phosphoribulokinase, sucrose phosphate synthase, and pyruvate orthophosphate dikinase, which reduces with the decreased leaf water potential (Bashir *et al*., 2021).

Natural stress adaptation strategies sometimes are insufficient to overcome the drought conditions. Modern methods to ameliorate drought stress include various agronomic, engineering, and biotechnological approaches. In previous years, numerous new experimental strategies at different levels of intervention in plant physiology and ecology have emerged, viz., film farming, development of drought-resistant crops, the use of nanoparticles, superabsorbent hydrogels and biochar, and applying plant growth-promoting rhizobacteria (Ahluwalia *et al*., 2021).

Transgenic plants

Genetic engineering provides an effective approach for generating the drought-resistant crop plants. Numerous earlier-mentioned and other regulatory genes implicated in stress-associated signal transduction metabolite production may be targeted via CRISPR (clustered regularly interspaced short palindromic repeat)/Cas9 technologies to develop stress-tolerant crop plants. The CRISPR/Cas genome editing tool based on bacterial and archaeal genomes has a greater potential to considerably affect plant productivity and tolerance under arid conditions. So far, CRISPR-Cas has gained adoption in almost 20 agronomically essential crops. The CRISPR/Cas9-based genome editing is more precise to genomic targets and less likely to change the genomic background of a variety (Zafar *et al*., 2020).

The CRISPR/Cas9-mediated gene editing, including betaine aldehyde dehydrogenase (OsBADH2), mitogen-activated protein kinase (OsMPK2), ABA-activated protein kinase-2 (SAPK2), and phytoene desaturase (OsPDS), showed their implications for improving the abiotic stress tolerance in rice crops. In *Phaseolus vulgaris*, the gene encoding the cleavage enzyme PvNCED1 is up-regulated by water stress and precedes the accumulation of ABA. In wild tobacco, the PvNCED1 expression results in an increase in ABA and its catabolite and phaseic acid. The dexamethasone-inducible promoter allows the generation of the crop plants with a transient induction of PvNCED1 with a markedly enhanced drought stress tolerance.

The TPS1 encodes trehalose-6-phosphate synthase, which is a key enzyme for trehalose biosynthesis in yeast. Trehalose affects the sugar metabolism, as well as osmoprotection against several environmental stress conditions. In potato, the constitutive expression of yeast TPS1 significantly improved drought tolerance. The glycine betaine osmolyte enables coping with environmental stresses through an osmotic adjustment. The betaine aldehyde dehydrogenase (BADH) gene from spinach over-expressed under the control of a stress-induced rd29 promoter. It also increased the fresh weight by 17%–29% and tolerance to drought and salt stress conditions in transgenic potato plants. Overexpression of the mothbean delta-1-pyrroline-5-carboxylate synthetase, an enzyme that catalyzes rate-limiting step in proline synthesis in tobacco, results in 10 to 18-fold enhancement of proline synthesis in transgenic plants, compared with control plants.

The transgenic plants demonstrated with an enhanced root biomass and flower development, as well as less decrease in osmotic potential of leaf sap under drought-stress conditions. Overexpression of ornithine δ-aminotransferase (OsOAT), proline, and arginine metabolism-related enzymes results in improved resistance to drought, osmotic, and oxidative stresses by enhancing pre-accumulation and ROS-scavenging in rice. Constitutive expression of the auxin-regulated gene involved in organ size (ARGOS8) under the GOS2 promoter in *Zea mays* enhances the yield under drought stress conditions. Late embryogenesis-abundant (LEA) chaperon protein gene OsLEA3-1 sustains normal induction from drought, salt stress, and ABA, protecting the cells from water-stress damage. Overexpression of sLEA3-1 results in higher grain yield in transgenic plants than in wild types under drought stress conditions (Shi *et al*., 2017).

Compared with the single-gene transformation, the multi-gene transformation strategy combines editing of several functional genes, contributing to drought resistance, and appearing more reasonable for improving drought resistance in crop plants. A good example of such an approach succeeded in advancing the flowering time and improving yield-related traits of Rht12 dwarf plants via the interactive effects between *Ppd-D1a* and *Rht12* gene modifications. Under deep sowing conditions, especially in water-limited areas, the semi-dwarf alleles Rht-B1b and Rht-D1b reduced the coleoptile length and seedling vigor, resulting in low yield and poor final plant biomass. The photoperiod genes play a vital role in flowering time and spike development. Introduction of photoperiod gene *Ppd-D1a* hastened the flowering time and enhanced the yield traits of Rht12 dwarf plants, suggesting that the combination of Rht12 and Ppd-D1a would be conducive for the successful use of the Rht12 genotype (Chen *et al*., 2018).

Seed priming

The same molecular signaling pathways incur activation in different stress conditions; therefore, response to one type of stress induces adaptability to another type of stress, with this phenomenon called cross-tolerance. Such cross-tolerance allows inducing stress signaling in seeds with physiologic stimuli mimicking stress conditions. As a result, in seeds, the induced molecular events, up to some extent, influence further stages of plant development, making it more resistant to drought stress. This stress tolerance method serves as a 'priming memory’ that reactivates during stress exposure and helps an individual respond to the subsequent stress tolerance more effectively in the next generation (Hussain *et al*., 2016). Post-translation modification is a possible 'stress memory' mechanism of the priming defense system, which increases transcription in drought stress responses and activates greater and faster gene expression.

Seed prefabrication, before sowing aimed to activate the pre-germinative metabolic and biochemical activities without radical protrusion, defined as seed priming. This helps ameliorate drought stress by adapting several strategies, such as early mobilization of seed food reserves, elongation of embryo cells, and activation of antioxidant enzymes, which eventually enhance seed germination. Seed priming also promotes synthesis of substances with antioxidant activity, i.e., ascorbic acid, vitamin E, carotene, and proline (Macovei *et al*., 2017).

Various priming methods include the use of hydropriming, osmopriming, chemopriming, nutrient priming, and hormonal priming. Hydropriming is a simple, cost-effective, and feasible technique that includes partial hydration of the seeds, followed by seed drying to the original moisture content before sowing (Singh *et al*., 2015). Rapid water uptake activates a series of biochemical activities, including the accumulation of osmolytes (proline, glycine-betaine, and polyamines) and hydrolytic enzymes (amylase, cellulase, and xylanase) that convert stored lipids, carbohydrates, and proteins to ATP for pre-germinative metabolic processes. Hydropriming clearly improves the seed germination, seedling emergence, early growth, vigor index, and seedling dry weight in wheat under drought stress conditions.

Hydropriming in upland rice reduced the growth period and improved the drought escape (Nakao *et al*., 2022).

Several bioactive compounds, such as nitrates, nitric oxide, hydrogen sulfide, melatonin, and polyamines are also useful in seed priming, aiming for abiotic stresses' amelioration. Among nanomaterials, metallic, biogenic metallic, and polymeric nanoparticles served as seed primers during nanopriming (Pereira *et al*., 2021). Chemopriming with sodium nitroprusside results in upregulation of antioxidants proline, phenolic compounds, and ascorbic acid, and a reduction in H_2O_2 levels, along with enhanced shoot length and 100-grain weight in wheat under physiological drought stress. $CaCl_2$ proved to be an effective priming agent, showing increased germination, net photosynthetic rate, growth, yield, and antioxidant activities, while decreasing Na^+ and H_2O_2 contents in wheat grown from primed seeds under drought stress conditions (Tabassum *et al*., 2017).

Osmopriming involves hydration of seeds in a low-osmotic aerated solution with different durations and water potentials. The low water potential of osmotic solution allows slow water imbibition and activation of pre-germinative metabolic processes. The commonly used osmotic solutions include KH_2PO_4, KNO_3, $CaCl_2$, $MgSO_4$, NaCl, KCl, mannitol, and polyethylene glycol (PEG), with PEG being widely used in osmopriming. Osmopriming results in earlier germination and seedling emergence, and osmopriming with PEG effectively improves the germination and fresh and dry weights of the plumule in caraway seeds (Mirmazloum *et al*., 2020). The 5% PEG in rice seed priming results in effective germination and seedling growth under dehydration stress, and the molecular markers of the antioxidant defense system showed a lower amount of ROS and lipid peroxidation than the control group (Khan *et al*., 2020).

Organic osmolytes include soluble sugars (glucose, fructose, and sucrose), sugar alcohols (mannitol and sorbitol), proline, and quaternary ammonium compounds like glycine betaine. These compounds comprised characteristics of multiple -OH groups, which facilitate the hydrogen bonding with water molecules in the cytoplasm. Osmolytes stabilize the cellular structure, act as antioxidants, and provide defense from ROS. Seed priming with mannose increases the antioxidant levels, reduces oxidative injuries, promotes the accumulation of reducing sugars for osmotic regulation, and improves drought tolerance (Hameed and Iqbal, 2014). Osmopriming with ascorbic acid boosts drought resistance in wheat due to its antioxidant action, phenols and proline accumulation, and significant improvement in leaf emergence and elongation, leaf area, chlorophyll contents, root length, and seedling dry weight.

Hormone priming with natural and synthetic physiologically active substances (auxins, gibberellins, kinetin, ABA, and ethylene producers) effectively enhances the activation of photosynthesis and bioproductivity and drought and salt tolerance. Hormones, such as polyamines, ethylene, ABA, kinetin, and salicylic acid reportedly benefit the crop stand under drought stress conditions (Rhaman *et al*., 2020). Seed priming technology allows breeders to successfully combine the physiologically active substances with nutrio- and osmopriming, ensuring a complex effect (Sarkar *et al*., 2021).

Biopriming involves seeds soaking in water containing microorganisms (bacteria and fungi) and their metabolic products. Solubilizing bacteria *Pseudomonas* spp., *Agrobacterium* spp., and *Bacillus* spp. release and mobilize the nutrients, contributing to an increase in the available forms of phosphorus and potassium in soil (Kumar *et a*l., 2020). Biopriming with liquid phosphobacterium induces the physiological and biochemical attributes in okra to mitigate drought tolerance. Wheat inoculated by *Burkholderia phytofirmans* showed an enhanced water use efficiency, higher assimilation rates, and elevated chlorophyll contents in water-deficit soils (Naveed *et al*., 2014).

In addition to the deleterious effects of drought on growth and yield, it makes the crop plants more susceptible to pathogens. *Fusarium culmorum*, which causes root rot and seedling blight in wheat, aggravates drought stress effects, resulting in increased leaf yellowing, decreased root and shoot growth, and a decline in biomass accumulation, as compared with an individual stress. Pre-sowing treatment with endophytic strains of *Bacillus subtilis* notably reduces (by 50%–80%) the incidence of disease development, increasing root and shoot length and fresh and dry biomass (up to 15%–40%) under drought stress conditions (Lastochkina *et al*., 2020).

Superabsorbent hydrogels

Superabsorbent hydrogels (SAHs) are soil conditioners that can retain and gradually release water over an extended time. Hydrogels reduce the osmotic pressure of soil and improve water supply, with 95% of the water absorbed by the hydrogel remaining available to the plants. The materials used to develop these hydrogels should be non-toxic, biodegradable, biocompatible, and cost-effective. The SAHs are cross-linked hydrophilic polymer networks that can absorb water that is 400 times greater than the polymer weight. In the polymeric chain of hydrogels, various hydrophilic groups, such as carboxyl, hydroxyl, sulfonates, sulfates, and phosphates are useful to absorb and retain extensive amounts of water. The SAHs found in the soil absorb the water during rainfall and provide a water reservoir near the root zone of crop plants for their survival under drought stress conditions (Tomášková *et al*., 2020). Hydrogels can serve as carriers for mineral fertilizers, growth stimulants, pesticides, and biopreparates, facilitating their gradual release to soil and providing a sustainable action (Guo *et al*., 2022).

Hydrophilic polymer hydrogels based on polyacrylamide and polyacrylates demonstrate a superior ability to swell in water (up to 1000 g H_2O/g dry polymer) and are effective for use to retain water in soils with light granulometric composition. Synthetic hydrogels' production is mainly from using acrylamide and acrylic acid. Chemical cross-linking of polymers, when carried out uses various methods, such as free-radical condensation polymerization, ultraviolet radiation, and cross-linking using small molecules. Polyacrylate and polyacrylamide hydrogels added to soil (in 0.2%–0.3%) increase the water-holding capacity of soils of various genesis, composition, and dispersion, with the greater effect being achieved in non-saline sandy substrates. Despite general benefits to the soil, gels based on polymers and copolymers of acrylamide and acrylic acid are not biodegradable, and their use and exposure to environmental factors result in their degradation. Destruction of acrylamide gels results in generation of microparticles and toxic by-products that can be neurotoxic and carcinogenic (Cheng *et al*., 2024).

Alginates are structural components of brown seaweeds and capsular polysaccharides of soil bacteria. When isolated from algae, their conversion into more stable salt forms arises mostly into sodium alginate, which is a linear molecule comprising (1-4)-linked D-mannuronate and L-guluronate residues with -COOH and -OH functional groups. Alginate is water soluble; however, it does not dissolve in organic solvents and acidic solutions with pH < 3. Such functional properties of alginate as gelling and water-retaining capacity, storage capacity, and solubility depend upon the guluronic acid content. Calcium cations bind guluronic acid residues through carboxyl groups, which result in gelation.

The concentration of $CaCl_2$ and the crosslinking time are the most important variables affecting the swelling properties of alginate-based hydrogels. The swelling degree of an alginate hydrogel prepared from a 2%–3% alginate solution cross-linked with 0.2% $CaCl_2$ for 10 min is 55 g of distilled water per 1 g of dry hydrogel in 24 h. Soil conditioning with such gel improves the lettuce growth under drought stress conditions. Biodegradation of alginate is successful by alginate lyases which are widespread in invertebrates, bacteria, and fungi. Endoalginate lyases have several divisions into polyguluronate, polymannuronate, and bifunctional alginate lyases specific for 1-4-glycosidic bonds between residues of both mannuronic and guluronic acids. Exoalginate lyases cleave oligosaccharides of alginic acids to monosaccharides (Belik *et al*., 2018).

Chitosan is a polycationic polysaccharide obtained from the shells of crustaceans by deacetylation of chitin.

Chitosan macromolecules consist of randomly linked D-glucosamine and N-acetyl-D-glucosamine, linked together by beta-1,4 glycosidic bonds. The chitosan molecule can bind hydrogen ions due to numerous free amino groups. As a result of the amino groups protonation, chitosan is poorly soluble in water; however, it can easily dissolve in dilute organic and mineral acids, i.e., acetic, formic, and citric acid. Preparing composites of chitosan with other products, such as gum, starch, and alginate, is a convenient method to improve its properties for slow release of active ingredients. Chitosan induces tolerance to abiotic and biotic stresses and exerts antiviral, antifungal, and antibacterial effects in various crop plants (Hidangmayum *et al*., 2019).

Chitosan depolymerization proceeds by hydrolases, highly specific chitosanases, and nonspecific enzymes, such as lipases and cellulases. In natural environments, microbial extracellular enzymes, chitosanases, continue secretion by bacteria and fungi. Complex hydrogels synthesized by crosslinking of different biopolymers are also a subject of intensive research: lignosulfonate, sodium alginate, and konjaku flour demonstrated 41.23 g/g maximum water absorption. The said composition has proven to increase the proline levels and photosynthetic capability of tobacco plants under drought stress conditions and could prolong the growth time (up to 14 days), which significantly enhanced the mass harvest (Song *et al*., 2019).

Hydrogels composed of polysaccharides, such as sodium alginate, chitosan, starch, and cellulose, can be beneficial as carriers for microorganisms. The hydrogel microstructure retains substantial amounts of water, promoting bacterial survival and further colonization of the plant rhizosphere. Association with beneficial soil microbiota improves maintenance of soil composition, nitrogen fixation, phosphate solubilization, and release of phytohormones (Pathania *et al*., 2020). Some pathogens can also compromise drought tolerance. Under mild drought stress conditions, plant defenses against pathogens attain successful activation. However, under severe drought stress, the infection can be aggravated due to the release of cellular nutrients into the apoplast. Toxins of *Uromyces phaseoli*, the cause of leaf rust in *Phaseolus vulgaris*, result in stomata malfunctioning, compromising water stress tolerance.

Plant growth-promoting rhizobacteria associated with plant roots include spp. *Pseudomonas, Bacillus, Rhizobium, Bradyrhizobium, Pantoea, Azospirillum, Acetobacter,* and *Burkholderia*. These microorganisms are capable of counteracting pathogenic microflora and act as biostimulants promoting plant growth, development, and production. *Paenibacillus polymyxa* enhances the drought tolerance of *Arabidopsis thaliana*. *Bacillus amyloliquefaciens* had been applicable to several commercial crops and revealed the remarkable effects of increasing plant growth, disease resistance, and salt and drought tolerance. Xerophytic plants can be essential sources of drought-tolerant microorganisms. *Bacillus* spp. drought-tolerant rhizobacteria strains isolated from the rhizosphere of guinea grass can induce proline accumulation and glutathione reductase activity and alleviate drought stress (Moreno-Galván *et al*., 2020). Application of the drought-tolerant rhizobacteria can help overcome wheat productivity losses in drought prone areas.

CONCLUSIONS

Drought is an environmental stress factor that affects crop plants at multiple stages and negatively impacts the metabolism, plant growth and development, and eventually the yield. Seed priming is a simple, cost-effective, and environmentally friendly technology to counteract the deleterious effects of drought stress conditions. Commercialization of superabsorbent hydrogels is still in its nascent stages, and further research is essential under field conditions. The strategies to overcome drought effects are now intensively evolving. Future research should address reproducible experiments in field conditions and the development of optimized protocols for commercialization of new techniques.

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